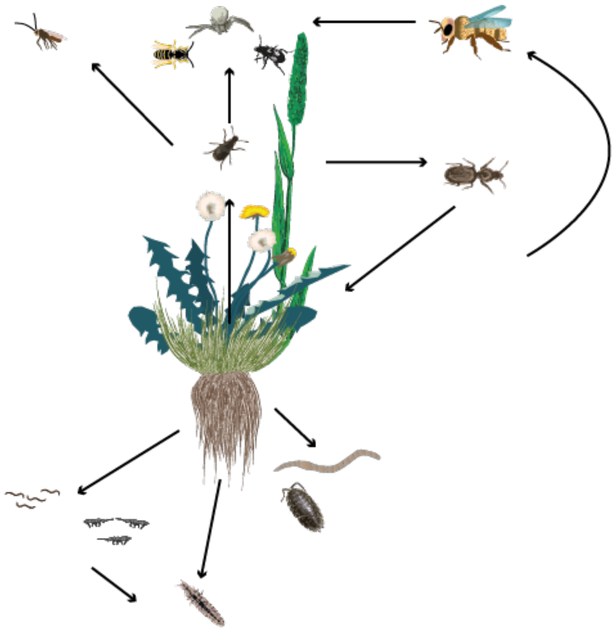
Defining Agroecology



A Festschrift for Teja Tscharntke

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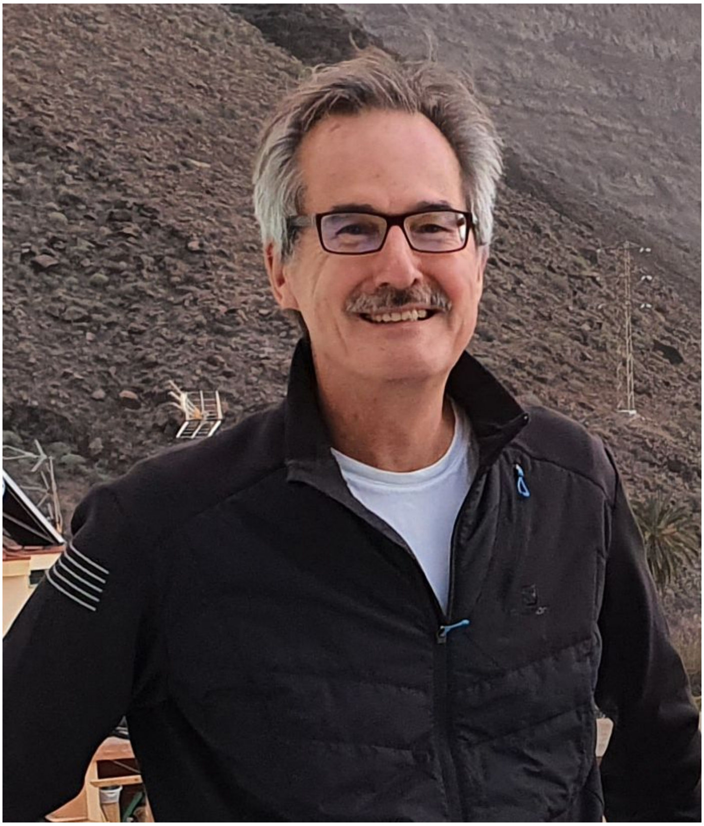

Prof. Dr. Teja Tscharntke (around 2015 or so)

Preface

When Teja Tscharntke, Professor for Agroecology at the University of Göttingen, retired in 2020, the planned festive activities had to be cancelled, due to the SARS-CoV2 pandemic. Regrettable as that was, it also offered a new chance for the production of a "Festschrift" in Teja's honour for a year (or two, as it turned out) later.

The title of the Festschrift came naturally. Although Gliessman (in a 2018 editorial in *Agroecology and Sustainable Food Systems*) wrote about defining the *term* agroecology, it is the work of Teja that defines the *science* of agroecology.

This Festschrift collects an array of work inspired, influenced, instigated by the work of Teja Tscharntke, and/or by him personally. To locate the influence Teja may have had on the reader, the Festschrift starts with an academic biography. The contributions are organised along the five themes we identified as describing Teja Tscharntke's work: (i) landscape ecology; (ii) pollination; (iii) biocontrol (and multitrophic interactions more widely); (iv) food security; and (v) socio-ecological systems. Also, the back-matter contains a bibliography of Teja's own publications (at time of editing).

When inviting contributions to this Festschrift, we were thrilled by the geographical as well as scientific spread of the contributions: from Sweden to Madagascar, from ecological theory to economic reality, from young to less young colleagues.

We like to thank all colleagues who contributed to this Festschrift, either directly and visibly as authors, or indirectly and less visible as friends, proof readers and motivators. We hope that Teja, and anybody interested in his lines of research, will enjoy this rich mixture of applied ecology.

June 2023

Carsten Dormann, Freiburg
Péter Batáry, Vácrátót
Ingo Grass, Hohenheim
Alexandra-Maria Klein, Freiburg
Jacqueline Loos, Lüneburg
Christoph Scherber, Bonn
Ingolf Steffan-Dewenter, Würzburg
Thomas Wanger, Hangzhou

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Teja Tscharntke – An academic biography

Stefan Vidal, Klaus Hövemeyer, Ingo Grass, Ingolf Steffan-Dewenter & Catrin Westphal

Studies and first steps in ecology

Teja Tscharntke grew up in a small town called Harsum near Hildesheim, Lower Saxony, Germany, as the youngest of four siblings. His father was a respected village doctor, his mother a housewife. It seem to have been a peaceful and common childhood, as no particular events were reported about his school years, which ended when he graduated from high school.

After his military service, which he completed with the rank of lieutenant, he was drawn to study at the University of Gießen, starting in 1973. At that time, his career as a biologist was not yet set in stone, as he also pursued the study of sociology in parallel. After his intermediate diploma, he moved to the University of Marburg, where he completed his thesis in the subject of sociobiology in 1978 with the title "*Bürgerinitiativen und Staat*",[1] a 184-page work with a bibliography of nearly 800 citations! In parallel he began his studies of biology at the University of Marburg, which he successfully finalized in 1981 with a thesis on a xerothermal arthropod community in the ecology research group led by Prof. Dr. Hermann Remmert.

The time of the studies in Marburg were at the same time also the political stirring years with numerous extra-university activities; however, this did not stop Teja from persistently attending his biology lectures and internships and pursuing his degree in this subject as well.

---

[1] "Citizens' Initiatives and State". See also Teja's full bibliography in the appendix of this Festschrift.

Dissertation and Habilitation

In March 1981 he moved to Hamburg University to join the research group of Prof. Dr. R. Abraham, at those times specificly known for his research on parasitic Hymenoptera. Here he started his PhD work but here he also met his future life-long partner Dr. Susanne Asche immediately in May (at the Dance into May; it must have been already in the morning).

Although he worked on his doctoral thesis in a very concentrated and goal-oriented way, he still had time for various side activities (e.g. recording of Aculeata in the nature reserves of Hamburg or the publication of his first paper (*Zur Arthropodenfauna eines xerothermen Steilhanges am Sonderrain bei Bad Wildungen (Nordhessen)*, Philippia, 1983).[2] He also found time to take an active interest in politics and to participate in the founding of the Hamburg variant of what later became the Green Party.

Those were the times when, tormented by horseflies, which as dark clouds above him indicated his position in the reeds, he collected reed stalks, harbouring the gall midge *Giraudiella inclusa* and their parasitoids, in the large reed beds of the nature conservation area Haseldorfer Marsch, Schleswig-Holstein. The huge data set collected here within three years resulted in his PhD thesis entitled "*Die Gallmücke* Giraudiella inclusa *(Diptera, Cecidomyiidae) im Nahrungsnetz des Ökosystems Schilf (*Phragmites australis*): Wechselwirkungen zwischen den Populationen von vier trophischen Ebenen*".[3]

Uncommon for this time, the results of this thesis were published in, for example, *Oikos*, (Changes in shoot growth of *Phragmites australis* caused by the gall maker (Diptera: Cecidomyiidae)), *Journal of Animal Ecology* (Coexistence, tritrophic interactions and density dependence in a species-rich parasitoid community), and *Ecology* (Cascade effects among four trophic levels: bird predation on galls affects density-dependent parasitism), respectively.

Soon after the PhD-defence in 1985 he was appointed an assistant professorship position at Karlsruhe University (now Karlsruhe Institute of Technology, KIT), where he started to work from September onwards.

In April 1992 he submitted his Habilitation thesis at the Zoological Institute I at Karlsruhe University entitled "Herbivoren-Parasitoiden-Gesellschaften an Gräsern (Poaceae): Vielfalt, Dynamik und Interaktionen",[4] and received the *venia legendi* [5] in Zoology.

Professorship in Göttingen

In 1992 he received three offers for professorships, in Hamburg, Gießen and Göttingen. The latter position he then took in 1993 and held it until his retirement in 2021. During this time, Teja has developed an unprecedented research activity in the field of agroecology, concentrating, among other things, on the relationship between biodiversity and ecosys-

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[2] "Arthropods of the xerothermal slope of Sonderrain near Bad Wildungen (Northern Hessia)".

[3] "Galling midge *Giraudiella inclusa* (Diptera, Cecidomyiidae) in the food web of reed (*Phragmites australis*) ecosystems: population interactions across four trophic levels." This wasn't a time for snappy PhD titles.

[4] "Herbivore-parasitoid communities on grasses (Poaceae): Diversity, dynamics and interaction"

[5] The "right to lecture" at the university.

tem functions, particularly herbivory, predation, parasitism and pollination, as well as multitrophic interactions and quantitative food webs. These research activities resulted in numerous papers published across all high-ranking scientific journals. Since 2015, he is ranked continuously among the top 1% most cited scientists in "Environment/Ecology" and "Plant & Animal Science" (Highly Cited Researcher, Web of Science, ISI Thomson Reuters/Clarivate Analytics).

Landscape-pattern of biodiversity and onwards

With new concepts and innovative study designs, Teja made major and highly influential contributions to landscape ecology. Early starting points were fragmentation studies with potted *Trifolium* plants published in Science (Kruess and Tscharntke 1994) and the consideration of neighbourhood and isolation effects for the colonisation of set aside fields (Gathmann et al. 1994). A major breakthrough was his recognition that the wider landscape context, in addition to local habitat characteristics, might shape species communities and their biotic interaction. Teja´s first PhD student from the Faculty of Agricultural Sciences at Göttingen University, Carsten Thies, performed experiments with potted oilseed rape plants and demonstrated that pest control benefits from higher proportions of non-crop habitat in the landscape (Thies and Tscharntke 1999). A next step was the consideration of multiple spatial scales, thereby linking landscape effects to foraging or dispersal distances of organisms (Steffan-Dewenter et al. 2002). After the first pioneering study, the landscape concept was applied to a broad range of taxa and ecosystem functions and summarised in highly cited conceptual papers by Teja and co-authors (Tscharntke et al. 2005, 2012).

Expanding from the seminal studies focussing on landscape composition, i.e. area coverage of organic agriculture, semi-natural habitats or mass-flowering crops, the landscape *configuration* came into focus, too. In various studies, Teja aimed at disentangling the effects of landscape composition and spatial configuration showing that small-scale agricultural landscapes are of great importance for conservation of biodiversity and ecosystem services (e.g. Tscharntke et al. 2021). Lately, he further applied landscape ecological concepts in urban contexts showing that increasing amounts of impervious areas result in impoverished species communities and ecosystem services (Wenzel et al. 2020). Teja also explored novel research approaches to assess landscape-wide patterns of species diversity using grid sampling. Nowadays, the legacy of Teja's work is demonstrated by a multitude of research groups across the globe that use diverse modifications of these pioneering landscape study designs in a wide range of temperate and tropical ecosystems (see also the article by Poveda et al. in this Festschrift).

Tropical agroecology

Teja Tscharntke's research activities in the tropics started in the late 1990s. At this time the agricultural and forestry faculties at Göttingen University had long-term contacts to Indonesian universities. A group of researchers came together to develop plans for the implementation of a Collaborative Research Unit. Teja became quickly involved and made several preparatory trips to Indonesia. He was fascinated by the different culture, the beautiful diversity of tropical insects and a multitude of exciting agroecological research topics. The decision was made to focus on tropical rainforest margins at the border of Lore

Lindu National Park in Central Sulawesi. The first expectations to find forest margins with diverse forest gardens turned out to be rather romantic. Instead, quite intensive and rapidly expanding coffee and cacao agroforestry systems in the neighbourhood of the national park were selected as focal study systems, together with primary and secondary forests.

After a first non-successful application a revised proposal titled "*Stabilität von Randzonen Tropischer Regenwälder in Indonesien*" was funded by the Deutsche Forschungsgemeinschaft (DFG) and started mid 2000. Teja's project (*Die Folgen der Landnutzung für den Insekten-Artenreichtum und Pflanze-Insekt-Interaktionen*) focused on butterfly, bee and legume pod communities and their biotic interactions. The first phase was followed by two more funding rounds of the SFB 1687 Storma until 2009 (summarised in Teja's only books: Tscharntke et al. 2007; Tscharntke et al. 2010). The subsequent CRC 990 Efforts ("*Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems*") moved its study region to Sumatra (a colleague stated that it was definitely not selected for touristic reasons) and has again been running for three phases from 2010-2023. The early studies in Indonesia have laid the ground for Teja's highly successful and influential agroecological research that benefited from transdisciplinary collaborations and landscape concepts developed in Germany. Later, Teja expanded his tropical activities to many places across the world including Ecuador, Madagascar, South Africa, India, Bolivia, and Peru.

Editor-in-Chief of Basic and Applied Ecology

In the late 1990s, members of the Ecological Society of Germany, Austria and Switzerland (GfÖ) became increasingly dissatisfied with the Society's Annual Proceedings ("Verhandlungen"). They felt that too many articles published were of questionable quality and regretted the low international perception, which was assumed to be due to German being the sole publication language.

The GfÖ-Board finally decided that the proceedings should be turned into a journal, published in English – with a German summary ("Zusammenfassung"), making the transition less abrupt: "Basic and Applied Ecology" was born. Teja Tscharntke was appointed Editor-in-Chief in 1999, assisted by five editors and an editorial board of 27 members. The first two issues appeared in 2000, followed by two volumes of four issues per year. In 2003, volumes were enlarged to comprise six issues. This was also the first year for which an impact factor (1.577) became available.

Early in 2004, Klaus Hövemeyer joined the journal, helping with the increasing amount of work. This was the time when shelves of folders containing hundreds of manuscripts covered the walls of Teja's office, while thousands of Euros were spent on postage and packing for correspondence with the authors and reviewers. The journal switched to online submission in 2006, and this generated a plethora of emails starting "Lieber Teja, ..." and "Lieber Klaus, ..." in the following years. In 2009, the journal expanded to eight issues per year, and this continued to be the size of the journal till the present day.

In December 2022, Teja stepped down as the Editor-in-Chief of Basic and Applied Ecology, after 23 years at the helm. During this time, 158 issues were published, containing 1561 peer-reviewed papers and 246 book reviews, and an impact factor of 3.735 (2022) was achieved. Teja put a lot of effort in encouraging colleagues to organize a Special Issue or prepare review papers. Finding authors for the Invited Views in Basic and Applied Ecology, some of which became highly cited papers, was one of Teja's major concerns.

Recently, the Editorial Board was re-organized with Subject Editors bearing more responsibility for organizing the review process and Ingo Grass took over as Editor-in-Chief in 2023. All the editors will continue to preserve Basic and Applied Ecology as an international forum for the many disciplines of ecology, ensuring a fair and smooth review process for our authors and reviewers.

Awards and honours

Teja received several outstanding honours and awards:

- In 2018 he was awarded the International Fellowship for Distinguished Scientists by the President of the Chinese Academy of Sciences (CAS).
- In 2020 he received the Marsh Award for Ecology by the British Ecological Society. The award is given for outstanding research achievements that have had a significant impact on the development of the science of ecology.
- In 2020 he received the Royal Entomological Society Award for Insect Conservation, in recognition of "outstanding and exemplary lifetime contribution in Insect Conservation".
- In 2021 he was awarded the Medal of Honour of the Society for Ecology (GfÖ) "for outstanding and forward-looking achievements in ecological research".

The scientific impact of Teja's work, and his personality, reaches far beyond his own working group. As the contributions to this Festschrift indicate, Teja's scientific legacy spans the entire world, and has inspired (agro)ecologists in many countries.

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Part I
The Landscape Ecology of Biodiversity

Chapter 1

The landscape perspective in agroecology – history and recent advances

Annika Hass, Matthias Spangenberg, Kerstin Wiegand & Catrin Westphal

Abstract The decline in biodiversity is largely attributed to the intensification of agriculture, even as crop production remains reliant on ecosystem services. As a response to this challenge, agroecology investigates biodiversity patterns, species interactions, ecosystem functions and services within agricultural systems. Over recent decades, agroecology has advanced significantly, adopting a landscape-oriented approach that enables the incorporation of essential dynamics occurring across different spatial scales. In this review we examine pivotal advancements in agroecology and pinpoint influential studies that have shaped contemporary research at larger spatial scales. We highlight four major developmental steps in this field:

1. Habitat Loss and Fragmentation: This section discusses how habitat loss and fragmentation impact species populations and biodiversity patterns. It emphasises the need to consider both habitat amount and isolation effects, introducing the concept of the habitat amount hypothesis to explain the combined effects of patch size and isolation.
2. Scale-Dependent Effects of Landscape Composition: We explore how landscape composition (the proportion of different habitat types) affects biodiversity and ecosystem services. We describe the introduction of the concept of analysing multiple spatial scales and highlight the importance of considering resource availability at landscape scales.
3. Interactions Between Local and Landscape Management: This section discusses studies that investigate how local and landscape factors interact to influence biodiversity and ecosystem services. It emphasises the need to consider both local habitat management and the surrounding landscape context to achieve effective biodiversity conservation measures.
4. Disentangling Different Landscape Components: We discuss the significance of considering both landscape composition and configuration (spatial arrangement of habitats)

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in understanding biodiversity patterns. We underscore the importance of careful study design to disentangle the effects of different landscape components.

We conclude by outlining potential future directions for agroecological research across spatial scales, including the importance of landscape design, capturing ecological processes using multiple sampling sites per landscape, and the need for interdisciplinary studies that consider ecological, economic, and social aspects in agricultural systems. These advancements will play a pivotal role in safeguarding biodiversity and ensuring more sustainable crop production in the future.

1.1 Introduction

Agricultural intensification has been identified as one of the main drivers for biodiversity decline (Newbold et al. 2015; Outhwaite et al. 2022) with detrimental consequences for species interactions, ecosystem functions and services (Balvanera et al. 2006; Dainese et al. 2019). The aim of agroecological research is to better understand how different agricultural practices affect biodiversity, how biodiversity can be promoted in agricultural systems and how biodiversity contributes to agricultural production. Moreover, agroecological research aims at finding solutions for halting the loss of farmland biodiversity while compromising food production as little as possible (Gliessman 2006; Altieri 2019). The term agroecology emerged at the beginning of the 20th century (Wezel et al. 2009) and focused initially on the study of different taxonomic groups, their interactions and how they were affected by agricultural management at the local scale (e.g. Tischler 1965). However, subsequently, it was proposed that ecological processes and interactions among species frequently operate on spatial scales that extend beyond individual habitats (Kareiva and Wennergren 1995; Tscharntke et al. 2012). Hence, a significant advancement in agroecological research involves surpassing these localised attributes to comprehend the composition of species communities. In the late 1990s, the need for a landscape-scale perspective has been proposed by distinct fields such as metapopulation ecology, theoretical ecology, and landscape ecology (Turner 1989; Gustafson 1998; Hanski 1998; Wiegand et al. 1999).

Teja Tscharntke has actively pursued and advanced the landscape perspective in ecology (Tscharntke et al. 2005). Since the late 1990s and early 2000s, a growing body of research has accumulated to underscore the significance of larger spatial scales for biodiversity patterns, species interactions, ecosystem functions and services in agricultural systems as demonstrated by seminal studies (e.g. Thies and Tscharntke 1999; Kremen et al. 2002). It became evident that many species occurring in agricultural fields use multiple habitats for foraging, hibernation or different life stages because of the high management intensity and frequent disturbances in agricultural fields. For example, in agricultural landscapes, species can spill over from (semi-)natural habitats into croplands where they provide important ecosystem services, such as biological pest control and pollination (Rand et al. 2006; Blitzer et al. 2012). Thus, for spillover processes the distance between species habitats and agricultural fields is a major factor determining species interactions and the provisioning of ecosystem services. The investigation of such distance effects (i.e. habitat fragmentation) represented one of the first steps of the integration of landscape ecology and agroecology.

This combination of agroecology and landscape ecology is not only important for science, but also for policy guidelines for both biodiversity conservation and the strategic management of services and disservices within agricultural areas. These recommendations encompass insights into the most effective landscape settings for implementing biodiversity schemes (the intermediate landscape-complexity hypothesis; (Tscharntke et al. 2005, 2012; Batáry et al. 2011) and the landscapes that are particularly conducive to achieving robust biological pest control or pollination services (Dainese et al. 2019). Therefore, the landscape perspective has played a major role in developing a vision of more sustainable agricultural systems and will also be essential for the future (Landis 2017; Pe'er et al. 2022). Examining historical progression and tracing the evolution of the landscape perspective within agroecology is important to achieve a more profound comprehension of the diverse approaches and progressions, thereby offering valuable insights for shaping forthcoming research and policy endeavours.

The aim of this review is to identify the most influential studies that form the basis of modern agroecological research at landscape scales and that have initiated and advanced important developments. Further, we identified four major developmental steps of research approaches that integrate landscape ecology and applied ecology with a focus on biodiversity, species interactions and ecosystem service provisioning in agricultural systems. These developments resulted in novel perspectives concerning the conservation-oriented management of agricultural landscapes.

1.2 Methods

To identify the most influential studies combining landscape and agroecology we used the following search string in Web of Science:

```
(fragmentation OR isolation OR radius OR buffer OR
"landscape heterogeneity" OR "landscape complexity" OR
"landscape simplif*" OR "landscape composition" OR
"landscape configuration")
AND (biodiversity OR "species richness")
AND agricultur*
```

We repeated this search for different time periods to find the most influential papers along the timeline. We divided the time periods in a period before 1990 and then used 5-year steps (1950-1989, 1990-1995, 1996-2000, 2001-2005, 2006-2010, 2011-2015, 2016-2020, 2021-2023). Within each time period, we sorted the results by the number of citations and decided first by checking the titles and then the abstracts whether the topic of the papers was appropriate. We searched per 5-year period to be able to reconstruct the historical development and to compare the number of citations for papers which had been published at a similar time period. Included papers needed to have a focus on landscape scale effects on biodiversity and/or ecosystem functions and services in agricultural systems. All finally included papers had at least 300 citations with the exception of the two most recent papers (Martin et al. 2019; Sirami et al. 2019) which both received more than 200 citations (25

August 2023). Based on these papers we identified four major topics which have advanced landscape ecology in agricultural systems (Fig. 1.1):

1. Habitat loss and fragmentation
2. Scale-dependent effects of landscape composition - the circles
3. Interactions between local and landscape management
4. Disentangling different landscape components

We assigned each paper to one of these topics and then further selected the most influential studies per topic. In the period from 1950-1989 no papers matched our search terms. Moreover, we added a few other studies which were highly influential and highly cited, but did not match our search terms (Thies and Tscharntke 1999; Fahrig 2003; Westphal et al. 2003; Chaplin-Kramer et al. 2011; Tscharntke et al. 2012). Finally, we aligned all highly influential papers on the timeline sorted by the thematic group (Fig. 1.1).

1.3 Habitat loss and fragmentation

Considering land use intensification through agriculture and other land use changes, early simulation studies demonstrated that habitat fragmentation affects species population mainly through decreasing proportions of suitable habitat patches and increasing isolation between habitats at landscape level (Andrén 1994). The degree to which habitat loss and isolation affect species populations depends on the habitat requirements of the species and their dispersal ability (Lambeck 1997). Lambeck (1997) was one of the first authors who introduced the concept of landscape management and landscape design to conserve multiple focal species that differ in their spatial habitat requirements. He suggested that different landscape parameters, such as landscape composition (required amount of suitable habitats) and configuration (habitat connectivity), need to be included in studies and subsequent conservation schemes for most sensitive and demanding focal species.

Inspired by the simulation studies of Andrén (1994), Steffan-Dewenter and Tscharntke (1999) tested the hypothesis that habitat fragmentation affects bee populations and impairs pollination services through changes in plant-pollinator interactions. Using experimental habitat islands, they demonstrated that high habitat connectivity is important for diverse bee communities and the stability of pollination services. Fahrig (2003) reviewed the growing body of empirical habitat fragmentation studies and found that habitat loss, measured as decreasing availability of suitable habitats at landscape scale, is a consistent driver of biodiversity losses while habitat fragmentation, decreasing connectivity, can have varying (positive and negative) effects on biodiversity. Hence, she emphasised that both landscape-scale processes should be considered independently in future studies on habitat fragmentation. This concept of differential effects of habitat loss and fragmentation has been adopted in subsequent empirical studies. Helm et al. (2006) even added a temporal perspective to the analysis of habitat loss and fragmentation using the flora of fragmented calcareous grasslands (alvars) as model system. They found that historic patterns of habitat size and connectivity predict the species richness of vascular plants in alvar habitats, indicating an extinction debt due to delayed responses of plant species to habitat fragmentation. Building upon this study, Krauss et al. (2010) demonstrated later that different trophic

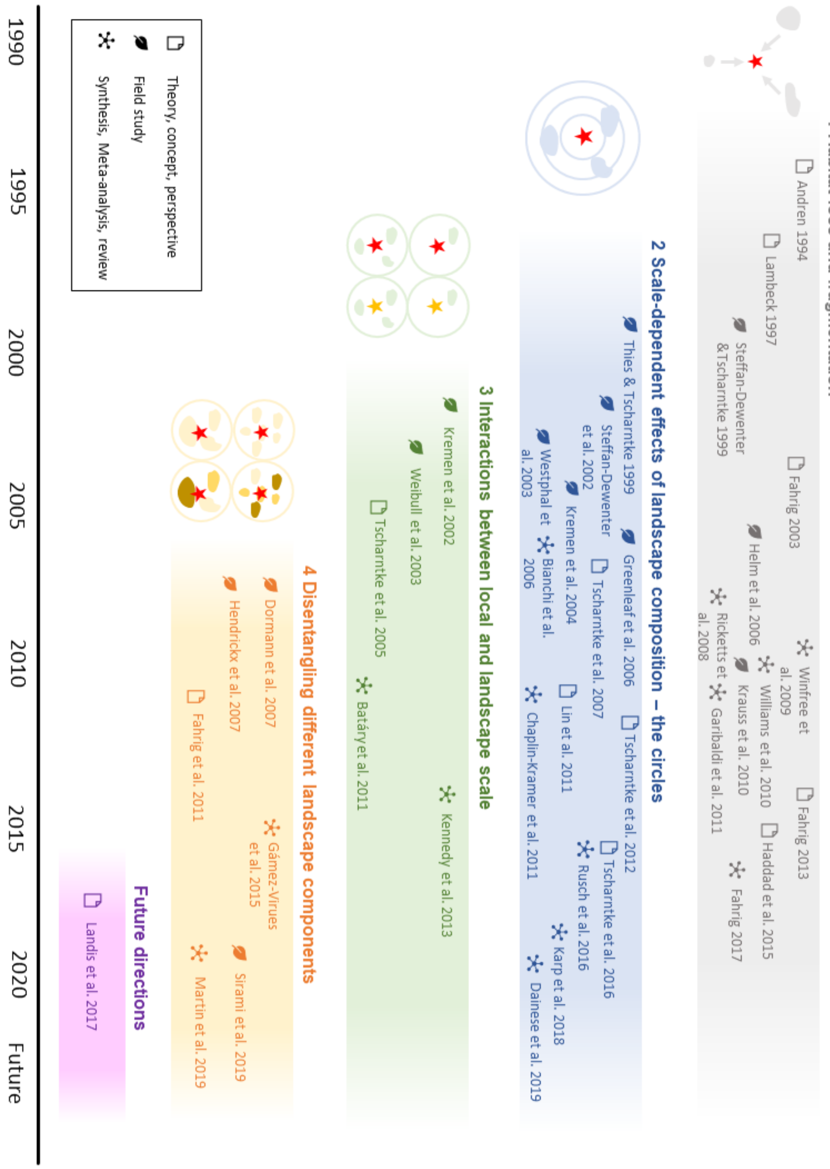

Fig. 1.1: Highly influential studies with a landscape perspective in agroecology along the timeline of their publication date.
]

levels show distinct temporal responses to habitat loss at local and landscape scale. In contrast to vascular plants, short-lived butterflies respond to present habitat size and thus do not show evidence for an extinction debt.

Focusing on pollinator communities and the delivery of crop pollination services, Ricketts et al. (2008) synthesised evidence from 23 studies on habitat fragmentation. They found negative effects of habitat isolation on both richness and visitation rates, with visitation rates declining more than pollinator richness. Subsequently, Garibaldi et al. (2011) focused their global synthesis on the effects of habitat isolation on the temporal and spatial stability of pollination services. They showed that not only the stability of flower-visitor richness and visitation rates but also the stability of the fruit set is negatively affected by habitat isolation.

In their meta-analysis, Winfree et al. (2009) examined the effects of multiple anthropogenic disturbances on bee abundance and richness. They found that habitat loss has significant negative effects on bees only in extremely simplified areas with low proportions of (semi-)natural habitats and thus is context dependent. Williams et al. (2010) also synthesised the effects of different anthropogenic disturbances on bee communities and included different functional traits in their analyses. Their findings indicate that the responses of bees to habitat loss were influenced by nest location and sociality, with above-ground nesting and social bees being most affected. Synthesising results from forest fragmentation experiments around the world, Haddad et al. (2015) demonstrated that habitat loss and isolation reduce biodiversity in general and also impair key ecosystem functions. Importantly, they found that the effects amplify over time and are most pronounced in the most isolated and smallest forest fragments.

Findings of empirical studies controlling for habitat amount indicate that habitat fragmentation, i.e. more numerous and smaller habitat patches covering the same area as a single large patch, often has positive effects on biodiversity (reviewed by Fahrig 2017). Different mechanisms, including increased habitat diversity or functional connectivity, positive edge effects, extinction debts or reduced competition, can result in such positive effects of several small habitat patches on biodiversity patterns. However, it is not yet fully understood under which specific conditions several small or single large habitat patches are most beneficial for biodiversity conservation.

Habitat loss and fragmentation play an important role in structuring species communities in agricultural landscapes. Research on habitat loss and fragmentations focuses only on suitable habitats, their connectivity and the amount of habitats in the surrounding landscape (habitat availability hypothesis: Fahrig 2013). However, species use different habitats within their activity ranges and respond to their spatial composition and configuration. These considerations led to novel research approaches focusing on the effects of landscape composition on species communities and the provisioning of ecosystems services.

1.4 Scale-dependent effects of landscape composition – the circles

Land consolidation and intensification of agriculture affect habitat amount and habitat conditions in agricultural systems. Moreover, such land use changes often result in the simplification of traditionally more complex landscapes that comprised a great variety of different managed and unmanaged habitats with often small patch and field sizes. Considering the evidence that these land use changes have been shown to be one of the main causes of biodiversity loss (IPBES 2019) which in turn leads to changes in the provisioning of ecosystem services (Cardinale et al. 2006), it became evident that in addition to local management the surroundings of the fields must also be taken into account in agroecological studies. Moreover, evidence from theoretical studies (Kareiva and Wennergren 1995; Wiegand et al. 1999) and the trophic-level hypothesis of island biogeography (Holt et al. 1999) motivated the inclusion of the landscape context in agroecological studies to better understand biodiversity patterns and the provisioning of ecosystem services. First landscape-scale studies focused on the proportion of suitable or unsuitable habitats at single spatial scales. The seminal study by Thies and Tscharntke (1999) could demonstrate that not only the presence of semi-natural habitats, such as field margins or fallows, adjacent to crop fields but also low shares of annual crops in the surrounding landscape (radius 750 m) improved biological pest control services in oilseed rape, resulting in lower crop damage. The study of Thies and Tscharntke (1999) motivated manifold follow-up studies on the effects of landscape composition, i.e. the proportion of crops or semi-natural habitats, on biological pest control agents and the services they provided. The review by Bianchi et al. (2006) could show impressively that natural enemy populations benefit from non-crop habitats and that pest pressure is higher in simplified landscapes with low proportions of semi-natural habitats and high proportions of annual crops. Based on a growing number of studies, Tscharntke et al. (2007) reviewed different mechanisms, such as spillover processes, metapopulation and metacommunity dynamics, that need to be considered in targeted landscape management of natural enemies and pest control services. However, from the numerous studies that still followed, it also became clear that other factors besides landscape factors often influence biological pest control (Tscharntke et al. 2016). For instance, agricultural practices, insufficient amount of suitable habitats and low habitat connectivity can additionally affect natural enemy populations and their biological pest control services. Likewise, crop habitats can provide important resources so that semi-natural habitats do not play an important role for natural enemy populations during certain phases of their life cycle. These and other factors can cause inconsistent responses of natural enemies and their biological pest control services to landscape composition, as shown by a global analysis by Karp et al. (2018). Nevertheless, Dainese et al. (2019) found in another global analysis that higher proportions of arable land have negative effects on the richness of natural enemies resulting in reduced pest control and final production. From the first empirical study (Thies and Tscharntke 1999) to global analyses (Karp et al. 2018; Dainese et al. 2019), it became very evident that, in addition to local drivers, a landscape perspective is needed to understand the diversity patterns and provisioning of ecosystem services in agroecological studies that deal with changing agricultural landscapes.

Depending on individual traits and trophic positions, organisms respond to habitat availability at different spatial scales (Roland and Taylor 1997; Holt et al. 1999). Hence, diversity patterns and ecological processes manifest at particular spatial scales at which the organisms perceive and interact with the surrounding landscape (Wiegand et al. 1999). As these spatial scales are determined by landscape characteristics (composition and spatial configuration) and species traits and perception, they are difficult to identify. Building upon modelling and theoretical studies, Steffan-Dewenter et al. (2002) used a novel approach of a nested set of eight spatial scales, i.e. circular landscape sectors centred around a study plot with radii between 250 m and 3000 m, to analyse the effects of landscape composition on the species richness and abundance of three pollinator guilds. They found contrasting foraging patterns of solitary wild bees, bumblebees and honeybees that were related to the proportions of semi-natural habitats at different spatial scales. This study was the first empirical study that clearly demonstrated the need to analyse multiple spatial scales in studies targeting the effects of landscape simplification on different taxonomic and functional groups. Inspired by the seminal study of Steffan-Dewenter et al. (2002), other studies employed the multiple scale analysis to investigate scale-dependent effects of landscape composition, for instance, on pollen deposition and the stability of pollination services (Kremen et al. 2004), the diversity of arable weeds (Gabriel et al. 2005) and arable spiders (Schmidt et al. 2008) as well as on cereal aphid-parasitoid interactions (Thies et al. 2005). In an important meta-analysis on the effects of landscape composition on functional groups of natural enemies, Chaplin-Kramer et al. (2011) showed that generalist enemies responded positively to the proportion of non-crop habitats across all spatial scales (up to 3500 m radius) while the responses of specialist enemies were rather detected at smaller spatial scales. However, the observed positive relationships did not translate into pest control as pest abundance was not affected by landscape complexity (Chaplin-Kramer et al. 2011).

The above mentioned studies focused on the proportions of crop or non-crop habitats but did not differentiate between crop species. As flowering crops can provide valuable resources for pollinators, Westphal et al. (2003) employed the proportions of mass-flowering crops in their multiple scale analysis. They found that overall bumblebee abundance increased with the availability of mass-flowering oilseed rape at a large spatial scale (3000 m radius). However, individual bumblebee species respond to mass-flowering crops at species-specific spatial scales (Westphal et al. 2006). Greenleaf and Kremen (2006) added a temporal perspective in their study and found that pollination services in hybrid sunflower benefit from semi-natural habitats in the surrounding landscapes but also from continuous cultivation of mass-flowering sunflowers.

Stimulated by modelling studies, agroecological research started to incorporate landscape composition at single or multiple spatial scales to analyse the effects of land use change on biodiversity patterns and the provisioning of ecosystem services in agroecosystems. In a trend-setting review, Tscharntke et al. (2012) summarised knowledge of landscape-scale studies and suggested eight important hypotheses to stimulate further research on the landscape-moderated effects on biodiversity to develop solutions for biodiversity conservation and ecosystem service management. For example, multiple spatial scale analyses are used to investigate the multifunctionality of landscapes (Le Provost et al. 2023) and implications of future climate change scenarios on the resilience of agricultural land systems Lin (2011).

1.5 Interactions between local and landscape management

One important question motivated by studies at multiple spatial scales is how local and landscape scale characteristics interactively affect biodiversity, ecosystem functions and services. The first highly influential study taking both, local and landscape effects, into account simultaneously investigated pollination services in organic and conventional watermelon fields varying in their distance to natural habitats (Kremen et al. 2002). Only in organic watermelon fields near natural habitats the diversity and abundance of wild pollinators was high enough to provide sufficient pollination services for optimal yields. In contrast, organic fields with larger distances to natural habitat and conventional fields depended on pollination by managed pollinators (Kremen et al. 2002). This indicates that both local and landscape factors, as well as their combined effects need to be considered when planning for biodiversity conservation and high ecosystem service provision in agricultural landscapes.

Tscharntke et al. (2005) identified the importance of landscape structure on ecological interactions and processes influencing biodiversity at the local scale and pinpointed the necessity to consider landscapes for biodiversity conservation and promotion of ecosystem services. They hypothesised that landscape effects would differ between contrasting local habitat types as suggested e.g. by Weibull and Östman (2003), who found higher importance of landscape heterogeneity in conventional fields compared to organic fields. Consequently, the effectiveness of measures aiming at biodiversity enhancement such as agri-environment schemes would depend on the landscape context. According to their hypotheses, the effectiveness of biodiversity measures such as the extensification of local management would be low in cleared landscapes (<1% non-crop habitat) due to a lack of source populations. High effectiveness was expected in landscapes with medium complexity (1-20% non-crop habitat) as species are able to immigrate from the surrounding landscape. However, a low contrast between the measure and the surrounding landscape as in highly complex landscapes (>20% non-crop habitat) where high biodiversity could be expected throughout the landscape would lead to a decreased effectiveness (Kleijn and Sutherland 2003; Tscharntke et al. 2005). Batáry et al. (2011) expected that this dependence on the landscape context might be the reason for the variable effects that conservation measures have on biodiversity Kleijn et al. (2006). In their meta-analysis they found evidence for the landscape dependence of the effectiveness of agri-environment schemes. Measures implemented in cropland such as organic farming increased the abundance and species richness across different taxonomic groups more in simple compared to complex landscapes (Batáry et al. 2011).

Based on the theory and meta-analysis, the interactive effects of local and landscape scale variables were further analysed in a global synthesis for crop pollinators (Kennedy et al. 2013). They synthesised the data from 39 studies and estimated landscape resource quality by using a modelling approach (Lonsdorf et al. 2009). Both local diversity at the field scale and resource availability at the landscape scale were strong predictors of bee species richness and abundance. Moreover, lower effectiveness of landscape scale resources was detected in locally diverse fields, supporting the intermediate-landscape complexity hypothesis.

Overall, the pioneering studies on interactive effects between local and landscape scale variables (Kremen et al. 2002; Weibull and Östman 2003; Tscharntke et al. 2005; Batáry et al. 2011; Kennedy et al. 2013) have strongly advanced our understanding of biodiversity in agricultural landscapes at larger spatial scales. Moreover, by demonstrating the higher effectiveness of biodiversity measures, such as agri-environment schemes, in simple landscapes compared to complex landscapes, they provided important policy recommendations for conservation measures in farmland.

1.6 Disentangling different landscape components

Landscape composition (the amount or diversity of different habitat types) and configuration (the spatial arrangement of habitats) had already been identified as important landscape characteristics during the beginning of landscape scale research (Lambeck 1997). However, early field studies investigating landscape effects on biodiversity and ecosystem services mostly focused on the amount of (semi)-natural habitat or the percentage of non-crop habitat (Thies and Tscharntke 1999; Steffan-Dewenter et al. 2002). Thus, the focus was more on landscape composition, neglecting landscape configuration. However, the spatial arrangement of habitats within the species' dispersal range can be essential for determining biodiversity (Fahrig et al. 2011). As configuration is crucial for habitat connectivity, it represents a combination of the landscape circles and the habitat fragmentation approach.

One early and highly influential study therefore aimed at disentangling different landscape components (Dormann et al. 2007). In this pan-European study, the authors could show that community similarity of various taxa responded not only to the percentage of semi-natural habitats, but also to interactive effects between the intensity of land use at the landscape level and the spatial arrangement of semi-natural habitats. For example, highest homogenisation of bee and true bug communities was found in landscapes with high pesticide use and high fragmentation of woody habitat types, probably due to reduced dispersal and promotion of generalist species (Dormann et al. 2007). Hence, landscape configuration was introduced as a measure for habitat fragmentation. Hendrickx et al. (2007) also focused on different landscape components and highlighted their importance not only for alpha, but also for beta diversity.

In their perspective paper, Fahrig et al. (2011) build on this importance of configurational heterogeneity. They identified a lack of suitable studies to disentangle the effects of compositional and configurational heterogeneity on biodiversity, as both are often correlated in real landscapes. They proposed explicit study designs by selecting landscapes along independent gradients (Fahrig et al. 2011). This work inspired large field and synthesis studies to test the independent effects of configuration and composition. Martin et al. (2019) synthesised the data of 49 studies and found that edge density was of major importance for abundances of pollinators and natural enemies of pests. Arthropod abundance was highest in landscapes with high configuration (edge density) and composition (percentage of semi-natural habitat) indicating interactive effects of both. Moreover, they found that high configurational heterogeneity does not correlate with reductions in yield.

Moreover, Fahrig et al. (2011) highlight the possible importance of compositional and configurational heterogeneity of the crop area for biodiversity (e.g. crop diversity or field border length), as previous studies had mainly focused on (semi-)natural habitats. This hypothesis was tested in a large international field study, confirming the high importance of configurational heterogeneity and interactive effects between different landscape components (Sirami et al. 2019). By selecting 435 landscapes in 8 contrasting regions of Europe and North America along independent gradients of crop diversity and mean field size, they could clearly disentangle the positive effects of reduced field sizes and thus higher configurational heterogeneity across different taxa from landscape composition effects. Crop diversity also had a positive effect, but only in landscapes with high cover of semi-natural habitats (Sirami et al. 2019).

The highly cited studies have drawn our attention to the fact that landscapes are complex and that careful study design is necessary to disentangle different landscape components such as land use intensity, landscape composition or landscape configuration. In particular, configurational heterogeneity has been identified as an important and previously often overlooked landscape characteristic determining biodiversity. Other studies have confirmed this importance by showing that in particular small and therefore less mobile species benefited from high edge density (Gámez-Virués et al. 2015). Moreover, ecosystem services like pollination can be increased (Hass et al. 2018), leading to higher crop yields (Magrach et al. 2023).

1.7 Outlook and future directions

During the last two decades, the landscape perspective in agroecology has been introduced and developed vibrantly (despite initial scepticism within the scientific community, personal observations). This led to major scientific achievements with practical relevance for agricultural production and biodiversity conservation in agricultural landscapes. However, achievements in practical implementation that improve conditions for biodiversity have been very limited. For example, the loss of typical farmland birds or grassland butterflies could not be stopped or reversed in Europe (Gregory et al. 2019; Warren et al. 2021). This may be one of the reasons why the recent suggestion by Landis (2017) that agro-ecological landscape research should focus on landscape design has received much attention. So far, spatial aspects are usually not considered in the implementation of agri-environment schemes or conservation measures although it is widely known that the effectiveness of such measures largely depends on the landscape context (see section 1.3) and even on the interplay between different landscape components (see section 1.4; Pe'er et al. 2022). This may be due to a lack of knowledge on how to put this theoretical knowledge into practice. Recently, novel agri-environment schemes emerge that target the collaborative implementation of measures at the landscape scale (Geertsema et al. 2016; Pe'er et al. 2022). Therefore, future research will need to focus on how to design multifunctional landscapes that optimise biodiversity conservation and agricultural production most efficiently in close collaboration with farmers and other stakeholders.

Moreover, landscape ecology in farmland has described dilution and concentration effects (Holzschuh et al. 2011), which might have distorted results of earlier studies. For example, introduced flower fields could attract pollinators from the surrounding landscape without increasing landscape scale population sizes (Kleijn et al. 2018). These effects cannot be detected by using the most common approach of only one sampling site at the center of a landscape, but requires the sampling of multiple sites per landscape (e.g. Beyer et al. 2020). This approach has already been used earlier (e.g. Dormann et al. 2007) and it has been argued that this is necessary to capture the ongoing ecological processes at the landscape scale (Marini et al. 2019; Scherber et al. 2019) and might be a future direction of landscape ecology in farmland.

Overall, future agro-ecological research will face the challenge of developing solutions for the ongoing biodiversity crisis in farmland. These challenges cannot be solved by agroecologists alone while ignoring social and economic components. Particularly interdisciplinary studies that focus on the interactions of ecological, economic and social impacts of possible interventions at relevant spatial scales will be crucial for more sustainable agricultural systems.

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Chapter 2
What did we learn from meta-analyses about farmland arthropod conservation?

Péter Batáry, Riho Marja, René Gaigher, Ingo Grass & András Báldi

Abstract Quantitative evidence syntheses appeared in agroecological research in the early 2000 and gained momentum during the last decade for summarising the growing knowledge about the importance of farmland biodiversity conservation. Among other evidence syntheses, meta-analyses have a significant role in quantitatively synthesising findings of primary studies, typically in the frame of systematic reviews. Here we provide a global overview via a scoping review of the essential quantitative synthesis studies testing land-use extensification or diversification effects on arthropod biodiversity. Most meta-analyses showed a positive impact of the studied different extensification or diversification measures on arthropod species richness, with varying effects depending on the studied arthropod functional group, ecosystem, measure type and landscape context. Our findings highlight a serious research gap from the tropics, envisage future directions of agroecological meta-analyses, and provide recommendations for insect conservation in farmland. Finally, we finish our review by emphasising the importance of closing the science-policy gap in order to support the transformative change in the European food system.

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2.1 Introduction

Arthropods are undergoing global population declines and extinctions due to a range of interacting stressors including habitat loss, habitat degradation, and climate change (Cardoso et al., 2020; Harvey et al., 2022). Agricultural intensification is among the top proximate drivers of these processes (IPBES 2019). Production areas that are intensively managed through e.g. heavy tillage, mechanisation, intensive grazing, short crop rotations, and high levels of agrochemical inputs represent an inhospitable environment to most arthropods (Tscharntke et al. 2005a; Desneux et al. 2007; Geiger et al. 2010). Along with this, farmland simplification has greatly reduced the resources available to farmland arthropods. Consolidation of crop fields has led to increased field sizes and the loss of non-crop elements, such as hedgerows and field margins, which provide essential resources for arthropods (Fahrig et al. 2015). Furthermore, crop and livestock diversity loss means farmland has become increasingly homogenised (Sirami et al. 2019).

A wide variety of conservation interventions ranging from targeted, individual measures to more holistic farmland conservation programmes, have played a critical role in mitigating these impacts. These include extensification approaches that aim to reduce in-field management intensity, and diversification measures that aim to re-introduce complexity in agroecosystems at the local and landscape scales, and at temporal scales (Schellhorn et al. 2015; Tamburini et al. 2020). However, there is great variation in success between agroecosystem types, taxa, landscape context and spatial scale considered (Birkhofer et al. 2014; Dainese et al. 2015; Tscharntke et al. 2005b; Tuck et al. 2014).

Synthesising research evidence is vital to identify knowledge gaps and showcase best practices in agroecology. There is a surprisingly great diversity of research or knowledge synthesis methods from simple, narrative reviews through focus groups to systematic reviews and quantitative meta-analyses. Dicks et al. (2017) identified and described over 20 such synthesis methods in environmental sciences, which all review, condense and communicate evidence-based findings vital for the science-policy interface. Two strongly linked methods stand out in responding to scientific ecological or conservation biological questions with their low risk and strong synthesis outcome: systematic reviews and meta-analyses. Systematic reviews identify, appraise, select and synthesize all high-quality relevant research evidence (Haddaway et al. 2018). Furthermore, systematic reviews often use meta-analysis as a statistical technique to combine results of the eligible studies, where effect sizes are calculated for the individual primary studies to put them on the same scale, and heterogeneities (random or systematic, e.g. by environmental moderators) among these effect sizes are tested in meta-analysis models (Gurevitch et al. 2018). Meta-analyses emerged in the 2000s in ecology (also in agroecology; see Pywell et al. 2003), and have become a standard, well-known and highly accepted method during the last decade with an ever-increasing number of published articles, even though there is still a high need to improve their quality (Philibert et al. 2012; Koricheva and Gurevitch 2014).

Here, we aimed to perform a scoping review for meta-analysis studies on farmland arthropod conservation to extract the evidence base by putting all relevant meta-analyses on the same scale. Scoping reviews, also termed quick scoping reviews, use a step-wise methodology following an a priori protocol and is similar to systematic reviews and maps but in a simplified process to produce information in a short time period (Dicks et al. 2017).

According to Munn et al. (2018), the scoping review is suitable for identifying knowledge gaps by scoping a body of literature, clarifying concepts or investigating research. For our review, we performed a systematic search for identifying the potential agroecological meta-analyses studying local and/or landscape scale management effects on arthropod diversity. We put all selected meta-analyses on the same scale (either percentage of change or percentage of explained variance) for better comparability to draw general conclusions (Spake et al. 2022). If it was available in the selected meta-analysis studies, we also summarised effects on different functional groups, landscape moderation effects, and occasionally we also considered effects on yield and profit data (but we did not search explicitly for ecosystem services).

2.2 Methods

In the scoping review, we followed the PICO (Population, Intervention, Comparison and Outcome) framework for considering and scoping for relevant search terms, with which we can identify relevant meta-analysis studies investigating local and landscape scale intensification or extensification effects on them (Higgins & Green, 2008). The population in this broad topic is various groups of arthropods in any kind of agricultural ecosystem, including temporary and permanent crop systems and managed grasslands, but we did not use any taxonomic group or insect or arthropod as a search term to apply a rather sensitive search. Also, instead of using many different intervention and outcome terms, we searched for the term meta-analysis. Finally, we used biodiversity and species richness as outcome terms to focus on community-level studies. Based on these, our search term combination was the following, which we used in topic search of ISI Web of Sciences (WoS), Science Citation Index on 05.01.2023: "(agri* OR grassland OR farmland OR agroforestry OR vineyard) AND (biodiversity OR "species richness") AND meta-analysis". Additionally, we made a refinement in WoS by excluding hits based on the document type. Thus, we excluded corrections, editorial materials and data papers, obviously not containing meta-analyses, but we also excluded early access studies.

This resulted in 402 potential articles. We set up the following inclusion/exclusion rules for the screening process. We included studies investigating the effects of any kind of agricultural activity at the local or landscape scale on species richness or species diversity of arthropods (i.e. we excluded meta-analyses on plants and vertebrates). Some meta-analyses analysed effects on biodiversity in general, but if most effect sizes used in the meta-analyses were on arthropods, we included them. Furthermore, we excluded agricultural expansion studies, where the reference level at the local scale is the natural habitat and agriculture is only a general land conversion impact (e.g. agriculture vs. forest or grassland vs. forest). In connection with this, we also excluded fragmentation studies. Finally, we included only primary meta-analyses using standard effect sizes (Hedges' d or g, log response ratio or Pearson's r). After title filtering based on the above criteria, we identified 127 potential meta-analyses, which were refined to 82 meta-analyses after abstract filtering. After full-text filtering, we included 24 meta-analyses in our scoping review, but also added one meta-analysis relevant to the topic, but not located in WoS: Gonthier et al. (2014). This meta-analysis was not detected because, quite unexpectedly, it did not mention the keyword "meta-analysis", but PB as well as Teja were co-authors.

All of the 25 meta-analyses grouped effect sizes based on population (e.g. functional groups of arthropods) or intervention (e.g. different agri-environment schemes) or population (species richness or abundance, the latter was not a search criterion) to test them in summary or subset analyses or by using them as a moderator in meta regressions. Therefore, we extracted effect sizes from each meta-analysis, which was first of all on arthropod species richness. In many meta-analyses, arthropods were the focus. Thus we extracted effect sizes directly from the main analyses. Still, there were many other meta-analyses with a broader focus, where we extracted effect sizes from the subset or side meta-analyses. Besides, we also extracted effect sizes about abundance, especially to put effects on them in relation to those on species richness. From some meta-analyses, we were able to extract yield and profit data, which are highly relevant in agriculture and of major interest to Teja (Batáry et al. 2017; Gong et al. 2022).

We extracted the above-identified effect sizes (Hedges' d or g, log response ratio or Pearson's r) together with their 95% confidence intervals (CI) from all meta-analyses, mostly from forest plots with PlotDigitizer 2023, but a few cases from text or tables. We converted standardised mean differences (Hedges' d or g) to Pearson's r correlation coefficient (Borenstein et al. 2009). We then calculated R^2 from r and multiplied it by 100 to get the percentage of explained variance. We provide Cohen's benchmarks for Person's r and the corresponding percentage of explained variance below for interpreting effect sizes: $r < 0.1$ (<1%) -- very small effect; $0.1 \leq r < 0.3$ (1-9%) — small effect; $0.3 \leq r < 0.5$ (9-25%) moderate effect and $r \geq 0.5$ (>25%) large effect (Cohen 1988). Finally, in the case of the log response ratio, we calculated the percentage of change by taking the exponential of this effect size, from which we subtracted one, and then multiplied by 100 to get the percentage of change (Pustejovsky 2018).

We extracted 75 effect sizes altogether from the 25 summarised meta-analyses. We classified them based on population two-fold. First, which taxonomic or functional groups were studied, i.e. arthropods in general or pests, natural enemies, pollinators or detritivores. Second, which agroecosystems were studied, i.e. croplands, grasslands, permanent crops (agroforestry, vineyard) or a mixture of them (typically without differentiating cropland and grassland). We also classified studies based on outcome terms, i.e. species richness, abundance, biodiversity (considering species richness, abundance or even biomass together), yield or profit. Finally, we grouped all studies into three major groups based on intervention into so-called intensification or extensification comparisons, organic farming, which is often a main focus of many meta-analyses, and remaining specific measures in the often specific agroecosystem, such as grazing, reduced tillage or vineyard vegetation management.

2.3 Results and Discussion

In general, extensification measures showed positive effects on species richness and abundance of arthropods with varying effects depending on population, intervention type and outcome (Fig. 2.1). Organic farming also showed positive effects on arthropod species richness, but with a substantial loss of yield (Fig. 2.2). Finally, specific measures showed varying effects on arthropods dependent on the measure in the different agroecosystems (Fig. 2.3).

2.3.1 Extensification meta-analyses

Investigating the extensification meta-analyses in detail, Attwood et al. (2008) performed one of the earliest agroecological meta-analyses and highlighted that the type of agroecosystem can moderate the effectiveness of different measures. They found strong effects of extensification on grassland arthropods when they compared natural grasslands with the probably strongly impoverished fauna of improved grasslands. A similar comparison of reduced input cropping vs. conventional cropping turned out to be less effective with weaker effects, but later meta-analyses often showed similar effects (see below). In contrast, Shackelford et al. (2013) did not differentiate agroecosystems, but instead investigated local and landscape scale complexity together on species richness vs. abundance. They found that effects on species richness of arthropods and also natural enemy arthropods are more expressed (10% increase) than on abundance (2-3% increase). Another comparison was performed by Batáry et al. (2011) with the authorship of Teja, who tested his well-known landscape complexity hypothesis (Tscharntke et al. 2005a), which expected in a qualitative review that agri-environment management (AEM) is moderated by landscape complexity (often measured as a share of cropland or semi-natural area). Indeed, Batáry et al. (2011) could demonstrate that AEM effective supports species richness (also that of arthropods) in simple landscapes, but not in complex landscapes, which was only valid in croplands, but not in grasslands. The mechanism behind this is the spillover of organisms among habitats for resource complementation, often studied by Teja (Rand et al. 2006; Tscharntke et al. 2012). After this meta-analysis, a few follow-up meta-analyses also partly tested landscape moderation effects. For example, Scheper et al. (2013) confirmed this finding in the case of pollinating insects with a more expressed effect in simple landscapes of this mobile functional group (although they also found a small increase in complex landscapes). In addition, they also considered extremely simplified, so-called cleared landscapes, where agri-environment schemes were not at all effective due to the largely absent species pool (see landscape species pool hypothesis in Tscharntke et al. 2012). Furthermore, Gonthier et al. (2014, with Teja as co-author) showed a stronger local extensification effect on abundance than local extensification or landscape scale complexity effects on species richness or landscape-scale complexity effect on abundance. This was further investigated by Marja et al. (2022, also with Teja as co-author) with paired data design, who could show that increasing landscape complexity enhances species richness of farmland arthropods, whereas AES also enhances their abundance.

Batáry et al. (2015), in their review paper about the European AESs classified the various AEM based on whether they are applied in actively managed agricultural land as in production AEM, such as low-input farming vs. if they are applied on land taken out-of-production as out of production AEM, such as flower strips or hedgerows. They showed that out of production AEM, as a greener measure, supports species richness (also that of arthropods) more than in production AEM. Nevertheless, there might be a scale issue, as the out-of-production AEM is typically limited to a small area of the original

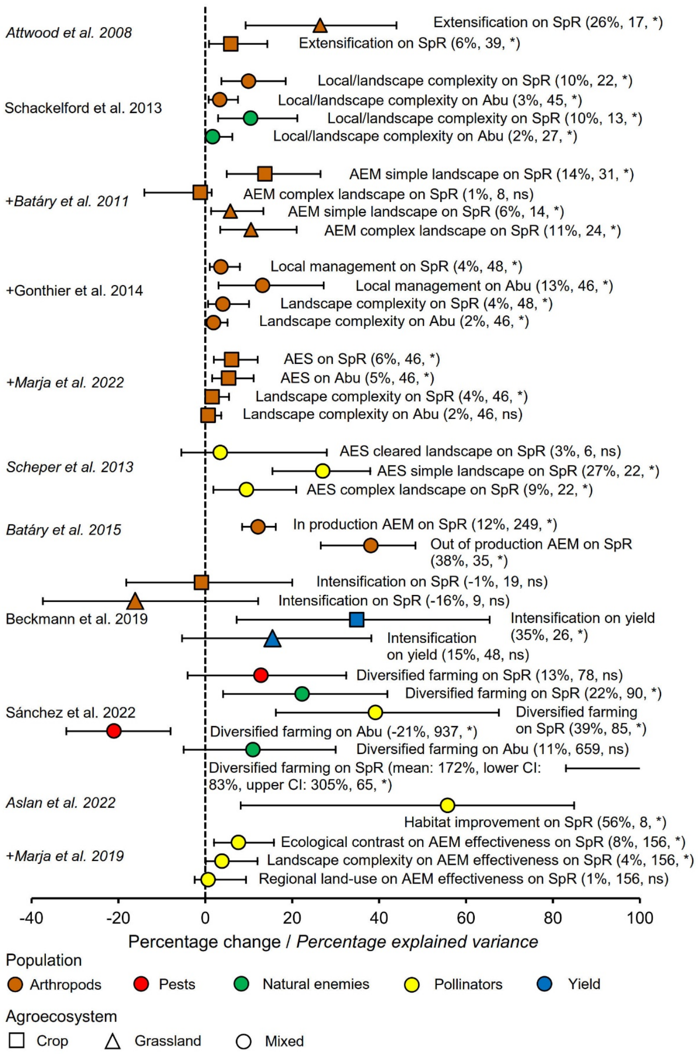

Fig. 2.1: Forest plot showing the main findings of meta-analyses testing different extensification measures on arthropod diversity (or yield) expressed as percentage change/percentage explained variance (reference in italics). Numbers in parentheses show the mean change, number of observations (i.e. effect sizes), and significance *: $p < 0.05$ and ns (if 95% CIs bracket zero the effect is not significant). AES: agri-environment scheme, AEM: agri-environmental management, SpR: species richness, Abu: abundance. Note: In contrast to all meta-analyses, Beckmann et al. (2019) tested intensification as intervention against lower land-use intensity as control. Effect size and Cis for pollinator abundance of Sánchez et al. (2022) is presented as text in the figure given the large effect. + indicates co-authorship of Teja.

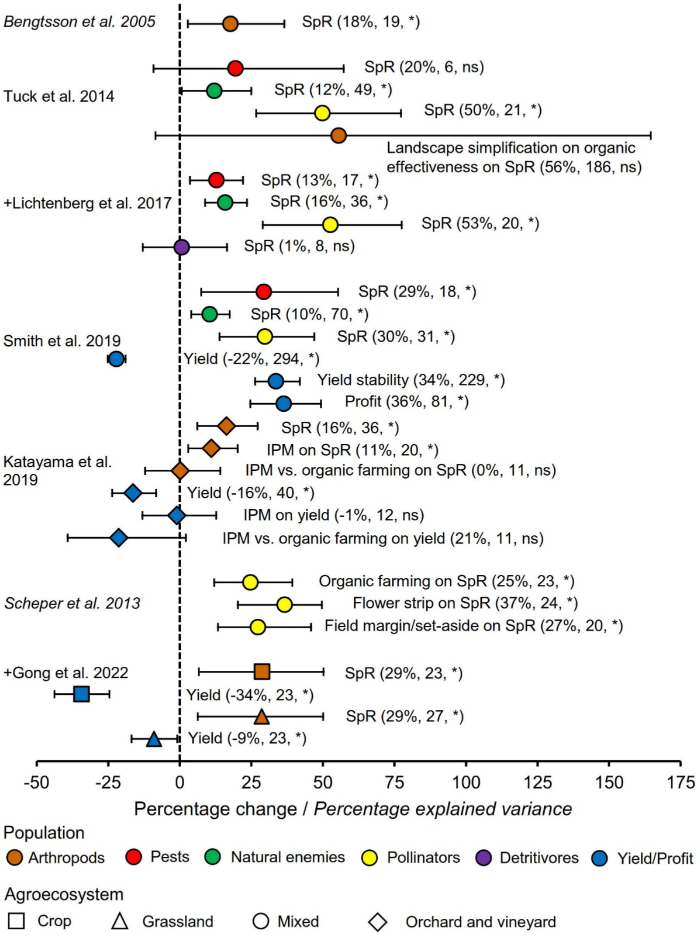

Fig. 2.2: Forest plot showing the main findings of meta-analyses testing organic farming on arthropod diversity (or yield and profit) expressed as percentage change/percentage explained variance (italics). See Fig. 2.1 for explanations.

field, whereas the in production AEM to the whole field, which complicates the outcomes dependent on which scale (transect, field, farm or even yield amount) is considered (Batáry and Tscharntke 2022).

Beckmann et al. (2019) considered intensification a bit unusual as an intervention and compared it to extensive systems as control. Nevertheless, their finding can also be interpreted as the opposite of extensification, and these largely confirm former meta-analyses. Intensification decreased the richness of arthropods, especially in grassland ecosystems (cf. with the finding of Attwood et al. 2008), but yield could be increased more in crops than in grasslands. This suggests that grasslands are probably more sensitive to intensification, and also that yield is hard to improve there. In a related meta-analysis, Sánchez et al. (2022)

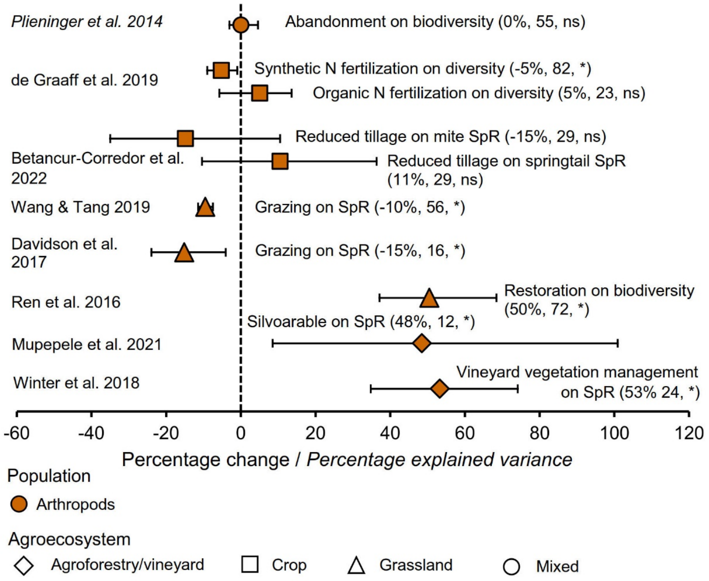

Fig. 2.3: Forest plot showing the main findings of meta-analyses testing specific farming measures on arthropod diversity expressed as percentage change/percentage explained variance (italics). See Fig. 2.1 for explanations.

studied diversified farming (also a mixture of all kinds of extensification measures, such as intercropping, and agroforestry) on different functional groups of arthropods. They showed a strong negative effect (−21%) on pest abundance, but a non-significant increase (11%) in natural enemy abundance (their species richness increased by 22%). Furthermore, they found that diversified farming increased pollinator richness by 39% (Aslan et al. 2022) also showed a large effect), and their abundance extremely by 172%. This latter surprising finding should be investigated further by a future meta-analysis by testing different agroecosystems and measures as moderators. Nevertheless, this meta-analysis also highlights that extensification or diversification schemes can have more expressed effects on more mobile organism groups, such as pollinators, and that these measures can shape biological control by suppressing pests and/or supporting their natural enemies. This cannot function well in given cases, as hypothesised by Teja (Tscharntke et al. 2016), which needs to be tested in future meta-analyses too. Finally, Marja et al. (2019, with Teja as co-author) studied the effects of European AEM on only pollinator richness. Besides the known landscape moderation effect, regional land-use intensity does not moderate AEM effectiveness, but the ecological contrast between the studied intervention and control measures is the most important in moderating this effectiveness. Large contrast cases, e.g. flower strip vs. conventionally managed field, showed somewhat stronger, but in general weak effect than low contrast cases, e.g. grassy field margin vs. conventional farming.

2.3.2 Meta-analyses on organic farming

Organic farming is a widely tested management measure in agroecology, with a lot of studies originating from the Agroecology group of Teja (e.g. Schmidt and Tscharntke 2005; Holzschuh et al. 2008; Batáry et al. 2012), which are often considered in different meta-analyses as a primary source. Organic farming, with its relatively clear local management extensification by mostly abolishing agrochemicals, is in the EU a common AES measure (Batáry et al. 2015). Even though organic farming can increase species richness, quite probably due to more individuals registered there, compared to conventional farming, this comes with a cost of lower yield, as detailed below. Therefore, Teja and his alumni recently emphasised the importance of landscape scale measures and relativised the importance of organic farming (Tscharntke et al. 2021). The meta-analysis studies start with Bengtsson et al. (2005), who found a moderately positive effect on arthropod richness. Its updated and amended meta-analysis by Tuck et al. (2014) showed 12% increase for natural enemies and a much stronger (50%) increase for pollinators, while a non-significant increase for pest richness. They also showed a strong landscape moderation effect on organic farming effectiveness, with higher effects in simpler landscapes, but this effect was not significant. Lichtenberg et al. (2017), with co-authorship of Teja) showed that organic farming effects also depend on the functional group considered, with no effects on detritivores, and increases for pests (13%), natural enemies (16%) and again especially for pollinators (53%). In contrast, Smith et al. (2019) found a stronger effect on pests (29%) than on natural enemies (10%), highlighting the fact that both groups are attracted by organic farming with variable diversity in contrast to the conventionally managed systems. While here not summarized, the global synthesis of Dainese et al. (2019) showed that increased richness of natural enemies resulted in a improved biocontrol (see results by crop diversification in the second-order meta-analysis of Beillouin et al. (2021), and similarly higher diversity of pollinators results in increased pollination success (but see Kleijn et al. 2015).

Smith et al. (2019) also tested the effects on yield and showed a 22% decrease in organic farming, but with higher yield stability (34%) and an increased profit (36%). Katayama et al. (2019), who studied orchards and vineyards, showed a 16% decrease in yield for organic farming, but basically, no yield loss in IPM compared to conventional farming. Both alternative measures increased arthropod richness, organic by 16%, IPM by 11%. Interestingly, when they compared organic farming directly with IPM, they showed no change in species richness, but the yield was still 12% lower (not significantly) in organic farming than in IPM. Thus we agree with their conclusion that integrated farming may be a crucial component of regional conservation planning in orchard/vineyard landscapes.

The earlier discussed Scheper et al. (2013) also tested the effects of other extensification measures besides organic farming on pollinator richness. They showed that organic farming, as well as, field margins and set-asides increased species richness by ca. 25-27%, but flower strips boosted them more with an increase of 37%. Nevertheless, as emphasised earlier, this greener measure might have less expressed impact at larger scales, therefore, combining these different measures is desirable (Grass et al. 2019). Finally, Gong et al. (2022), with Teja as co-author) also tested yield and species richness outcomes of organic farming and showed that organic farming increases species richness by 29% in crop and grass agroecosystems, but there is a stronger yield loss in crops (34%) than in grasslands

(9%). This study also highlights a similar yield-biodiversity trade-off in crops, but with a smaller intensification for closing the yield gap in grassland ecosystems, we might lose more species.

2.3.3 Meta-analyses focusing on specific interventions in different ecosystems

It is welcome that more and more meta-analyses pop up, which test specific agroecosystems, interventions or populations, and can respond to more detailed questions. Plieninger et al. (2014) highlighted the threats of land abandonment in the Mediterranean and found a slight increase in biodiversity (species richness and abundance, without differentiating among them), although not for arthropods. Therefore, they concluded that there is no one-size fits all solution for nature conservation, but there is a strong context dependency. Another specific meta-analysis by de Graaff et al. (2019) investigated the effects of fertilisation on cropland arthropods and found a 5% decrease in their richness due to artificial fertiliser, and a non-significant 5% increase due to organic fertilisers. The high amount of N fertilisers, often coupled with intensive pesticide use in conventional systems, resulted in a strongly reduced diversity and cover of arable wild plants Kleijn et al. (2009), which forms the basis of food webs for the arthropod fauna. Also, in croplands, Betancur-Corredor et al. (2022) showed a non-significant decrease (−15%) and increase (11%) of reduced tillage for mite and springtail richness, although positive effects on their abundances were more obvious (not presented). Thus, reduced tillage has great importance in soil conservation, especially in times of climate crisis.

Extensive grazing has enormous importance in the maintenance of natural and semi-natural grasslands Báldi et al. (2013), Kormann et al. (2015), and Torma et al. (2023), especially in Europe, where large megaherbivores are strongly missing on grasslands Pärtel et al. (2005). Wang and Tang (2019) showed in their global meta-analysis that increased grazing intensity (vs. enclosed control) negatively affected arthropod species richness resulting in a 10% decline. Similarly, Davidson et al. (2017) studying the grazing intensity on salt marshes showed a negative effect on arthropod richness (−15%). Furthermore, a meta-analysis on grassland restorations (including grazing exclusion as a passive method) in the Tibetan plateau, where overgrazing is a serious issue, found a positive effect on arthropod richness with 50% increase Ren et al. (2016). Future meta-analyses on grazing should focus on tipping points in grazing intensity and consider the contrast between grazed vs. control areas.

In silvo-arable systems, where crops are grown among trees, Mupepele et al. (2021) were able to show strong positive (48%), but highly variable effects on arthropod richness, where researchers compared this agroecosystem to temporary crops without trees. Thus the high variability made it hard to draw strong conclusions about these measures. Nevertheless, including trees and shrubs in the cropping systems might provide food resources, shelters, overwintering sites and, in general, habitats for many arthropods, as also suggested by Teja for small habitat fragments (Tscharntke et al. 2002). Finally, Winter et al. (2018) showed several ecosystem service benefits of vineyard inter-row vegetation management, which also supports biodiversity, including arthropod richness, by over 50% increase compared to conventionally managed (tilled, mulched, herbicide-controlled) vineyards. Furthermore, they found no trade-off between grape yield and quality vs. biodiversity or other ecosystem services highlighting the importance of establishing locally adapted diverse vegetation cover in vineyard inter-rows. This latter, specific meta-analysis is an exceptional example, which could provide a reasonably clear management and policy suggestion.

2.3.4 Knowledge gaps

Despite the remarkable progress in our understanding of measures promoting farmland biodiversity, in no small part due to the work of Teja and his colleagues, knowledge gaps remain. Much of our knowledge stems from the temperate agricultural landscapes of Europe and the US, including the meta-analyses considered in this book chapter (tremendous geographic bias). By contrast, we have little knowledge on the state of farmland biodiversity and ecosystem services in most tropical regions, where many studies still focus on conservation of natural habitats, especially forests (Gibson et al. 2011; Lewis et al. 2015; Barlow et al. 2018). This is despite the significant role of farmland biodiversity and associated ecosystem services (e.g., pollination, biological pest control) for tropical agriculture, and in particular smallholders, as emphasised by many studies of Teja's group (e.g. Klein et al. 2003; Hoehn et al. 2008; Maas et al. 2013; Li et al. 2022). In addition, recent research shows that agricultural land-uses in the tropics are much more biodiverse than previously assumed (e.g. Wurz et al. 2022). However, influential ecological theories developed by Teja and colleagues, such as the intermediate landscape complexity and the dominance of beta diversity hypotheses (Tscharntke et al. 2012), remain largely to be tested in tropical human-modified landscapes.

2.3.5 Future meta-analysis directions

The methodology of both systematic reviews and meta-analyses develops quickly (O'Dea et al. 2021). For instance, machine learning has been speeding up the screening process of systematic reviews (Farrell et al. 2022). Although, most (agro)ecological meta-analyses use univariate models, i.e. a single moderator, more and more complex models also testing interactions (e.g. Marja et al. 2019) are possible with the ever increasing number of primary studies and developing statistics. For example, second-order meta-analyses have recently appeared also in agroecology (Tamburini et al. 2020; Beillouin et al. 2021), but these might be biased by including partly overlapping primary meta-analyses. One criticism of meta-analyses, in general, might be that given their often simplistic design, they are less helpful in explaining mechanisms. Luckily, with more and more data from similarly designed studies, this can be achieved by path analyses, namely applying meta-analytic structural equation modelling (as summarized by Wang and Tang 2019). Hence, besides the still increasing number of meta-analyses, we expect more specific ones, which might improve our understanding more how spatial and temporal scale management diversification actions can maintain and support farmland biodiversity and their services to achieve societal and policy changes, ultimately a transformative change. Finally, we expect that the importance of increasing the temporal stability of meta-analyses will increase in the future, as accumulating new evidence (additional effect sizes) can change the magnitude or even the sign of the effects, but in general, increases its robustness (Koricheva and Kulinskaya

2019). A promising solution is the maintenance of living systematic reviews already existing in health science (Elliott et al. 2017).

2.3.6 Recommendations for insect conservation in farmland

The analyses here highlight several emergent trends which may help guide insect conservation in farmland. Diversification practices focussing on increasing heterogeneity (structural, compositional, and temporal) at the local scale effective enhance arthropod diversity under most scenarios. Within-crop diversification practices such as mixed cropping, complex crop rotations, silvopasture and agroforestry improve arthropod resource diversity and continuity (Tamburini et al. 2020; Iverson et al. 2014), as do measures that focus on areas outside of the production fields such as flower strips, set-asides, field margins and hedgerows which show particular promise for boosting arthropods (Batáry et al. 2015). Despite substantial variation among systems and focal organisms, measures that focus on reducing management intensity in the production areas, such as organic farming, IPM, reduced tillage and low-intensity grazing soften the agricultural matrix for arthropods and may be especially effective in combination with diversification measures (Tscharntke et al. 2021). In addition, more hospitable crop fields may also facilitate greater arthropod dispersal across farming landscapes, with essential benefits for arthropod migration and adaption to climate change.

In the regions that were assessed, complexity at the landscape scale was less influential on farmland arthropod diversity than local-scale practices (Marja et al. 2022; Gonthier et al. 2014). Nonetheless, landscape-scale practices such as maintaining natural and semi-natural vegetation patches increase arthropod diversity in the species pool and are especially important for more mobile organisms (Gonthier et al. 2014), also bearing in mind that many species of conservation significance are supported in such areas (Tscharntke et al. 2002).

Our study highlights the variability among specific individual practices. An important focus area is to identify highly effective targeted practices that consistently enhance arthropods within certain agroecosystems, e.g. sensitive inter-row vegetation management in perennial crops such as vineyards (Winter et al. 2018).

2.4 Outlook

The evidence is more robust if the synthesised studies cover more systems (habitats, biogeographic regions, socio-economic environments, etc.). For example, the loss of farmland heterogeneity was suggested as the key factor behind bird population decline (Benton 2003), but this was based on West European experiences. Báldi and Batáry (2011) showed that the contrary might be valid in the semi-natural grasslands in Central Europe. Thus, the biogeographical coverage may modify the outcome, which policy makers may use. We recommend to be more comprehensive in research syntheses to reach higher relevance for policy, for example, with the more effective inclusion of non-English sources (Amano et al. 2023; Steigerwald et al. 2022). Another way is — what we applied in this study and demonstrated its usefulness – when results of several meta-analyses were synthesised, thus getting a more comprehensive and robust result than previous meta-analytical studies. Finally, we emphasize the temporal aspects of accumulating research evidence, which might change meta-analysis results (Koricheva and Kulinskaya 2019), with living systematic reviews providing a potential solution (Elliott et al. 2017).

However, all these meta-analyses are scientific publications, thus, not in the policy arena. Considering the robust nature of the evidence that a meta-analysis can hold, it is crucial that this evidence is guided through the science-policy interface for utilisation in policy developments. As farmland arthropods provide essential ecosystem services, such as pollination, pest control and soil fertility, this evidence could directly impact food security and sustainability of farming systems beyond the conservation of farmland biodiversity. Thus, the evidence may also contribute to the relevant European and global policies. For example, the EU's ambitious goals in the Biodiversity and Farm to Fork strategies are impossible to achieve without the application of knowledge on the effects of landscape and local scale factors on the functioning of arthropod groups. Acknowledging and including this in the Common Agricultural Policy may make the desired change to support transformative change in the European food system (European Commission: Directorate-General for Research and Innovation 2020). Therefore, a more effective interface to facilitate the flow of evidence from science to policy is badly needed to provide increased robust knowledge immediately to the hand of policymakers (Bertuol-Garcia et al. 2018).

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Chapter 3

Ant assemblages in human-modified landscape in southwestern Brazilian Amazon

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Abstract The diversity patterns and ecological functions of ant assemblages change systematically in response to both anthropogenic impacts and the regeneration of habitats following such impacts at several spatial scales (e.g., 1 m^2 to 50 km^2). Here, we present the main results of biodiversity and ecosystem function studies developed by the Ant Ecology group at the Federal University of Acre in southwestern Brazilian Amazon over the last 10 years. We assessed the response of ant diversity to forest cover at a landscape scale using two approaches: i) within circular areas, by analysing gamma, alpha and beta diversity metrics (composition variation within the landscapes) and ii) between circular areas, by analysing beta diversity among them and partitioning it in replacement and nestedness components. Furthermore, we assessed the response of species richness of habitat ant guilds (forest specialists, generalists, and open-habitat specialists) to this forest cover gradient. Additionally, we evaluated the ecological function of ants in contrasting environments (forest and pasture) regarding seed removal. Landscapes with higher forest cover had higher gamma and beta diversity. The larger the difference in the forest cover between landscapes, the higher the beta diversity, a trend that was mainly driven by species replacement. Finally, landscapes with low forest cover had higher species richness of open-habitat and generalist ants, and landscapes with higher forest cover had more forest specialist ant species. We also found that, although the percentage of seed removal was higher in pasture, these species were low quality seed dispersers. Therefore, we recommend that future studies about human-modified landscapes consider investigating the maximum forest loss that assures the dominance of forest specialist ant species and high-quality ecosystem functions.

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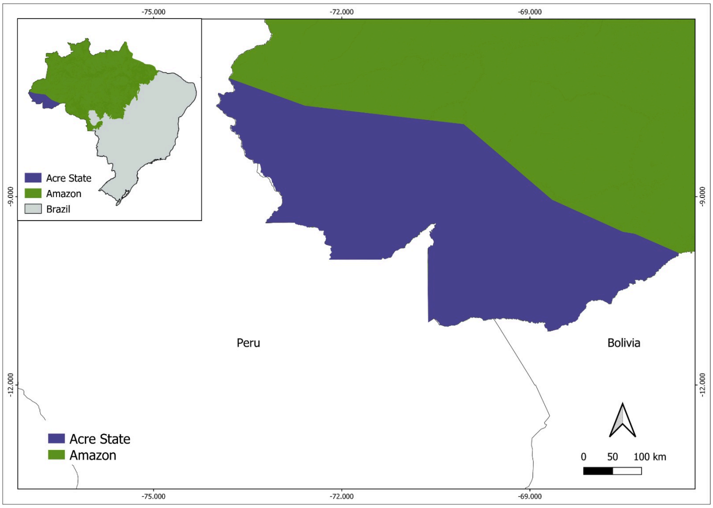

Fig. 3.1: Acre state in southwestern Brazilian Amazon.

3.1 Introduction

The southwestern Brazilian Amazon comprises southern Amazonas state, Acre state and part of Rondônia state. In the eastern portion of this region, along the Acre River basin there is the trinational border among Brazil, Peru and Bolivia (Fig. 3.1).

The climate along the Acre River basin is equatorial, hot and humid. The average annual precipitation is 1,900 mm and mean altitude is 290 m (Acre 2012). The most common vegetation in the region is open ombrophilous forest (Perz et al. 2015). Additionally, the natural ecosystems also share the same impacts, which the major is forest-pasture shifting.

Additionally, the natural ecosystems also similar human pressures, especially forest-pasture transitions. Consequently, there are high levels of deforestation and fragmentation (Mendoza et al. 2015), affecting species loss and hampering ecosystem functions (Fontenele and Schmidt 2021; Silva da Costa and Schmidt 2022). However, as it is not possible to determine the response of all biodiversity to alterations caused by human activities, organisms that have demonstrated clear and predictable responses to anthropogenic impacts have been used as indicators.

One of these groups are ants, which play key ecological roles in terrestrial ecosystems (Lach et al. 2010; Del Toro et al. 2012), such as moving and redistributing more than 50% of the resources (e.g., plant and animal derived organic material) in tropical forests (Griffiths et al. 2018). In addition, the diversity patterns of ant assemblages and ecological functions change systematically in response to both anthropogenic impacts and habitat regeneration (Andersen and Majer 2004; Philpott et al. 2010) at several spatial scales (e.g. 1 m^2 to 50 km^2) (Paolucci et al. 2012; Solar et al. 2016).

Specifically, gamma and beta diversity of ant assemblages are related to changes in vegetation types in natural landscapes (Spiesman and Cumming 2008; Campos et al. 2011;

Marques et al. 2017; Schmidt et al. 2017). In general, ant assemblages in human-modified landscapes possess low gamma diversity (Solar et al. 2015) and are primarily composed of generalist species (Sobrinho and Schoereder 2007). These generalist species are tolerant to the conditions of open habitat and are widely distributed within these landscapes (Paolucci et al. 2017), resulting in no changes in alpha diversity (Escobar-Ramirez et al. 2020) and low beta diversity (Solar et al. 2015; Paolucci et al. 2017). Additionally, forest and generalist ant species also differ in their ecological functions, such as the potential role for seed dispersion (Fontenele and Schmidt 2021), which affects plant species populations.

Here, we present the main results of biodiversity and ecosystem function studies developed by the Ant Ecology group at the Federal University of Acre in the last 10 years in the southwestern Brazilian Amazon. The studies are about the response of ant diversity to a forest cover gradient at the landscape level. We observed the ant diversity patterns with two approaches: i) within each landscape, which the metrics considered were gamma, alpha and beta diversity (composition variation within the landscapes) and ii) among landscapes, where the beta diversity was assessed among the landscapes and partitioned in replacement and nestedness components. Furthermore, we searched the response of species richness of habitat ant guilds (forest specialists, generalists, and open-habitat specialists) to this forest cover gradient. Additionally, we verified the ecological function of ants in contrasting environments (forest and pasture) regarding seed removing. The full description of sampling design and statistical analyses output can be found in the Fontenele and Schmidt (2021), Silva da Costa and Schmidt (2022), Santos Martins et al. (2022), and Sales and Schmidt (2023).

3.2 Ant diversity along a forest-cover gradient

The forest cover gradient analyzed is in the Chico Mendes Extractive Reserve (RESEX Chico Mendes), a sustainable use conservation unit located in the southeast of the state of Acre, Brazil. The reserve encompasses approximately 970,550 ha and is covered by open forest (73%) and dense forest (27%). Since its establishment, RESEX Chico Mendes has undergone widespread changes in land use, which have resulted in deforestation, habitat fragmentation, and degradation (Mascarenhas et al. 2018). The economy of RESEX Chico Mendes is based on the harvesting of Brazil nuts (*Bertholletia excelsa*) and latex (*Hevea brasiliensis*), and on low-intensity timber management (Acre 2006). Between 2000–2018, 14.4% of the reserve's forest cover has been lost, mainly driven by pasture establishment (Milien et al. 2021). Livestock has become an increasingly common economic activity to supplement family income, and pastures now cover a significant part of the protected area (Negret 2010; Mascarenhas et al. 2018). Finally, although reserve administration has made efforts to control deforestation within RESEX Chico Mendes, many pasture areas have been illegally established (Mascarenhas et al. 2018).

We established 12 circular areas at 5-km intervals along the access road to the core area of RESEX Chico Mendes in Assis Brasil. This access road extends from the urban region of Assis Brasil to the right bank of the Iaco River, for a total of 75 km. Each circular areas had a radius (r) of 500 m, which resulted in an area of 785,398.16 m^2. According to Spiesman and Cumming (2008), landscape variables measured at circular areas with radius of 500 m

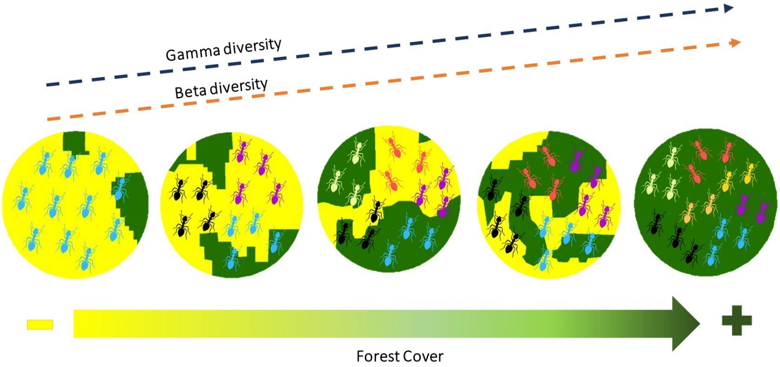

Fig. 3.2: Ant diversity along forest cover gradient in RESEX Chico Mendes, Assis Brasil, Acre, Southwestern Brazilian Amazon. Forest cover is a key driver of spatial heterogeneity, which in turn positively affects gamma and beta diversity.

explain the greatest amount of variation in ant assemblage data. This spatial scale has been used in landscape-scale studies of ant assemblages (Ahuatzin et al. 2019) and is a geographic space in which ant species coexistence is determined by their dispersal capacity among different habitat types (Schmidt et al. 2017). The forest cover in the 12 circular areas ranged between 13% to 100% (Fig. 3.2).

We also established four radial transects, oriented by the four cardinal points, within each circular area. We distributed four sampling points at 100 m intervals along each transect, with the first sampling point located 100 m from the centre of each the circular area. Thus, each sampling area had a total of 16 sampling points. In each sampling point, the ants were sampled by pitfall trap at ground level. The pitfall traps remained in the field for 48 h (Bestelmeyer et al. 2000). Ants collected in traps were stored in ethanol (96%) for processing, mounting, and identification.

Within the circular areas, we found a positive relationship between forest cover percentage and gamma diversity; however, increasing forest cover did have a statistically significant relationship with alpha diversity. Increasing forest cover also led to increased beta diversity inside the circular areas (Fig.3.2; for statistical analysis see Silva da Costa and Schmidt 2022). Among the circular areas, increasing difference in forest cover correlated with increases on beta diversity, which the main component was species replacement. The number of forest habitat ant species ranged from three to 24 species, while the number of generalist species ranged from 13 to 27, and the richness of open-habitat species from zero to six in each circular area. With increasing forest cover, the number of forest habitat species increased while the number of open habitat species decreased. Richness of generalist species did not vary as a function of forest cover (Fig.3.3; for statistical analysis see Santos Martins et al. 2022).

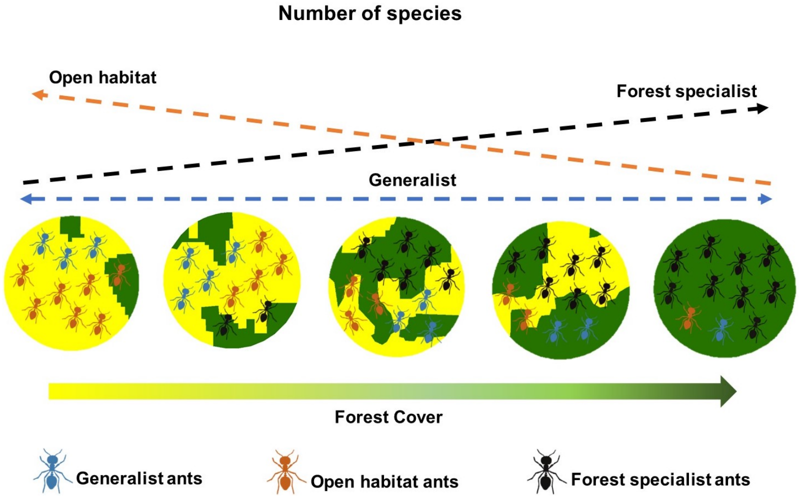

Fig. 3.3: Response of habitat ant guilds to forest cover gradient in RESEX Chico Mendes, Assis Brasil, Acre, Southwestern Brazilian Amazon.

3.3 Ecological function of ants in contrasting environments: forest and pasture

We verified the ecosystem function of ants in contrasting environments (forest and pasture) in the Rio Branco region in the state of Acre in the southwestern Brazilian Amazon (Fig. 3.1). The native vegetation of the region is characterized by several different forest types, including dense ombrophilous forest and open ombrophilous forest with bamboo and palm trees (Acre 2012).

We used seed removal as surrogate for ant ecosystem function in both environments. We conducted experiments on ant seed removal in 10 forest habitats and in adjacent pastures, which is the primary type of habitat matrix in the region. Due to the lack of a sufficient amount of naturally-occurring myrmecochorous seeds (i.e. plants that have seeds with an elaiosome a lipid-rich appendix) in the study region and difficulties with storing seeds during the implementation of the experiments, we used artificial seeds that exhibit similar characteristics to natural seeds for the seed-removal experiments (Bieber et al. 2014). For details on artificial seeds elaboration, please see (Fontenele and Schmidt 2021).

We established a 225-m transect with 10 sampling points spaced at 25 m intervals within each forest fragment and within pastures. We placed 40 artificial seeds at each sampling point — 20 in the morning (9:00 – 12:00 am) and 20 in the afternoon (14:00 – 17:00). We recorded seed removals for 20 minutes at each sampling point (three hours per period) and actively collected ants that removed the seeds from their original location using entomological forceps. We considered seed removal when seeds were moved for distances equal to or greater than 30 cm from their original location (Christianini and Oliveira 2010).

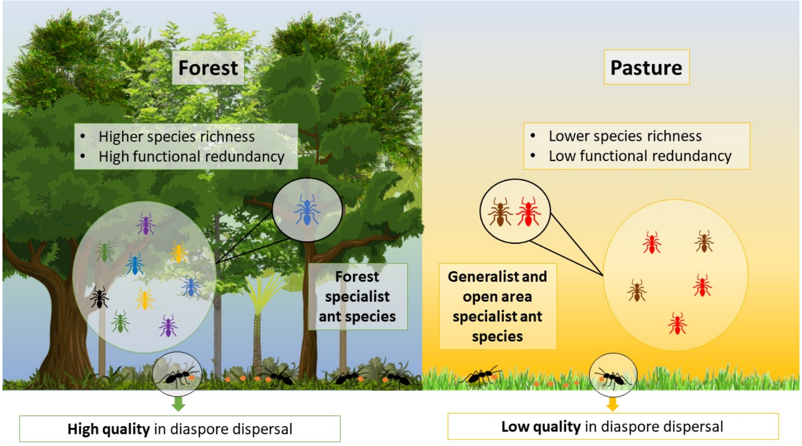

Fig. 3.4: Assemblages of seed-removing ants in contrasting environments (forest and pasture) in Rio Branco region, Acre, Southwestern Brazilian Amazon.

We observed more ant species removing seeds in forest (mean = 7.5 species) than in pasture (mean = 3.5 species) (Fig. 3.4). However, a higher percentage of seeds were removed by ants in the pasture than in forest (Fig. 3.4; see Fontenele and Schmidt 2021 for more detail). The ant species that removed seeds in the two environments were distinct. In pasture, the ant species that dispersed seeds were considered low-quality seed dispersers. Meanwhile, in the forest, the ant species that dispersed seeds were high-quality seed dispersers. These two seed dispersion ant guilds differed in body size, recruitment, elaiosome consumption, and seed removing distance (Leal et al. 2014a; Leal et al. 2014b). Low-quality seed dispersers had smaller body sizes (< 5 mm), consumed the elaiosome at the site (a behaviour known as cheating), and removed seeds for short distances via mass recruitment. High-quality seed dispersers had larger body sizes (> 5 mm), foraged solitarily, and removed seeds for long distances (i.e. greater than 5 m). Therefore, these ant guilds distinctly affected plant populations.

3.4 Main conclusion and directions

The differing observed responses of forest and open-habitat ant species richness to forest cover could be understood by winner-loser species replacement (Fig. 3.4). Human-induced changes (shifting of natural into fragmented landscapes) increase abundance and species richness of disturbance-tolerant species (winners: open-habitat ants in our case), who replace disturbance-sensitive species (losers: forest specialist ants) (McKinney and Lockwood 1999; Filgueiras et al. 2021). Additionally, this species replacement implies a nearly complete functional reorganization of communities with implications for ecosystem processes (Filgueiras et al. 2021). Moreover, we found out that generalist and open-habitat specialist ants are low quality seed dispersers due to granivorous seed predators and the movement of seeds for short distances (Fontenele and Schmidt 2021). Furthermore, the absence of a relationship between species richness of generalist ants and forest cover suggests the plasticity of these species, which provides them with high survival probabilities in landscapes with different forest cover.

While the state of Acre still has 80% of the original vegetation conserved (Acre 2012), it is in a process shifting forest into human-induced land uses (e.g., pastures) (MapBiomas 2020). Above, we presented the negative effects of this process on ant diversity and ecosystem functions. According to Arroyo-Rodriguez et al. (2020) it is necessary to manage human-modified landscapes such that the matrix has similar land cover to natural ecosystems to assure biodiversity and ecosystems functions.

We understand that the studies carried out by our research group until now have approached two extremes of a land use gradient: forest, the natural habitat in the region, as well as pasture, the major human-induced land use in the region, which present different conditions and resources than forest. However, between these extremes there are several other land use types, such as slash-burn agriculture, conventional crops, agroforestry systems, and forestry. Each of these land use types distinctly affect the ant assemblages. Thus, we expect that land uses that look like forest will share similar ant assemblages (Queiroz et al. 2020). In our future studies, we plan to analyze more land use types along this gradient to have more predictability about the response of ant assemblages and to determine the maximum level of forest loss in human-modified landscape that still preserves the dominance of forest specialist ants and high-quality seed dispersers.

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Chapter 4

Contribution of tropical forest fragments to ecosystem functions in adjacent smallholder maize farmland in Sulawesi, Indonesia

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Abstract Most farmers in tropical region are smallholders growing seasonal crops that are often prone to failure because of poor soil fertility or pest attack. Smallholders may benefit from ecosystem services provided by nearby natural and seminatural habitats which export ecosystem services such as decomposition and predator-mediated biological pest control. To evaluate the potential for spill-over of decomposition and predation services from forests to adjacent maize farmland in Sulawesi, Indonesia, we deployed cellulose baits (toilet rolls) and model plasticine caterpillars to assess decomposition and predation along transects from forest into maize farmland. Soil bulk density and the abundance of a key decomposer taxon, millipedes, were also recorded at the same sampling points. Rates of decomposition did not change significantly with distance into the crop from the forest edge. However, predation was substantially higher near the forest edge, indicating that predation of insect herbivores may spill over from the forest to adjacent maize farmland. Pest control services might provide an incentive for forest conservation efforts in human-modified tropical environments. However, whether predator and pest predation service spill-over is sufficient to limit outbreaks of agricultural pests requires further investigation.

4.1 Introduction

Agricultural growth and intensification constitute a significant risk to tropical forests (Carrasco et al. 2017; Gibbs et al. 2010), with about 6 million hectares of tropical forests currently converted for agricultural purposes (Mayaux et al. 2005). At the same time, reduced proximity of agricultural land to forests has the potential to impair important ecosystem functions and services (Tscharntke et al. 2005), including pollination (e.g. Klein et al. 2003), maintenance of soil fertility (e.g. Holle and Lewis 2022), and control of insect

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pests (e.g. Tscharntke et al. 2005). Integrating management for ecosystem functions into land-use planning in human-modified landscapes, including areas where agroecosystems and tropical forests co-occur, is important for long-term sustainability and improved social welfare (Harvey et al. 2008; Gardner et al. 2009; Power 2010).

Diversifying crops, for example through polyculture or agroforestry, is widely suggested as a potential solution to maintain ecosystem function integrity while producing adequate food (Scherr and McNeely 2008). However, such approaches are less suitable to seasonal crops such as maize, rice, soy, and wheat, which supply two-thirds of global food calories (Kim et al. 2019). Seasonal crops are more prone to crop failure than perennial crops; prominent causes of crop failure include soil degradation, pests and weeds (Crews et al. 2018), with crop monocultures especially susceptible (Ewel et al. 1991).

Soil fertility in agroecosystems is maintained by efficient nutrient cycling that relies on decomposition processes mediated by microbes as well as soil and litter invertebrates such as earthworms, millipedes and termites (Gray and Lewis 2014; Power 2010; Zhang et al. 2007; Both et al. 2017; Krishna and Mohan 2017). Similarly, while pests such as insect herbivores reduce yields in many tropical crops (Oliveira et al. 2014), their impacts can often be lessened naturally through top-down control from natural enemies such as predators, parasitoids, and pathogens, which provide an alternative to high-input and often environmentally harmful pesticides (Zhang and Adams 2011; Power 2010; Tscharntke et al. 2005). Arthropods and mammals dominate predation of insect herbivores in most tropical farming systems (Denan et al. 2020).

Here, we investigate whether ecosystem functions mediated by invertebrates are transferred from forest fragments to nearby agricultural land. We focus on ecosystem functions that can be beneficial for agricultural production: decomposition of plant material, and predation of herbivorous insects. Our focal landscape is a mosaic of patches of tropical forest and smallholder maize farmland in the province of Gorontalo, Sulawesi, Indonesia. Maize is one of the most widely planted and rapidly-expanding tropical crops (Phalan et al. 2013), and our focus on smallholder production is motivated by the observation that, although most farms are small and family-operated (Lowder et al. 2016), most research has concentrated on large-scale industrial agriculture (Reiss-Woolever et al. 2021). Maintaining the integrity of ecosystem functions in tropical smallholder monoculture is crucial because the initial step in forest conversion is often the conversion of intact forests to smallholder agriculture by rural farmers (López-Carr 2021).

Focusing on measures of decomposition and predation of caterpillars along transects at the transition from forest to farmland, we predicted that (i) decomposition and predation of caterpillars would decline with distance from forest, and that (ii) predation of caterpillars would have greater spillover than decomposition, because of the higher mobility of the organisms mediating this ecosystem function. discuss our contribution to this topic, specifically focusing on the combined impact of local and landscape diversification on yield.

4.2 Methods

4.2.1 Study site

Data were collected in Panua Nature Reserve (PNR) in the Pohuwato Regency (0°31' 59" N, 121°49' 30" E), Gorontalo Province, Sulawesi, Indonesia. This protected area is under threat from forest conversion to agriculture and mining, and illegal logging by local people living adjacent to the nature reserve. Data were gathered during the rainy season (January-March 2020) in forest and adjacent maize farmland near the edge of the PNR. Forest sites had experienced low-intensity selective logging of large and emergent trees, but retained closed-canopy structure. Maize farmland sites are managed by smallholder farmers within PNR and just outside its boundary. Dara collection started three weeks after planting, when maize stalks started to create locally-shaded microclimates. Fields used for maize in our study landscape are left fallow outside of the planting season (mostly the wet season) and can develop into either shrubland, bare ground, or grassland.

Eight line transects were established running from the forest edge into the maize farmland, with sampling sites within the forest (−10 m, −5 m) at the forest edge (0 m), and in the corn farmland (5 m, 10 m, 15 m, and 30 m). At each sampling site, decomposition rate, millipede abundance, predation of model herbivores, and soil bulk density were recorded. Data on decomposition (only) were additionally collected at 20 m.

4.2.2 Quantifying decomposition and related parameters

Decomposition occurs both on fallen leaves and on the woody portion of plants. At our study site, decomposition of cellulose is mediated by very high abundance of millipedes (*Salpidobolus* sp.) (Holle 2023). As a standardised cellulose substrate, single ply, unscented coreless toilet rolls were used to evaluate millipede consumption activity between February and March 2020 (Leitner et al. 2018). Three 5 g toilet rolls were placed at each site on each of the transects for total of 147 toilet rolls (7 transect lines × 7 distance variations × 3 toilet rolls). After two weeks, the remaining toilet rolls were collected, cleaned, sun dried, and weighed to determine the cellulose consumption rate.

To accompany decomposition measurements, we also recorded decomposer abundance and soil bulk density. Given that *Salpidobolus* sp. are the major invertebrate decomposers at this research site, we concentrated on estimating millipede abundance. Millipede abundance was evaluated by counting millipedes using 1 m × 1 m quadrats, randomly located more than 2 m apart at each sampling site (within 15 m of where decomposition was measured, and with similar vegetation and topographical conditions). Counts were taken on cloudy days following rain events the previous day. Since measured abundances varied greatly depending on environmental condition, counts were performed multiple times, and the maximum recorded abundance was used for analysis. Since long-term organic matter removal affects soil bulk density (Sayer 2006), we assessed soil bulk density by collecting 6 cm depth × 5cm diameter soil cores at each sampling site. Soil samples were dried completely in full sun before weighing, and soil density was calculated by dividing soil volume by soil dry mass.

4.2.3 Predation of caterpillars in relation to distance from forest

Model caterpillars made from plasticine are commonly used to evaluate predation of insect herbivores (Howe et al. 2009; Nurdiansyah et al. 2016; Denan et al. 2020), which reflects potential pest control services (Barbaro et al. 2017). Plasticine caterpillars were used to estimate predation rates from predators such as arthropods, birds, reptiles, and mammals. We rolled non-toxic plasticine modelling clay (Newplast light green) into a 3 mm diameter cylinder on a flat surface, cut it into 15 mm long sections, and shaped each into a curved caterpillar shape to mimic an 'inchworm' (family Geometridae) larva. Ten plasticine caterpillars were attached using UHU®adhesive to the upper surface of ten plant individuals (either maize plants, seedlings or small saplings), 1.5 m above the ground, and left for two days. Seven linear transects were established and three sets of ten caterpillars were deployed at each of seven positions running from the forest into the maize farmland: −10 m (within the forest), −5 m, 0 m (forest edge), 5 m, 10 m, 15 m, and 30 m (10 caterpillars × 3 replicates × 7 distances × 7 transects). There were 1440 plasticine caterpillars in total because none were placed at the 30 m distance on one of the transects.

Plasticine caterpillars were left in position for two days and then recovered to score for predator damage. Where caterpillars were missing the ground was searched to check for caterpillars that had fallen from the vegetation. Plasticine caterpillars re-collected from the vegetation and the ground are included in the analyses. Caterpillars were scored for the presence and type of bite marks. Where there was doubt about the identity of the predator, the bite marks were photographed for later identification using bite-mark identification guidelines (Low et al. 2014).

4.2.4 Data analysis

All statistical analyses and graph visualization were performed using R (R Core Team 2020). The effects of distances from the forest edge on the response variables were investigated using mixed effects models (using the `lme` function in the **lme4** package), with distance as a continuous explanatory variable and transect as a random effect. Response variables evaluated included cellulose consumption, predation of caterpillars, millipede abundance, and soil bulk density. As a two-column response variable for predation of caterpillars, we used the numbers of attacked and non-attacked caterpillars and specified a binomial error structure. Analysis was carried out separately for forest and maize farmland data points, with forest edge (0 m) data included with the forest data.

4.3 Results

Decomposition, decomposition-related parameters, and predation of caterpillars showed varied trends in relation to distance from the forest edge (Fig. 4.1). There was no significant trend in cellulose decomposition with distance from the forest edge within the maize farmland ($F_{1,51} = 0.5002$, $p = 0.4826$). However, in the subset of forest data points there was a significant decrease in decomposition with distance from the forest edge into the forest interior ($F_{1,48} = 9.042$, $p = 0.0042$). Millipedes were recorded only in the forest. Within the subset of forest data points, we found that millipedes abundance declined significantly towards the forest edge ($F_{1,39} = 19.203$, $p < 0.0001$). There was a marginally non-significant trend for forest soil bulk density to be higher closer to the forest edge ($F_{1,51} = 3.97$, $p = 0.051$), but no significant trend with distance within maize farmland ($F_{1,70} = 1.30$, $p = 0.258$).

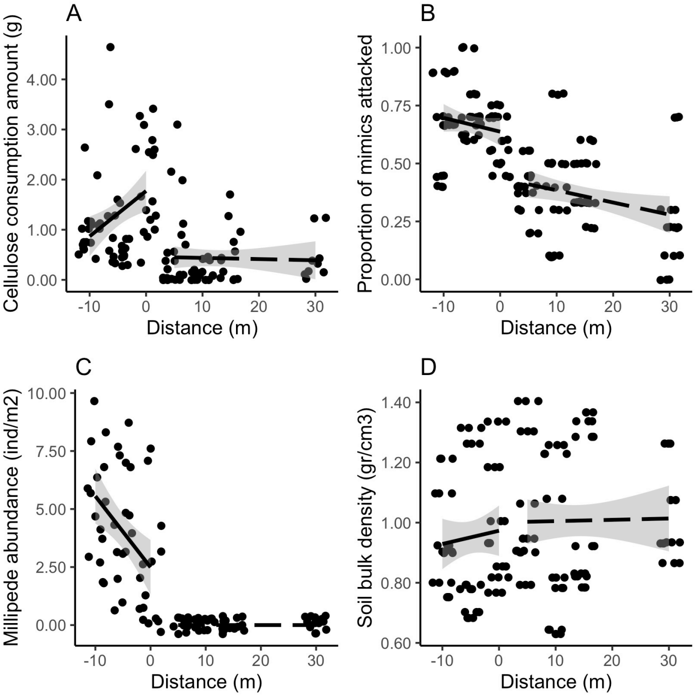

Fig. 4.1: Ecosystem functions and associated parameters in relation to distance from the forest edge (n=7 transects). A: cellulose decomposition; B: millipede abundance; C: soil bulk density; and D: predation of caterpillars. Data points are jittered to avoid points overlapping. Grey shading represents the 95% confidence interval for predictions from a linear model. Solid and dashed lines represent separate linear regressions for the forest data and maize farmland data, respectively.

We recovered 1377 of 1440 plasticine caterpillars (95.62%), of which 681 (49.5%) were predated. Predation of caterpillars declined significantly with distance into the maize farmland from the forest edge ($F_{1,73} = 5.6004$, $p = 0.0206$). The proportion of attacked caterpillars at −10 m, −5 m, 0 m, 5 m, 10 m, 15 m, and 30 m were 66.7%, 73.1%, 60.6%, 37.9%, 37.9%, 40.90%, and 25.9% respectively. In a separate analysis, attack rates were not related to distance from forest edge in the subset of forest data points (−10, −5, and 0 m from the forest edge; $F_{1,55} = 2.4$, $p = 0.127$). All predators that attacked plasticine caterpillars were invertebrates, primarily ants.

4.4 Discussion

Understanding the contribution of forest fragments to smallholder agriculture is critical for both forest conservation and the sustainability of rural livelihoods (López-Carr 2021). The ecosystem functions and associated parameters investigated exhibited different trends with distance from forest into farmland. In general, decomposition and its associated characteristics did not appear to rely on forest fragments, as evidenced by the lack of a trend for reduced decomposition at farmland sites further from the forest edge. However, predation of caterpillars was forest-dependent, with plasticine caterpillars being more likely to be predated close to forest fragments.

4.4.1 No evidence of spillover of decomposition services from forest fragments

Tropical forest fragments can spill-over their biodiversity to less diverse agricultural land nearby (Lucey and Hill 2012). This leads to the expectation that ecosystem functions will also be transferred, as the concept of biodiversity-ecosystem functioning (BEF) strongly links these two components (Hong et al. 2022). Although forest conversion to maize farmland is likely to alter litter decomposition (Attignon et al. 2004; Holle and Lewis 2022; Kagezi et al. 2016), cellulose decomposition did not change significantly with distance either in the forest or in the maize farmland (Fig. 4.1), suggesting that decomposition services measured in this way are not exported from forest to nearby farmland. Previous research in East African coastal forest landscapes found a similar trend, with no significant positive spillover effects of ecological functions from forest into agricultural land (Habel and Ulrich 2020).

Decomposition requires decomposers (Hättenschwiler et al. 2005), a substrate (Chomel et al. 2015), and a suitable environment (Hector et al. 2000; Oliveira et al. 2019). The absence of millipedes in the maize farmland could explain the absence of any trend in decomposition or soil bulk density, as millipedes are a key component of the decomposer community in our study landscape (Holle and Lewis 2022). It seems likely that forest millipedes are not moving from forest to forage in the farmland, and that the farmland itself is not supporting millipede populations. Millipedes can move from 19 to 123 m each day, depending on the species (Semenyuk and Tiunov 2019). These estimates reflect random foraging movements rather than targeted, directional foraging because millipedes lack effective receptors for detecting food at distance (Semenyuk and Tiunov 2019). Compared to the forest, the higher temperatures and lower humidity of the more open maize plantations may be inhospitable to millipedes or mean that they shelter in the soil during the day, leading to underestimates of their density. Alternative sampling methods such as hay-bait traps (Tuf et al. 2015) might be needed to provide more realistic density estimates. Furthermore, the supply of cellulose or woody detritus in the maize farming site was limited, resulting in a lack of decomposition substrate for decomposers. This will be exacerbated if farmers remove or burn organic matter within their fields, limiting resources and killing the decomposers associated with them.

To measure rates of decomposition of organic matter we used toilet rolls as cellulose baits. This method has been used widely to analyse termite decomposition activity (e.g.

Leitner et al. 2018), and we have found that it is also applicable to millipede-mediated decomposition (Holle 2023). Comparing rates of decomposition across a land-use intensity gradient in the same landscape, we found that using toilet roll baits and leaf litter to evaluate decomposition in different habitats yields similar results, with decomposition being higher in forest environments than in modified habitat types (Holle and Lewis 2022).

4.4.2 Spillover of pest control services from forest fragments

We found that tropical forest fragments contributed to predation of model pest insects in maize farmland. In contrast, two similar studies (Gray et al. 2016; Ferrante et al. 2017), found no pest control service spill-over from forest fragments into crops (oil palm plantations and maize farmland, respectively). In the studies by both Gray et al. (2016) and Ferrante et al. (2017), the forest sites comprised relatively small forest strips or fragments, whereas the current study was conducted at the edge of continuous tropical forest. It is possible that forest patch size influences the extent of spill-over of predation services. Reduced predation of caterpillars associated with smaller forest fragment is consistent with the trophic concept of island biogeography, which predicts that predators (and parasites) will decline the most in smaller habitat patches (Anderson et al. 2019), and supports the need to keep tropical forest unfragmented to sustain ecosystem functions. However, further research is needed to investigate whether predator and pest predation service spill-over is sufficient to limit outbreaks of agricultural pests.

4.5 Conclusions

Our study shows that ecosystem functions can spill-over from forest to nearby agricultural land, but that patterns differ for different ecosystem functions. These differences may be linked in part to the habitat fidelity of the species mediating different functions. Species associated with natural habitat (stenotopic species), those associated with farmland (cultural species), and those showing no strong association for either habitat (ubiquitous species) are transferred from natural habitat to the agricultural land through different pathways (van Schalkwyk et al. 2020). It is possible that decomposer communities, which rely on soil quality that differs markedly between habitat types (Delelegn et al. 2017) comprise stenotopic species that are influenced by marked difference in environmental conditions between forest and farmland (van Schalkwyk et al. 2020). In contrast, caterpillar predators are likely to be more ubiquitous and more mobile, allowing them to move more freely across habitat boundaries.

Of course, pest control and soil fertility maintenance are not the only ecosystem services relevant to forest regeneration and crop production; further studies on a broader range of ecosystem functions could contribute to a better understanding of how to manage human-modified landscapes more sustainably.

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Chapter 5

Landscape effects on plant-arthropod interactions in agroecosystems: building on Teja Tscharntke's legacy

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Abstract Teja Tscharntke and his Agroecology group have fundamentally changed our understanding of the impact that landscape composition and configuration have on arthropod conservation, plant-insect interactions, and ecosystem services. Here we summarize our work from the last ten years building on key theories and research findings from Teja's group to test the consequences of landscape mediated changes in arthropod populations on crop production, the context dependency of management practices, and the evolution of wild plants in agricultural landscapes. We focus on three main areas of research: 1) the relationship between landscape simplification and the diversity of arthropods that provide important ecosystem services and disservices, 2) how landscape simplification affects arthropod and plant functional traits with potential consequences for ecosystem services and wild plant evolution, and 3) expanding on the intermediate landscape hypothesis to include a broader range of local management practices and crop production responses. While Teja's theories and research results form the foundations of each section, we review our data that test these theories in different systems, generating new research venues and a more nuanced understanding of how landscape-scale processes affect ecosystem services, local management practices, and ultimately plant adaptation and crop production.

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5.1 Introduction

Over the past few decades, global land use has undergone a significant transformation, leading to more simplified landscapes with fewer natural areas and increased agricultural land. This transformation has resulted in forest and shrubland covering the same percentage of global land area (34%) as cropland and livestock production (34%) (Our World In Data 2021). It is now widely recognized that the landscape composition (the proportion of different land-use types in a landscape area) and configuration (the shape, size, and arrangement of different land-use types) can have far-reaching effects on the community composition of pollinators, herbivores, and natural enemies, with consequences on ecosystem services including yield. However, it was only in 1994 (Kruess and Tscharntke 1994) and 1999 (Thies and Tscharntke 1999) that Teja Tscharntke's group published two groundbreaking papers that revolutionized our understanding of how land-use changes can affect plant-herbivore interactions in agroecosystems. Kruess and Tscharntke (1994)'s study demonstrated how fragmentation reduces the abundance and richness of herbivores and parasitoids of red clover (*Trifolium pratense*) with consequences for parasitism rates. Thies and Tscharntke (1999)'s study showed how landscape composition, measured as the percentage of non-crop area within a 1.5 km radius, can increase parasitism rates and decrease damage to canola caused by the pollen beetle (*Meligethes aeneus*). Shortly after, in 2003, Klein showed the importance of another landscape configuration metric - forest distance - which can affect pollination services to coffee, mediated by an increased diversity of social bees closer to the forest (Klein et al. 2003). These initial papers provide the foundation for our current understanding of how landscape simplification affects insect populations and communities and its consequences for ecosystem function and services.

Teja and his group also influenced our understanding of spillover effects between natural and agricultural areas (Blitzer et al. 2012; Rand et al. 2006). Functional spillover, which refers to the transfer of functions provided by an organism to the habitat into which it moves, has been observed for ecosystem functions such as pollination and herbivory. Evidence of functional spillover between natural and agricultural areas and vice versa have been described for multiple ecosystem functions and services (Blitzer et al. 2012). Inspired by this work demonstrating that landscape simplification alters both insect community composition and distribution in the landscape, we have begun investigating if these changes in the insect community have cascading consequences for wild plant evolution in simple landscapes.

Given the overwhelming evidence that landscape simplification and agricultural intensification are major drivers of biodiversity loss and global change patterns (Wagner et al. 2021), which also negatively impacts yield (Dainese et al. 2019), interest has grown in ecological intensification practices that can replace current agricultural amendments for biodiversity and ecological practices. In 2005, Teja proposed that local conservation practice would interact with landscape simplification, impacting the effectiveness of local diversification strategies to recover biodiversity. The hypothesis suggests that only in landscapes of intermediate complexity will local diversification management improve biodiversity. Although initially proposed to enhance biodiversity, its importance for providing ecosystem services and yield quickly became apparent. Since its inception, this hypothesis has been cited over 2500 times and has significantly contributed to our understanding of the context dependency of local management practices, as we will elaborate on in a section below.

Although it would be impossible to review Teja's more than 450 articles comprehensively, we want to synthesize some of the most significant contributions made by Teja Tscharntke's Agroecology group since its inception in 1993. We aim to showcase how this body of work has inspired our research and influenced our understanding of various topics in landscape ecology. We begin by summarizing Teja's impact on our comprehension of the relationship between landscape simplification and the abundance and diversity of functionally important trophic groups like pollinators, herbivores, and natural enemies. We will then review our work in this field and describe how it has expanded upon Teja's research. Moreover, we explore the effects of landscape simplification on insect intra- and inter-specific functional traits and their impact on ecosystem services. In the second section, we present our current work on how landscape simplification affects functional traits of wild plants mediated by changes in the insect community, which can lead to wild plant adaptation. In the third section of this review, we summarize the contributions of Teja Tscharntke's group to our understanding of the interactive effect of local and landscape-scale factors on biodiversity patterns by reviewing the intermediate landscape complexity hypothesis. We discuss our contribution to this topic, specifically focusing on the combined impact of local and landscape diversification on yield.

5.2 Landscape effects on diversity, functional traits, and ecosystem services

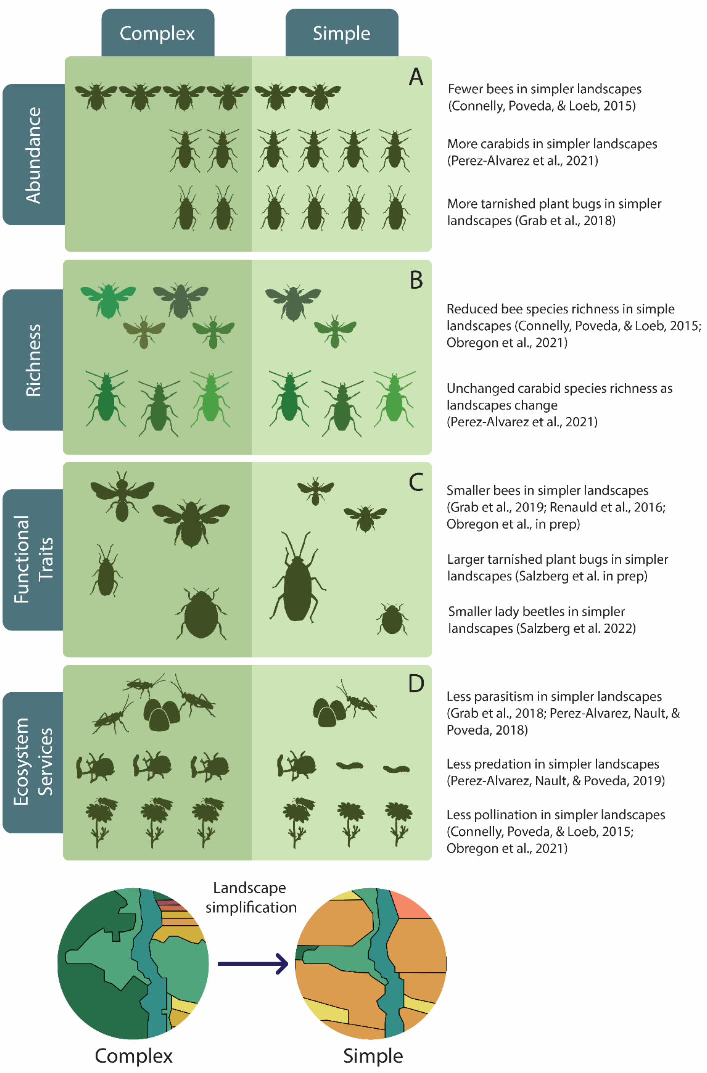
Teja and his group developed a body of ecological theory that set the direction for studying landscape-moderated patterns on biodiversity and its relationship to ecosystem functioning in agricultural systems. In a pioneering review, Tscharntke et al. (2005a) provided an overview of the relationship between biodiversity and ecosystem services. They emphasized the importance of considering large spatial scales in biodiversity conservation and argued that the functional role of biodiversity would only be apparent at such scales. This broader perspective is critical because population dynamics, community composition, and ecological interactions are dependent on processes at spatial scales larger than a single agricultural field.

Since these early efforts, significant empirical work has been conducted to support the notion that complex agricultural landscapes harbour diverse arthropod communities that sustain key ecosystem services such as pollination and biological pest control. For example, our research group has conducted several studies on the impact of landscape simplification on different groups of organisms and their associated ecosystem services. Our findings show that landscape simplification reduces the abundance and richness of bees in both temperate and tropical systems (Connelly et al. 2015; Obregon et al. 2021, Fig. 5.1A, B). In contrast, carabids (generalist predators) and tarnished plant bugs (*Lygus lineolaris*, a generalist herbivore) are more abundant in simple habitats than in complex ones (Perez-Alvarez et al. 2021; Grab et al. 2018b, Fig. 5.1A). These results highlight that landscape simplification can affect different groups of organisms in various ways. Importantly, our research demonstrated that landscape simplification affects more than just the diversity of arthropods, but also the ecosystem services they provide. For instance, we found that parasitism rates of crop pests in strawberry farms located in simple landscapes are lower than on farms with higher semi-natural cover (Grab et al. 2018a, Fig. 5.1D). We observed similar results in cabbage crops where agricultural simplification at the landscape scale reduced lepidopteran parasitism (Perez-Alvarez et al. 2018, Fig. 5.1D). These landscape-mediated changes in natural enemy and pollinator abundance and diversity have significant downstream consequences for crop yield beyond the intermediate ecosystem services of pest control and pollination (Connelly et al. 2015; Perez-Alvarez et al. 2018).

The composition of the landscape has an impact not only on the abundance and diversity of service-providing organisms but also their functional trait composition. A shift in functional trait composition can reveal effects on biodiversity beyond species richness and abundance, which are often overlooked by classical diversity measures. Additionally, analysing functional traits can offer insight into potential consequences for ecosystem services. Tscharntke and his colleagues have made fundamental contributions to understanding the effects of land-use changes on functional composition. For example, the highly influential work of Gámez-Virués et al. (2015) demonstrated that landscape simplification selects against species with specialized feeding habits, shorter activity periods, and smaller body sizes, highlighting the importance of preserving natural habitats to maintain functional diversity. While the importance of land use effects on individual traits and community trait composition was recognized well before Gámez-Virués' study (Kotze and O'Hara 2003; Persson and Smith 2011), the key contribution of this work was to reveal the negative impacts of landscape simplification using a trait-based approach across multiple traits and taxa. In subsequent work, Tscharntke and colleagues demonstrated how the filtering effects of landscape simplification on arthropod communities could also have significant implications for ecosystem service provisioning (Gagic et al. 2015; Galle et al. 2019).

These ideas have played a fundamental role in our group's research focus, motivating us to build upon these ideas and expand our understanding of landscape-driven changes in functional composition in two fundamental ways. First, we expanded our focus beyond community-weighted means and started considering the variability and skewness in trait values. For example, we have shown that landscape simplification affects the body size distribution of carabid communities, leading to concomitant effects on pest control (Perez-Alvarez et al. 2021, Fig. 5.1C). However, contrary to previous research (Fischer et al. 2021; Philpott et al. 2019), our study found that the numerical dominance of large-bodied species did not solely determine the magnitude of pest control. Instead, changes in the relative proportion of different size classes —that is, body size frequency distributions—are also likely to alter the strength of top-down control. Specifically, we found that communities with an even representation of small- and large-bodied species had higher predation rates than communities dominated by either large- or small-bodied species.

Second, our work initially focused on evaluating changes in functional trait composition across species due to species turnover but gradually extended to include within-species variation (i.e., intraspecific diversity). We investigated the impact of landscape simplification on body size variation in bee communities in the northern United States. The results showed that simplified landscapes were dominated by smaller individuals within species (Grab et al. 2019; Renauld et al. 2016). Similarly, in the tropical fruit lulo (*Solanum*



Fewer bees in simpler landscapes (Connelly, Poveda, & Loeb, 2015)

More carabids in simpler landscapes (Perez-Alvarez et al., 2021)

More tarnished plant bugs in simpler landscapes (Grab et al., 2018)

Reduced bee species richness in simple landscapes (Connelly, Poveda, & Loeb, 2015; Obregon et al., 2021)

Unchanged carabid species richness as landscapes change (Perez-Alvarez et al., 2021)

Smaller bees in simpler landscapes (Grab et al., 2019; Renauld et al., 2016; Obregon et al., in prep)

Larger tarnished plant bugs in simpler landscapes (Salzberg et al. in prep)

Smaller lady beetles in simpler landscapes (Salzberg et al. 2022)

Less parasitism in simpler landscapes (Grab et al., 2018; Perez-Alvarez, Nault, & Poveda, 2018)

Less predation in simpler landscapes (Perez-Alvarez, Nault, & Poveda, 2019)

Less pollination in simpler landscapes (Connelly, Poveda, & Loeb, 2015; Obregon et al., 2021)

Fig. 5.1: Effects of landscape simplification on arthropod communities and ecosystem services. The figure shows the (A) abundance, (B) richness, (C) functional traits, and (D) ecosystem services of, or provided by, arthropods across different insect groups we have studied over the years. Each icon represents a different insect group, variation in shade and size represents variation in richness and functional traits. The corresponding explanation and reference describing the landscape effects is provided on the right.

quitoense) in Colombia, we found that the stingless bee *Melipona fasciata* exhibits a reduced worker body size in farms surrounded by landscapes with less natural habitats (Obregon et al., in prep). Additionally, intraspecific variation in functional traits in response to landscape simplification could have meaningful effects on the provision of ecosystem disservices such as crop damage. For example, we found that simplified landscapes could increase the body size of herbivores, such as the tarnished plant bug (*Lygus lineolaris*) leading to higher herbivory rates in strawberry fruits (Salzberg et al. in prep). These findings emphasize the importance of integrating intraspecific trait variation into models predicting ecosystem function, as even minor changes in intraspecific traits can potentially exacerbate the functional consequences associated with species loss.

Given its significance to practical conservation biology and sustainable food production, the work of Tscharntke and colleagues has been a constant point of reference for our group. At the same time, it provides us with a theoretical framework that enables us to make plausible predictions to be tested and further refined. In this way, their research has immediate practical applications and contributes to advancing our theoretical understanding of how the composition and configuration of agricultural landscapes influence biodiversity and ecosystem services. Teja Tscharntke's research has also been instrumental in informing policy decisions and conservation strategies to preserve biodiversity and promote sustainable agriculture. These contributions to sustainable agriculture are far-reaching, extending beyond the scientific community to impact society at large.

5.3 Landscape effects on plant adaptation

The theoretical framework proposed by Tscharntke and his group does not just apply to conservation, agricultural systems, and crop production, as outlined above, but has far-reaching impacts on plant-arthropod interactions in natural systems. By altering the composition and distribution of arthropod communities throughout the growing season, landscape simplification can impact both the spatial and temporal dynamics of natural plant-insect interactions. Teja Tscharntke's group demonstrated that spill-over and spill-back of insect antagonists and mutualists have important implications for plant-insect interactions in natural habitat fragments (Blitzer et al. 2012; Gladbach et al. 2011; Tscharntke et al. 2005b). Mass blooming crops have been found to divert pollinators away from semi-natural habitats, resulting in a fitness cost for co-flowering wild plants (Holzschuh et al. 2011). Proximity also mediates insect interactions, as wild plants near a mass-blooming crop may have higher pollinator visitation than populations further from the crop (Chamberlain et al. 2013). Herbivore interactions with wild plants may be similarly affected by landscape simplification (Tscharntke et al. 2005b), however the direction of these patterns can be highly variable (Rosenheim et al. 2022). For example in maize, simplified landscapes were associated with a decrease in the abundance of a generalist herbivore and an increased abundance of a specialist herbivore, with consequences, especially for wild plant relatives of crops (Dong et al. 2020). While spillover from crops into natural systems remains largely understudied (Blitzer et al. 2012), some examples demonstrate greater herbivore pressure associated with close proximity to crops (McKone et al. 2001).

This work demonstrating changes in insect interactions with plants in habitat fragments led our group to investigate whether this may lead to altered selection of plant traits. Insects are well established as agents of selection on plant traits, with the outcome of selection relying on the combined contribution of both pollinator and herbivore interactions (Johnson et al. 2015; Ramos and Schiestl 2019; Sletvold et al. 2015). Therefore, shifts in insect interactions associated with landscape simplification are expected to alter the selection on plant traits (Schroeder et al. 2021). This has been demonstrated across plant populations where the introduction of a novel pollinator was found to alter floral trait evolution (Mackin et al. 2021). Across landscape types, pollinators have been found to select for larger flowers, with plants in pollinator rich landscapes producing larger and more numerous flowers than plants in pollinator limited landscapes (Brys and Jacquemyn 2012). Release from herbivore pressure similarly results in a reduction in plant defenses (Agrawal et al. 2012). However, insects do not interact with plants in isolation and ultimately it is the combined interactions of pollinators and herbivores that drive the outcome of selection on traits related to defense and attraction (Egan et al. 2021; Ramos and Schiestl 2019).

For the wild Brassicaceae species *Barbarea vulgaris* we have found changes in both plant trait expression and insect interactions across a gradient of increasing agricultural land cover. Plants grown in a greenhouse common garden from seeds collected across the landscape gradient exhibited changes in plant trait expression, where plants originating from simple landscapes were found to produce smaller flowers and have a smaller leaf area removed by caterpillar herbivores (Schroeder et al., in review, Fig. 5.2). When plants grown from a single parent plant were placed across the landscape gradient, plants placed in complex landscapes experienced greater herbivore pressure and higher pollinator visitation (Schroeder et al., in prep.; Fig. 5.2). While further work is necessary to directly link insect interactions as the driver of trait changes, this data supports the hypothesis that changes in the insect community driven by landscape simplification have consequences for wild plant evolution. Shifts in plant traits may also create eco-evolutionary feedback loops where plant adaptation further reinforces the unique insect interactions associated with simplified landscapes.

Drawing on the spillover and spillback framework developed by Teja Tscharntke and his group, we have a new theoretical framework that has the potential to shed light on plant trait evolution and the complex eco-evolutionary feedback loops between plants and arthropods across landscape gradients. By exploring the evolution of these interactions across landscape gradients, we are generating new insights into: 1) the relative roles of pollinators and herbivores as agents of natural selection, 2) the environmental context that shapes plant-arthropod evolutionary dynamics, and 3) the genetic mechanisms underlying population-specific differences in trait expression. In this way, the work of Tscharntke and his group has far-reaching implications not just for conservation biology and ecosystem services but also for our broader understanding of evolutionary ecology.

5.4 Building on the intermediate landscape complexity hypothesis

One of Teja Tscharntke's most important contributions to the field of landscape ecology has been the suggestion of multiple hypotheses that explain how human-modified

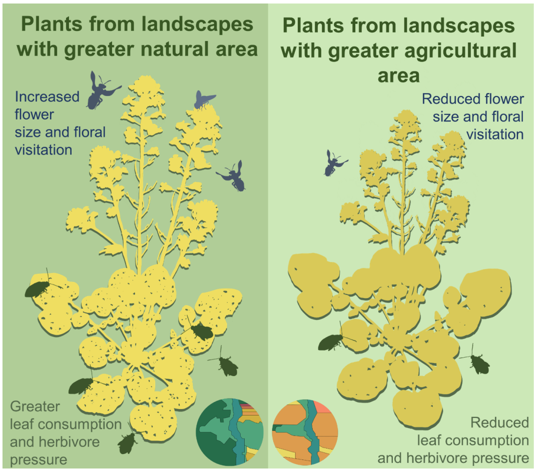


Fig. 5.2: Seeds from the plant *Barbarea vulgaris* were collected from across a gradient of increasing landscape simplification and grown together in a greenhouse common garden. Plants from landscapes with more natural land cover produced larger flowers and experienced greater leaf damage in an herbivore no choice bioassay when compared to plants originating from highly simplified landscapes. When sentinel plants grown from a single parent plant were placed across the landscape gradient, plants placed in landscapes with greater natural land cover experienced greater pollinator visitation and increased herbivore pressure than plants placed in more simplified landscapes.

landscapes determine the structure of ecological communities, ecosystem function, and services (Tscharntke 2012; Tscharntke et al. 2005a). One of his most influential hypotheses is the intermediate landscape complexity hypothesis, proposed in 2005 and formalized in 2012. This hypothesis suggests that the effectiveness of management practices to promote biodiversity conservation ultimately depends on the composition of the landscape in which they are implemented.

The development of the intermediate landscape complexity hypothesis grew from discussions of the effectiveness of large-scale agri-environmental schemes across Europe (Kleijn and Sutherland 2003) and was formulated based on concepts of source population availability and species dispersal limitations in fragmented, agriculturally intensified landscapes (Tscharntke et al. 2005a). The hypothesis proposes that management practices implemented in landscapes with intermediate complexity will be more successful at increasing diversity and ecosystem functioning relative to an unmanaged control than the same practice implemented in either a complex or highly simplified landscape. In complex landscapes, source populations are high and dispersal limitation is low, generating a high baseline level of diversity and functioning in these landscapes, a scenario in which local management changes would have little impact. In contrast, implementing a conservation practice in intermediate landscapes will increase local habitat quality relative to the baseline and facilitate dispersal resulting in a greater positive impact. In highly simplified or cleared landscapes, source populations are so low and dispersal limitation so high that local management would be unsuccessful in overcoming these constraints, consequently resulting in low expected effectiveness. The hypothesis therefore proposes a non-linear hump-shaped effectiveness curve across the landscape gradient (Fig. 5.3A).

The intermediate landscape complexity hypothesis has subsequently been evaluated in a range of systems, most of which have focused on the biodiversity responses from which the hypothesis was originally framed (Batáry et al. 2010; Jonsson et al. 2015; Martínez-Núñez et al. 2020). Our work has built on the original framing of the hypothesis to explore additional effects on ecosystem services such as crop pollination and biological pest control, as well as their impacts on crop production (Grab et al. 2018b; Obregon et al. 2021, Fig. 5.3B). We have also expanded the breadth of local management practices to include augmentative biological control (Perez-Alvarez et al. 2019) and push-pull practices (Poveda et al. 2019, Luttermoser et al. in prep.) where natural source populations and dispersal play a lesser role and thus alter the expectations for the shape of the landscape-effectiveness relationship.

The management practices included in the original conception of the intermediate landscape complexity hypothesis generally rely on recruiting organisms from surrounding source populations by increasing local habitat suitability. These practices rely less on synthetic inputs and include organic and reduced input production practices. The intermediate landscape complexity hypothesis proposes that these practices will be most effective when implemented in intermediate rather than simple or complex landscapes. (Park et al. 2015; Tscharntke 2012). Working in Colombia, we evaluated whether landscape context buffered the impact of pesticide use intensity on pollinator communities of a tropical and highly pollinator-dependent crop (*S. quitoense*). As expected, we found that complex landscapes buffered bee communities under low to moderate pesticide risk scenarios but were not able to buffer communities exposed to the highest pesticide risk. While reductions in pesticide risk were associated with increases in bee richness across all landscape contexts, the effects of these pesticide risk reductions on richness were strongest in complex landscapes (Obregon et al. 2021). These results highlight the context dependency of pesticide risk reduction interventions which, in this case, shows the greatest benefits in complex and species rich landscapes.

In addition to improving local habitat suitability by reducing risk factors, the intermediate landscape complexity hypothesis was also framed on practices that improve suitability by adding habitats and resources such as the hedgerows and field margins supported in the EU by the Common Agricultural Policy's subsidies for agri-environmental schemes. In the US, the Farm Bill program provides similar subsidies, including incentives for establishing perennial flowering habitats within farmlands for conserving pollinators and other beneficial species. Our work beginning in 2012 evaluated the effectiveness of field borders planted with native perennial wildflowers relative to control borders for pollination, pest control and crop productivity to strawberry in a relatively diverse farming region in New York, USA (Grab et al. 2018b). We expected to see the classic hump-shaped landscape-effectiveness relationship for benefits to pollination, biological control and crop yield and an inverse curve indicating the strongest reductions in pest pressure in intermediate landscapes. We found that pollinator abundance followed the expected pattern, but was the only response to do so. The landscape-effectiveness relationship was inverted for pest control as expected, but was shifted strongly above zero. This pattern suggests that wildflower planting did not result in significant pest suppression in any landscape

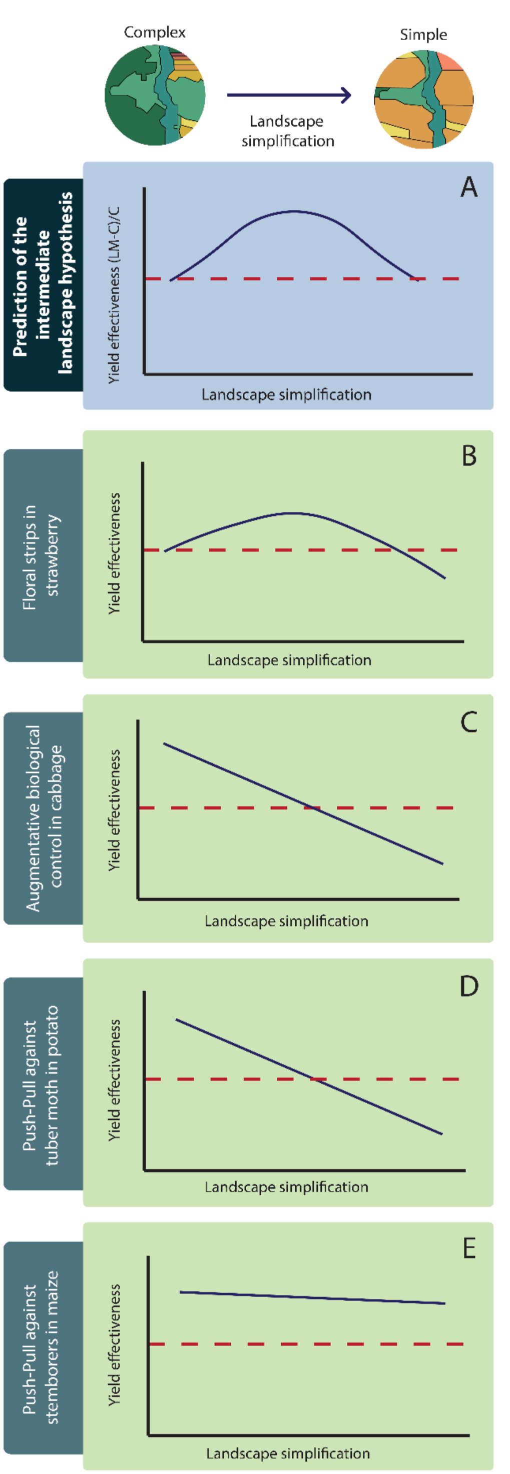


Fig. 5.3: Graphical representation of the context dependency of different local management practices in different crop systems. Yield effectiveness was measured as the difference between local management (LM) and control (C) yield over control yield. The red dotted line indicates where the local management and the control plots have the same yield. Values above the line mean that the local management plots has higher yields than the control plots, values below the line indicate that the local management plots have lower yield than the control plot. (A) Prediction of the intermediate landscape hypothesis predicting that in intermediate landscapes the benefits of a local management practice would be higher than in simple and complex landscapes. (B) In New York State, USA, floral strips aimed at increasing pollination and biological control increased strawberry yield in intermediate landscapes, but has no effects in simple or complex landscapes. (C) In cabbage systems in the same region, we find that in complex landscapes, the use of augmentative biological control increases yields in complex, but not in simpler landscapes. (D) In the Andean Region of Colombia a push-pull system aimed at reducing pest pressures by the potato tuber moth, is effective at increasing yield in complex, but not in simple landscapes. (E) The push-pull system developed for suppression of stemborer damage and striga weed in maize was slightly more effective in more complex landscapes, but showed high effectiveness across all landscapes.

context and that pest pressure was greater at sites with wildflower plantings particularly in landscapes with the lowest surrounding natural habitat cover. The primary pest in this system is a broad generalist which also benefited from the wildflower plantings adjacent to the focal crop. These benefits of wildflower plantings to the pest in terms of accessible alternative hosts and overwintering habitat may have been particularly great in more simple landscapes. The cost of wildflower plantings associated with increased pest pressure was apparent when considering yields and wildflower plantings were only expected to provide a benefit or neutral effect on yield in intermediate landscapes.

Much of our work builds upon the original conservation-based management practices proposed in the intermediate landscape complexity hypothesis. In addition to testing these practices, we have included strategies that directly augment populations of biological control agents, which reduces the assumptions of the original hypothesis based on source populations and dispersal limitations. One such practice is augmentative biological control, which is an increasingly common sustainable pest management strategy (van Lenteren et al. 2018). Unlike classical biological control, which aims to establish a self-sustaining population of the natural enemy, augmentative biological control involves periodic releases of natural enemies to supplement existing populations and provide short-term pest suppression. We expected augmentative biocontrol benefits to be greater in simple or intermediate landscapes than in complex landscapes, thinking that the high abundance of naturally occurring enemies in complex landscapes would make enemy augmentation redundant. Surprisingly, we found that releasing predators in complex, resource-rich landscapes resulted in fewer pests, less plant damage, and greater crop yield (Perez-Alvarez et al. 2019, Fig. 5.3C). Conversely, in simple landscapes, the addition of predators may lead to lower biocontrol and more damage to the crop due to antagonistic interactions between naturally occurring and introduced natural enemies. By creating favourable conditions for complementarity among augmented and resident enemies, complex landscapes strengthened pest suppression. Our findings suggest that augmentative biocontrol may be most effective in enhancing biological pest control on farms located in landscapes with contiguous natural habitats.

The array of ecologically intensified management practices we have evaluated also extends to those that rely on directly modifying the responses of pests themselves rather than relying on top-down control by recruited or augmented natural enemies. Push-pull systems rely on modifying host related cues by incorporating a highly attractive pull cue to move pests away from the crop with a deterrent push cue to repel pests from the crop (Cook et al. 2007). Frequently these are implemented as an intercropping system. In contrast to the hump-shaped expectation of the intermediate landscape hypothesis, we expected that under circumstances that are more challenging for specialist herbivores, such as complex landscapes with fewer host crops, behaviour-modifying management practices would be more effective at increasing yields relative to push-pull practices implemented in simple landscapes. We developed a Push-pull system to decrease potato tuber moth pressure in Colombian potatoes, consisting of an intercrop of an attractive (pull) tuber variety with a repellent garlic-pepper spray (push) that works as a conventional insecticide spray (Gómez Jiménez and Poveda 2009). We tested how landscape dependent this push-pull management practice is by planting it on 14 Andean farms located along a gradient of landscape simplification between 38 and 88% agriculture at a 1 km scale. Results show the effectiveness of the push-pull practice in increasing yield relative to control plots was greatest in complex landscapes. As the proportion of cropland in the landscape increased, the push-pull system became less effective (Poveda et al. 2019, Fig. 5.3D). We also tested the landscape dependence of a maize intercropping push-pull system used widely across Kenya. Although the push-pull system was highly effective in all landscape contexts, we found relatively weak landscape dependence with the practice also showing slightly greater effectiveness in complex landscapes (Luttermoser et al. in prep.). Again, the effect of push-pull was the most important factor for yield, outperforming control plots by 175% even in the most agriculturally-dominated landscapes. This landscape resilience could be due to push-pull's benefits primarily coming from plant effects managing pest abundance, and below-ground soil effects, rather than beneficial arthropods. While beneficial arthropods do contribute predation services in the push-pull system, their effect is relatively minor compared to the direct effect of the plant volatiles from the companion crops.

Although the initial intermediate landscape complexity hypothesis was proposed to test if biodiversity will benefit the most from local conservation practices in landscapes of intermediate diversity, its application to local management practices that use ecological intensification is undeniable. Our research has shown that the effectiveness of local management practices is highly dependent on the landscape context and that implementing these practices in intermediate landscapes does not always lead to the most benefits (Fig. 5.3). While the intermediate landscape hypothesis' predictions do not always hold true, its framework enables the design of context-informed management practices that can maximize benefits to both biodiversity and agricultural productivity. This is crucial for informing policy decisions at regional scales and promoting the adoption of sustainable land management practices.

5.5 Conclusions

Teja Tscharntke and his agroecology group have made a significant contribution to our understanding of landscape ecology, particularly by providing insights into the effects of landscape composition and configuration on arthropod conservation, plant-insect interactions, and ecosystem services. Their foundational theories have inspired further research in these areas, including our work exploring landscape composition's effects on crop production and plant adaptation mediated by changes in the arthropod community.

However, our findings suggest that achieving crop yield benefits from landscape composition is not simple. While complex landscapes tend to consistently benefit pollination services, other functional responses, such as biological control and pest damage, are more variable and depend on the type of semi-natural habitat, crop composition, crop system, and management intensity. Therefore, future research aimed at improving ecosystem services mediated by arthropods at landscape scales should focus on identifying the specific mechanisms driving plant-arthropod community responses to landscape simplification and how these responses vary across different habitats and management practices.

Moreover, our understanding of how landscape composition affects plant evolution mediated by changes in the arthropod community is still in its infancy. Changes in plant traits can affect insect traits and communities, creating eco-evolutionary feedback loops that are likely to change the evolution of plant-arthropod interactions along landscape simplification gradients. Future research in this area should include selection experiments on plants and arthropods and a clear understanding of the genetic changes that are occurring in organisms growing along the earth's land use gradients.

In summary, Teja Tscharntke's work has provided us with a valuable theoretical framework for comprehending the importance of biodiversity changes at the landscape scale. Nonetheless, further research is necessary to gain a more nuanced understanding of biodiversity patterns in agricultural landscapes. This will enable us to effectively use landscape metrics as predictors for management decisions that impact crop production, conservation, and plant-herbivore evolution. Our research group strives to honour Tscharntke's legacy by expanding our knowledge in this field and creating solutions for a more sustainable and equitable future for both people and nature.

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Chapter 6

Biodiversity friendly landscapes – A question with many solutions

Jan Bengtsson & Riccardo Bommarco

Abstract Building on some of Teja Tscharntke's key papers we discuss a number of complexities of farming systems and agricultural landscapes that we believe should be included in future studies of production landscapes. We contend that transformation of modern agricultural landscapes to biodiversity-friendly ones needs a combination of farming on-field measures, land-use practices and landscape measures, but also policies supporting less intensive production. We argue that in future research, landscape ecologists should acknowledge the multiple values of biodiversity, and abandon using simple species richness indicators for those values. Ecologists should rather focus on understanding what species and their interactions are actually doing in production ecosystems. Some myths in landscape ecology, such as global food scarcity, land sparing, and intensive farming being the benchmark for sustainable food production, are rejected. We show that the global agricultural system is entrenched in a productivist narrative that hinders development of more sustainable production systems. In order to change current agricultural systems towards sustainable production and biodiversity-friendly landscapes, we need a broader perspective that incorporates knowledge and understanding of social-ecological systems and processes. We exemplify this with four future scenarios for Swedish food systems that in different ways are suggested to contribute to biodiversity goals, though perhaps not exactly via the biodiversity-friendly landscapes envisioned by Teja and many other ecologists.

> "*Answers live their time. Questions come again and again.*"
> Samuli Paronen[1]

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[1] Paronen, S. (1974) Maailma on sana: Mietteitä. Translated from Finnish by Heljä-Sisko Helmisaari.

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6.1 Introduction

It is interesting how thoughts and ideas tend to develop in parallel in science. Starting from different points of departure we (Janne and Riccardo, together with a much missed Barbara Ekbom) developed an interest in agricultural landscape ecology in the mid to late 1990s. By the turn of the millennium we had discovered Teja Tscharntke who followed similar lines of thought.[2] What drew our attention and admiration was the ground-breaking paper in *Science* by Carsten Thies and Teja (Thies and Tscharntke 1999) that pointed towards research on how non-arable habitats in the agricultural landscape could be important for biological control of insect crop pests; a process now often called ecosystem service or Nature's Contributions to People (NCP), depending on the choice of conceptual framework.[3] However, examining our articles from that time, references to Teja are conspicuously rare until 2005, and if anything was cited, it was the Science paper. Teja was by then building his successful agroecological group in Göttingen with many interesting persons, and by 2006-08 we routinely referred to and were inspired by the quickly increasing body of excellent research led by Teja. When there was a EuroDiversity call for a "pan-European" project on biodiversity and ecosystem services from the now largely closed down European Science Foundation in 2004, it was an obvious choice to invite Teja and his group in Göttingen as a key partner. We called the project AGRIPOPES and we received funding for three years from late 2006.[4] It was during this time that we really

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[2] It could have made us competitors, but instead we became colleagues, collaborators and friends with Teja and many of the younger group of students and Ph Ds that he gathered around him in Göttingen. Janne came from a background in metapopulation ecology of waterfleas (*Daphnia*), being one in a long tradition of Swedish researchers who believed they could change the world with research in rockpools (see below), but happened to end up studying biodiversity and ecosystem services in forest and agricultural landscapes at the Swedish University of Agricultural Sciences by the late 1990s. Riccardo had a training in agronomy and had worked with crop protection and the population ecology of predators and their pest prey, and had initiated research on spatial ecology and the influence of landscape on population regulation in his PhD-studies mentored by Barbara Ekbom. (Rockpools are small water-filled depressions in bedrock along large areas of the coasts of Sweden, Finland and Norway, but also other countries such as Russia and Canada, being perfect models for fragmented populations such as *Daphnia* metapopulations (e.g. Hanski and Ranta 1983; Bengtsson 1989; Bengtsson and Ebert 1998). Other Swedish researchers studying rockpools include Fredrik Wulff, Björn Ganning, Jon Norberg, Eva Lindström, Silke Langenheder and – amazingly – Janne's collaborators Örjan Östman and Lars Gamfeldt, to name a few).

[3] IPBES advocates that the term Nature's Contributions to People (NCP) is used rather than ecosystem services (e.g. Díaz et al. 2018). It is argued that this is a broader and more inclusive term that puts higher emphasis on cultural links between people and nature, and recognizes other knowledge and value systems, while the term ecosystem services is too much based in an western and economic world view. Here we use these terms interchangeably as they have been used in the debates we refer to.

[4] The perhaps strange acronym AGRIPOPES stands for AGRIcultural POlicy-induced landscaPe changes: effects on biodiversity and Ecosystem Services. It's not been possible to trace exactly how the project emerged and how Teja got one of the key roles; the files on Janne's computers only date back to late 2004, when a full draft of thce application appears from the shadows. We believe that Michel Loreau's work in the ESF Linking Species and Ecosystems network played an important role, but the person who did most of the hard job to produce the apparently well-received application was Pablo Inchausti, then at CNRS in France. (As a side issue, the surprisingly positive reviewer comments included "a breath of scientific fresh air. The authors have a testable hypothesis, which, while not the most original, will certainly provide evidence for a much larger landscape of Europe than the typical country assessments'", "a novel, superior approach to anything I have seen at this level.'" and "a jewel to read … Amazing."). The project ran during

got to know Teja and his co-workers in Göttingen in person, with friendships that have continued. For example, Janne has a fond memory of a seminar and Christmas party in Göttingen in December 2008, and then taking a very early train back to Sweden the next morning. Riccardo vividly remembers the warm reception by Teja and his group at a visit in Göttingen. We remember Teja impressively balancing between on one hand scientific focus and high ambition, with on the other hand feasibility and pragmatic consideration of the students and available resources in AGRIPOPES.

Most of Teja's career, as we know it, has been built around questions on how to preserve, increase and use biodiversity and ecosystem services in managed landscapes – from landscape effects on natural enemies of crop pests and the dynamics of the trophic interactions involved (Thies and Tscharntke 1999), pollinators' use of landscapes (Steffan-Dewenter et al. 2002) and how this affects coffee pollination (Klein et al. 2003), to advantages (Gabriel et al. 2006; Holzschuh et al. 2008) and disadvantages (Tscharntke et al. 2021) of organic farming for increasing farmland biodiversity. These are all questions of high theoretical and practical importance that have inspired research globally, and are likely to have complex, localized or regionalized and often uncertain answers, partly because each answer is likely to represent particular perspectives, localizations, organism interactions, scales, times, and time-frames. To this is added the uncertainties of climate warming and the socio-political responses to climate change and biodiversity loss (IPCC 2014; IPBES 2019). Finally, the questions may also challenge many views on human-nature relationships in a fundamental way (Díaz et al. 2018; Biermann 2021).[5]

A reoccurring and important theme in Teja's research is the conviction that landscape composition, and especially the amount and quality of seminatural habitat outside arable crop land, is an important determinant of biodiversity in agricultural regions, together with farming practices and production systems on the arable land. This is especially emphasised in one of Teja's most cited papers (Tscharntke et al. 2005) in Ecology Letters,[6] in which most of the ideas were formulated that have been elaborated by him and many others for almost 20 years. Examples of still active research topics springing from this paper include the contrast between local and landscape intensification, the role of the landscape species pool and dispersal, and the varying effectiveness of agri-environmental schemes depending on landscape context. The latter suggests that farming system changes, such as transition to organic farming, will have larger effects on biodiversity and ecosystem services in simple than in complex landscapes. The article makes a strong case for both more extensive and traditional farming methods and land use systems, including benefits of managed non-crop areas, to increase biodiversity. In addition to more extensive farming methods, e.g. organic and regenerative practices, such managed semi-natural habitats have received large

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2007-2010 and included field studies in a N-S gradient from Estonia and Sweden to Spain, and E-W from Poland to Ireland, with two sites in Germany (former West and former East) and one each in France and the Netherlands. Several other European countries were also involved. Work from the project is still being published, the most recent articles are Emmerson et al. (2016) and Carmona et al. (2020). Riccardo and Janne take this opportunity to thank Pablo, Teja and the other PIs for the privilege to have worked with you.

[5] Also discussed in relation to biodiversity by Bengtsson and Hilding-Rydevik (2021) (in Swedish. A pdf is available from the first author on request, but it is in Swedish, and will not really make sense if you Google-translate it!)

[6] This paper has around 4000 citations, depending on which source is being used.

attention both in biodiversity science and policy, local and landscape management being regarded as complementary for supporting biodiversity in agricultural landscapes (e.g. Tscharntke et al. 2005; Tuck et al. 2014). More extensive farming methods have also been argued to have a number of other environmental and social benefits (e.g. Gomiero et al. 2011; Reganold and Wachter 2016; Seufert and Ramankutty 2017; Elmqvist et al. 2022).

In view of a seemingly general agreement on the complementarity of these two approaches, it was somewhat surprising when Tscharntke et al. (2021) argued that measures and policies at the landscape level was the major or even overriding factor for supporting biodiversity in agricultural landscapes, in comparison with extensification of farming practices and farm production systems on the arable land. The 2021 article elaborated their view on how "biodiversity-friendly" landscapes can be created. We will use the 2005 and 2021 articles as starting points for a discussion of some problematic issues when dealing with conservation of biodiversity and ecosystem services in human-dominated production landscapes. We refer especially to landscapes dominated by western types of agriculture that have been overwhelmingly transformed since the 1950s into a productivist industrial agriculture, to a large extent driven by large agrobusinesses aligned with policies (or no-policies) that have favoured intensification (e.g. Clapp 2015, 2021b,a).

Our aim here is not to question Teja's work, but rather to build upon it by highlighting a number of unresolved and difficult issues that Teja in various and sometimes contradictory ways has addressed, but at times also avoided in his career. We discuss the directions and questions asked and not asked in agricultural landscape ecology that has grown to a large field of research globally, to a great extent inspired by the work and approaches of Teja and his students. The main point we make is that creation of the "biodiversity-friendly" landscapes suggested by Tscharntke et al. (2021) and many other landscape ecologists is unrealistic without a major change in *farming systems*. We argue that in fact it is only possible if combined with a socio-political transition towards environmentally sustainable farming, along with climate-smart diets, biodiversity-friendly landscape management and reduced and recirculated waste (e.g. Billen et al. 2021).[7]

6.2 What is this thing called a biodiversity-friendly landscape?

Tscharntke et al. (2021) discuss what a "biodiversity friendly" agricultural landscape should look like, by giving examples of features that such landscapes should contain. They divide these features into "measures essential for biodiversity-friendly *farming*", "*land-use* practices" and "*landscape* measures" (our italics). We find it useful to divide what can be done to enhance biodiversity into these categories, since the societal drivers and actors are different. However, their paper largely focused on – or was interpreted often as – contrasting organic farming and landscape measures for biodiversity as *opposing* strategies. We contend that

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[7] We base our view on a system perspective that emphasises something that is hidden or even actively forgotten in the biodiversity-farming discourse, namely that the system we want to change is a social-ecological one. Since our view also implies some hypotheses about the future – which cannot be known and tested now, we can only provide a chain of arguments based on what we presently know about the ecology of agricultural landscapes and social-ecological food production systems. By necessity, but in our case explicitly, this is based on a political view on agriculture, food and biodiversity that, albeit vague, is transcending the organisation of the present agricultural systems. But in which direction?

this framing of the biodiversity-friendly landscapes question is misleading. It will most likely not provide the answers needed for enhancing biodiversity in modern agricultural landscapes.

Farming measures include *what farmers can do* on or in the direct vicinity of *their arable land*. Such practices include crop diversification and crop rotations, cover crops and green manure, intercropping, agroforestry (combining trees and crops in arable fields), reduced tillage and reduced pesticide use, fertilising with organic amendments, and integrating livestock into farming systems. All these have significant positive consequences for biodiversity.

Crop fields are key habitats for a large number of organisms, many of which contribute to a number of ecosystem services. In particular, soil organisms and insects with life stages in the soil contribute to processes beneficial for farmers, such as earthworm bioturbation and redistribution of organic material, microbial decomposition and nutrient release, biological regulation of pests, pollination, crop health, and regulation of water storage and purification (e.g. Brussaard et al. 2007; Hanson et al. 2016; Smith et al. 2021; for pollinators see Carvalheiro et al. 2021; Christmann 2022). These processes are mainly dependent on the organisms performing them being present right there in the soil *in the crop field*, where farming practices shape the local communities and how they function (e.g. Riggi and Bommarco 2019; Viketoft et al. 2021; Torppa and Taylor 2022; Heinen et al. 2023).

However, we know rather little about how farming practices affect biodiversity and ecosystem services when changed at larger spatial scales. More organic farming in the landscape can increase weed diversity (Rundlöf et al. 2010), and positively affect predatory insects and predation rates (Inclán et al. 2015; Muneret et al. 2018), but sometimes only marginally (Petit et al. 2018). It also increases diversity of pollinators such as butterflies (Rundlöf et al. 2008). Because of the positive effects on biodiversity and ecosystem services of local field management, it is likely that landscape effects of biodiversity-friendly farming practices will emerge if implemented at larger scales than fields and farms. Indeed, recent research demonstrates that increasing crop diversity in the landscape can enhance pollinators and predatory arthropods and the pest suppression they provide (Redlich et al. 2018; Raderschall et al. 2021). Such positive effects on beneficial organisms could be further enhanced if landscape level crop diversity is combined with establishing or restoring seminatural habitats such as hedges, grasslands or non-arable vegetation near the arable land (Aguilera et al. 2020). Research on up-scaled farming practices beyond organic farming and diversified cropping would shed light on the main hypothesis of Tscharntke et al. (2021) that landscape effects of non-crop habitats is the main driver of biodiversity in agricultural landscapes.

While changes in many of the biodiversity-friendly farming measures sound simple, they are in practice difficult to achieve in the short term, because most farmers are locked in their present farming systems and their practices (see section 6.4 below). Rather than simple policy changes, they often need larger incentives and support to move away from an input-intensive production with few annual crops to a more diverse production system, which all alternatives compatible with biodiversity-friendly and sustainable farming are likely to be (Tamburini et al. 2020). Farmers need support with, for example, knowledge, infrastructure, breeding and genetics, suitable technologies and markets for a greater diversity of crops and agricultural products. Also, biodiversity-friendly farming measures are (and can only be) related to actual practices on either arable fields or adjacent semi-natural managed habitats such as grasslands. Such grasslands need to be incorporated in the farm management to be maintained in the landscape (cf. Bengtsson et al. 2019).

Land-use practices, on the other hand, are only partly under the control of farmers. One reason is the fact that farmers are restricted to certain ways of farming because of market forces and policies, and hence land use is difficult to change. Also, practices are often determined by local factors, such as soil type, topography and the presence of other biotopes that cannot be converted to arable fields, such as dry meadows, semi-natural grasslands, riparian elements and forests. Land use is greatly affected by the governing socio-economic milieu – how farming is expected to be made by the farmer, neighbouring farmers and larger society, and how farmers perceive their own role and identity (e.g. Ahnström et al. 2013; Ortman et al. 2023). Larger changes in land use usually require changes in farmers' mind-sets. They are more likely either towards the end of investment periods for buildings and machinery (often around 20 years), when farms are transferred to a new generation, or if societal and other external pressures are large enough to shift the farmers' views on how their farming should be made. Hence, policies need to be aligned with strong incentives (or regulations) and investments in knowledge and infrastructure to produce a transition. We have a role model for such changes in the relative success of organic farming since the 1980s to transform farming systems at the farm level.[8]

Finally, *landscape composition* and configuration are even more difficult to change by individual farmers. Farms are placed in particular landscapes that determine what is possible to do and what can be changed. Landscapes in plains and prairies are fundamentally different from landscapes with hills and river valleys or mountain landscapes, and farming needs different measures and policies to be changed. The ecological consequences of such differences were thoroughly discussed in Tscharntke et al. (2012), but they did not discuss the policy requirements for transformation in different landscapes. And this was not discussed much in Tscharntke et al. (2021) either. Landscapes often determine what types of farming that can be performed under particular socio-economic, environmental and climatic conditions. Despite all the machinery and technology available, to accomplish large transitions into biodiversity-friendly landscapes requires a coordinated effort at the societal level, often invoking changes in culture, ideology, society and relations between humans and nature, and adaptation to local conditions. Such changes in societal and farmer minds-sets will take time, often decades. Tscharntke et al. (2021) had some suggestions for positive changes within present landscapes, i.e. within present farming systems, such as increasing the amount of semi-natural habitats mainly by decreasing arable field size, and supporting traditional but "uneconomic" land uses such as semi-natural grasslands. However, larger landscape transformations require substantial concomitant changes in farming and food systems, which their and many other ecologists' framing of the issue

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[8] It can be discussed how successful this transformation was, and if organic farming can manage to break out of the general intensification trap. Note that organics, like other suggested sustainable farming systems, such as regenerative, permaculture, etc. is only concerned with the farmed area, i.e. arable fields and grasslands, and can hardly be anything else. While these systems affect how agricultural landscapes look, they do not have prescriptions that extend outside the agricultural land to how other biotopes are managed.

— (organic) farming measures vs. landscape measures -– does not recognize.[9] Landscape transformation entails a transformation of farming systems and society because it requires breaking out of the straitjacket of intensified agricultural systems. It is time that ecologists working in agricultural landscapes begin to grapple with these issues.

What this useful distinction of measures for biodiversity-friendly landscapes implies is that transformation of agriculture to become biodiversity-friendly needs a set of complementary actions and policies that ensure that farming measures, land-use practices and landscape measures are aligned with each other. They are complementary approaches and hence not useful to contrast against each other. Many of the comments on the Tscharntke et al. (2021) article in Trends in Ecology & Evolution (e.g. Brühl et al. 2022, Marrec et al. 2022, Stein-Bachinger et al. 2022; see also Mupepele et al. 2021) hint at this, but it needs to be more explicitly stated. *If transformation of agricultural systems to biodiversity-friendly landscapes is the goal, there is no conflict between farming on-field measures, land-use practices and landscape measures.* All are needed since they complement and will strengthen in each other during transformations to future sustainable farming systems.

Most of the landscape and farming elements and practices that can be considered for making landscapes more biodiversity friendly are nicely summarized by Tscharntke et al. (2021, their tables 1 and 2): a larger diversity of biotopes in the agricultural landscape, de-intensification of farming through crop diversification and less use of fertilizers, using pesticides, herbicides and antibiotics only as a last resort, increased use of semi-natural and semi-managed habitats such as less productive grasslands and woodlands for livestock (many grazing animals like feeding on young trees), expanded areas of field edges, and so on. So what's the problem? It is that the 2021 paper, in contrast to many earlier of Teja's writings, seems to drive a wedge between landscape composition and biodiversity-friendly farming. It does so by constructing a narrative of opposition, or trade-off, between biodiversity increase from existing (albeit imperfect) organic farming and other on-farm practices vs. a non-existing conventional intensified farming system, in which measures increasing landscape complexity are hypothesised to be possible to add within the present production systems.

In many ways the farming systems that would be most likely to fit with the landscape vision of the "biodiversity-friendly" landscapes are deceptively similar to organic farming in mixed landscapes (Tscharntke et al. 2021). But alas no! The authors distance themselves from organic farming, implicitly arguing for intensified farming[10] and extensification at the landscape level. Their arguments are ambiguous and seem to us a combination of wishful thinking – intensification of farming can actually provide more space for biodiversity – and unsupported suggestions, such as pesticide use being as common in organic farming as in conventional, that crop rotations are similar in conventional and organic farming, that organic yields have to be consistently lower than conventional, and that less intensive farm-

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[9] We use organic farming as representative for several alternative farming systems to intensive industrial farming dependent on fertilizers, pesticides, herbicides, and technology machinery, entailing monocultures and large farming units. Organic is – for good and bad – the most articulated system among these alternatives, but not the only one, neither necessarily the desired endpoint.

[10] At least keeping the present level of intensification on the arable areas, which to us is contradictory to the tables 1 and 2 in Tscharntke et al. (2021).

ing systems, in contrast to conventional ones, are immutable and impossible to improve.[11] A friendly interpretation is that the authors really wanted to emphasize their point about landscape being important for biodiversity, which we basically agree with. This point was also made by (Estrada-Carmona et al. 2022), who highlighted that multifunctional agriculture at the farm as well as landscape levels is needed for biodiversity and ecosystem

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[11] The critical remarks on the TREE paper from others (Brühl et al. 2022; Marrec et al. 2022; Stein-Bachinger et al. 2022) discuss this in more detail, but the replies to the criticisms from Tscharntke et al. (2022c,a,b) are in our view weak and defensive, written to maintain the priority of their landscape view while de-emphasizing farming and land-use practices. Also, some of the propositions of Tscharntke et al. (2021) rest on a selective reading of the literature, which for some issues is in conflict with their propositions. Some examples are:

1. As Brühl et al. (2022) and Stein-Bachinger et al. (2022) point out, while organic farming uses pesticides, levels are much lower and of qualitatively different types which, apart from copper, are less negative for the environment and human health. Pesticide residues in organic products are much lower than in conventional ones (Mie et al. 2017; Benbrook et al. 2021), but not zero. In their response (Tscharntke et al. 2022b) just dismisses this point by juxtaposing pesticide use and landscape effects, as if a choice has to be made between one or the other (see also point 5 below).
2. Crop rotations of organic farming were stated to be only slightly longer than conventional (15%), but selecting this figure misses the point that crop rotations in organic farming usually is more functionally diverse and includes leys which enhance both soil carbon and soil biodiversity (obvious in Figs 1 and 2 in Barbieri et al. (2017). Also, crop rotations are locally adapted in ways not captured by regional means. For example, in agriculture-dominated landscapes in Sweden typical organic crop sequences are 5-7 years long (Cederberg et al. 2011: `https://www.diva-portal.org/smash/get/diva2:943924/FULLTEXT01.pdf`), but sometimes slightly shorter, on average 4.8 years in Chongtham et al. (2017), compared to common conventional rotations in the same areas which are usually 3 years with functionally more similar crops (cereals and oilcrops but rarely leys or legumes). In addition, organic crop rotations in marginal regions are often short because farming largely consist of leys (feed for animals) interspersed with annual crops, resulting in low crop diversity and rotation length but a less intensively managed and more biodiversity-friendly landscape overall.
3. The higher food production argument for conventional farming is only true if we accept that conventional intensive farming is the baseline, as discussed in the main text. This inconsistent logic should at least have raised a warning sign. Crop diversification can, as actually mentioned in Tscharntke et al. (2021), to a large extent decrease the yield differences (see above).
4. We do not downplay the worry about organic intensification mentioned by Tscharntke et al. (2021). That conventionalization breaks with “organic principles” should obviously be a matter of concern, and has been discussed by researchers (e.g. Darnhofer et al. 2010; Chongtham et al. 2017). We believe it can be explained as part of the lock-in problem discussed later in this chapter (section 4). The present food system, in which organic food production is embedded, is rigged for intensification no matter the farming methods.
5. As a side issue on pesticides, there is probably a pervasive influence of landscape-wide use of pesticides, as suggested by the results in Geiger et al. (2010). After this study was published, Janne and Barbara Ekbom were invited to the Swedish Chemical Inspection (Kemikalieinspektionen), because it was one of the first studies that had examined landscape-wide negative effects of pesticide use. They told us that ‘no studies underlying the registration and permission for pesticides were done at larger scales such as landscapes, and most were short time plot studies’. Janne was surprised while Barbara stoically agreed. However, the Geiger et al. (2010) study was not designed to answer exactly that question, although it suggests landscape-wide effects of pesticides across the nine European landscapes studied. This point is reinforced by Brühl et al. (2022) and Stein-Bachinger et al. (2022). The landscape-wide effects of pesticides on biodiversity and ecosystem services deserve more research, as does the landscape-wide effects of organic or regenerative farming.

services. However, relationships between agricultural practices and landscape measures on biodiversity are likely to be complex,[12] and need a more in-depth analysis than the simple species richness comparisons in the 2021 article.

6.2.1 Some productivist agriculture myths — food scarcity, land sparing, and non-sustainable baselines

Global food scarcity is often invoked as an argument for further agricultural intensification, contrasting yield deficits in especially organic farming compared to present intensive farming. However, the argument is not used when discussing other issues, such as grain or soybean being used as feed for pigs and poultry, when it could be used for humans directly. It assumes that present yields from intensive farming are sustainable, despite the fact that enough food is produced globally, but the distribution is unequal (Holt-Giménez and Altieri 2013)[13]. Almost a billion people are too poor to obtain food at the same time as up to 50% of the arable land area is producing feed for animals in the developed world (Öborn et al. 2011; Poore and Nemecek 2018; Harwatt et al. 2023); up to 70% of soy bean production is fed to pigs and poultry (*ibid.*). Hence food scarcity and yield arguments for intensification fail, at least in the short run and given that we can control climate change, which of course is uncertain but another story.[14] In this intensification narrative it is common to reject any alternative farming system as not being able to meet a purported "need" for more food production.

Another myth that has engaged landscape ecologists and agricultural researchers for too long is that intensifying agriculture will make it possible to spare more land for biodiversity, often framed as a land sparing–land sharing dichotomy (Green et al. 2005; Fischer et al. 2014; Kremen 2015). However, the land sparing–sharing debate should be laid to rest for several reasons: The conflict is largely constructed and usually poorly conceptualized because these choices are not mutually exclusive and outcomes depend on context, scale and on the subject of interest – biodiversity, ecosystem services, other environmental and social consequences (Fischer et al. 2014; Kremen 2015; Grass et al. 2019; Billen et al. 2021; Sidemo-Holm et al. 2021). In addition, different actors in the debate have communicated mainly within their "closed clusters", i.e. on one hand a land sparing group, better funded and with a philosophy dominated by biodiversity conservation, associated industry and practices of intensive agriculture, and on the other hand a land sharing group emphasising

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[12] The AGRIPOPES project did analyse the effects of landscape complexity and farming intensity on biodiversity as species richness at local and landscape levels (e.g. Flohre et al. 2011). The results were indeed complex and varied between the three organism groups, i.e. birds, carabids and plants. On the other hand, and not consistent with Tscharntke et al. (2021), Carmona et al. (2020) found that functional diversity of plants was more affected by intensification at the field scale than at the landscape scale. There is scope for more research on these issues. Marja et al. (2022) to some extent refuted the basic hypothesis in the 2021 article, but also highlights that different taxa respond in different ways to landscape and management.

[13] Holt-Gimenez reports that around 50% more food was produced than needed to feed everyone by 2008 (quoting FAO figures). This is still reported by the UN (`https://news.un.org/en/story/2019/10/1048452`) and consistent with the per capita figures in Our world in data (`https://ourworldindata.org/food-supply`). However, it may not be the case in a warmer world with approx. 10 billion people by 2050.

[14] See the current IPCC report, and the fact that CO_2-emissions still are increasing (Liu et al. 2023).

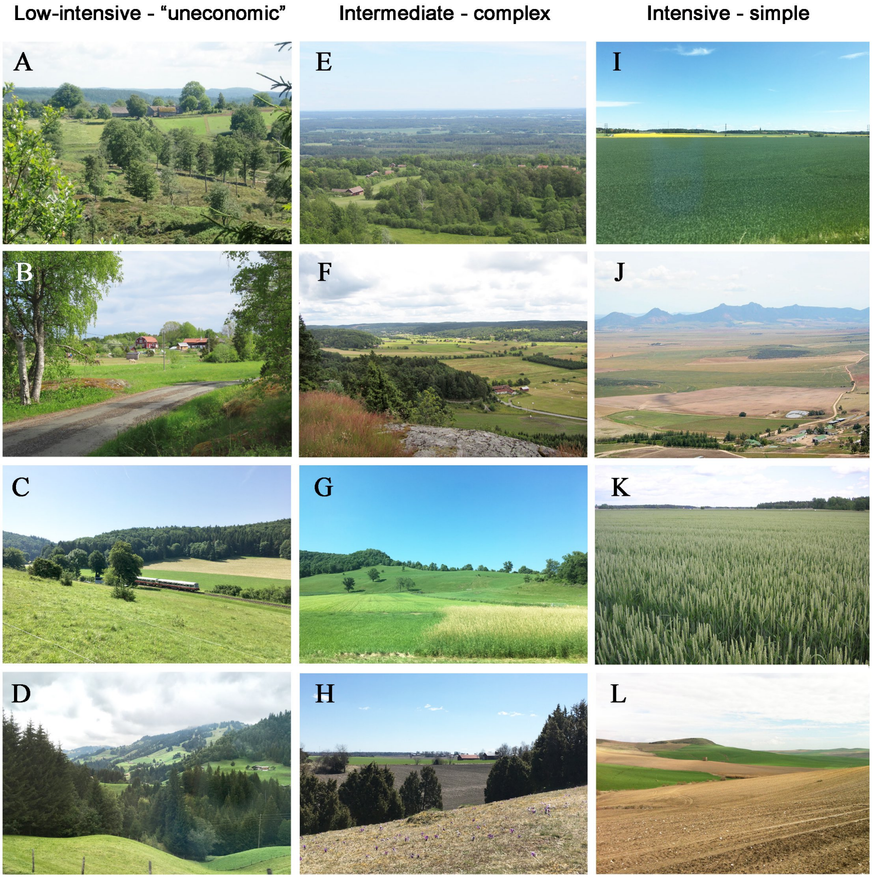

Fig. 6.1: Examples of landscapes managed with different intensities and different landscape composition, from older, low-intensive and "uneconomic" management (left column, A-D), modern landscapes in areas with more complex underlying natural conditions (mid column, E-H) to intensively managed industrial agriculture landscapes (right column, I-L).
Left column: A, recreated old landscape in SW Sweden. B, mosaic coastal landscape in E Sweden. C, grasslands in SW Germany. D, mountain landscape in central Switzerland.
Mid column: E, mosaic landscape with managed forest and intensively managed arable areas in Västergötland, Sweden. F. mosaic rift valley landscape with agriculture along rivers, and forest on the hills where arable cropping is impossible, SW Sweden. G, mosaic landscape with forest and medium intensive agriculture, Driftless area, Wisconsin, US. H, mosaic landscape with semi-natural grasslands on sandy soils and intensive agriculture on adjacent clay soils close to Uppsala, Sweden.
Right column: I, intensive conventionally managed landscape on fertile clay soils, SE of Uppsala, Sweden. J, wheat production landscape with small remnants of threatened renosterveld vegetation, north of Capetown, South Africa. K, wheat fields somewhere in Uppland, Sweden. L, cereal production landscape with no natural biotopes left, near Cordoba, Spain. [Photos by Jan Bengtsson, except J (Suzaan Kritzinger-Klopper) and K (Johan Bengtsson-Palme/Camilla Winqvist)].

ecosystem management, ecosystem services and functions, and sustainable agriculture (Loconto et al. 2020). Furthermore, and importantly, intensification sold as efficiency suffers from the problem of the rebound effect or "Jevons paradox". By increasing land-use "efficiency", the actual outcome of land sparing intensification will likely be that *more land is intensified* to produce even cheaper food, and hence ev'en less land will be available to set aside for biodiversity (see also next paragraph). This was pointed out already by Perfecto and Vandermeer (2008), and the general concept of decoupling has been efficiently debunked by e.g. Parrique et al. (2019) and Vadén et al. (2020). Without strong regulation (Wackernagel and Rees 1997) the intensification in land sparing scenarios will just lead to more sections of the landscape becoming intensified.[15] Clearly, other solutions are needed for modern industrial agricultural landscapes to be transformed to sustainability and biodiversity-friendliness. We need to move away from deceptively straight-forward and elegant, but empirically unfounded, trade-offs which has proliferated especially around the selected contrast between conventional and organic agriculture, but not between other forms of agriculture for which such trade-offs may be equally strong if not stronger.

A final comment on land sparing and intensification is appropriate. It relates to the food production question, and whether alternative systems such as organic or regenerative or even low-pesticide/herbicide farming systems can produce the amount of food "needed" in the future. It assumes that intensified systems – monocultures that are fertilized, sprayed, mechanized and supposedly efficient – are the benchmark that all other farming systems should be compared with.[16] But this requires, firstly, that we do not count the disservices or externalities of the intensified systems, such as eutrophication by dumping nitrogen and phosphorus into inland waters and the sea, contributing to global warming by releasing greenhouse gases into the atmosphere,[17] and exposure to pesticides and herbicides to human and non-human life.[18] And secondly, that we believe that continued intensification is a possibility in an increasingly resource scarce world (Moore 2008; Cordell et al. 2009; Herrington 2021).

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[15] Land sparing proponents may argue that such regulations are possible, but it's hard to see how this can occur in the current situation of policies and land use lock-in, so this remains pure speculation, but maybe possible under a transformed food and land use system. Note that decoupling arguments are assuming that Jevons paradox won't happen, which is why these arguments are valid for both issues.

[16] To this can be added the proposition by (Benton and Bailey 2019) that the current food system is inefficient because of the drive for efficiency at the farm level (interpreted as yields), meaning that changes in diets could free up very significant natural resources and reduce agriculture's impact on both environment and human health. So efficiency arguments are dubious when discussing yields vs. biodiversity, because efficiency is a contested issue and depends on which system level you are analysing (see also van der Werf et al. 2020, as regards LCA and biodiversity).

[17] Agriculture, not only but mainly modern farming systems and land use changes, contributes to approximately 30-40% of total GHG emissions, of which more than half is linked to animal production (Xu et al. 2021; Lynch et al. 2021). Past land-use change from forests to agricultural land has also contributed to the present high CO_2-levels.

[18] It is sometimes argued that pesticide risks for humans are negligible, but this is not the case for those who work with or are repeatedly in contact with pesticides or herbicides, as the recent debates about glyphosate shows. See also Mie et al. (2017).

6.3 Biodiversity is multifaceted and multidimensional

Landscape ecology and especially policy addressing biodiversity continues to be largely based on diversity measured as species richness of different taxa. However, while richness appears relatively simple to measure and give a value – much of the lay and public discussion on biodiversity is based on this notion -– it is also deceptive. It suggests that biodiversity is one measurable thing, when it is actually extremely complex, composed of thousands of species and other taxa with different requirements on the environment, with interactions dependent on local and landscape features, and having different effects on each other and the environment. There are many facets to this questions. We focus on two, firstly on which biodiversity we might be interested to preserve and secondly how to account for organisms and taxa having different requirements.

The reasons to be concerned about biodiversity can be many, and varies among individuals and actors in society. A primary reason can be that biodiversity and the species and populations that make it up has intrinsic existential value, even if we cannot find any human values for it. This is a valid argument, although it still forces us to discuss what it means in practice when we work in production landscapes dominated by agriculture or forestry.

A related argument for safeguarding biodiversity is the value we ascribe to biodiversity as rare, threatened or red-listed species, not for their intrinsic value but for some possible human benefits of this part of biodiversity in an uncertain future. For example, they contribute to option, insurance or resilience value, or many species, including rare ones, may be needed for ecosystems to function well in a future that we cannot know and therefore not tell exactly which species will be needed. These species have also been argued to be evidence that our landscapes are managed sustainably and well.[19] This view of biodiversity values of rare species is quite common among ecologists and biologists, who often also ascribe to a pure existential value of biodiversity.

Another reason, more oriented towards direct human benefits, for conservation of biodiversity is related to the part of biodiversity that contributes ecosystem services (NCPs) of benefit to farmers and society, for example, food production and the regulation and maintenance of underlying ecosystem services. Among those are biological control and pollination, where the research of Teja and his colleagues has been pioneering. Some of these ecosystem services are dependent on species that are common in other landscape elements than arable land, that are not or less intensively managed. However, other ecosystem services beneficial for farmers, landowners and society are not primarily sustained by species in non-farmed habitats. In particular, many soil processes are dependent on the organisms performing them being present and sustained right there in the soil, on the field. These processes and organisms play an important role in sustainable farming methods (e.g. Brussaard et al. 2007).

Still another argument for the usefulness of biodiversity is related to the *planned diversity* that farmers, forestry or urban planners can be interested in, often in terms of yield, biomass production or environmental benefits when plant diversity is increased. Examples include longer and more complex crop rotations, mixtures, agroforestry, intercropping,

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[19] By e.g. Carl Folke in discussions at scientific meetings, and it is a compelling argument.

the use of catch and cover crops, integration of leys and grassland in the farming system, or diversification of crop species at the farm level. Here potentially common species can be used by farmers for higher yields or other benefits by smart farming or forestry practices (see above; also e.g. Gamfeldt et al. 2013; Jonsson et al. 2019, as regards forestry).

Finally, as highlighted during the Covid-19 pandemic (2020-2022), many humans use nature and hence parts of biodiversity for recreation and health reasons, in far-away national parks and nature reserves as well as urban, near-urban and countryside nature areas. These reasons for biodiversity conservation have – just like ecosystem services –been undervalued in economic valuation (TEEB 2010; UK National Ecosystem Assessment 2011; IPBES 2019, 2022), as well as planning.

All these arguments are valid and matter. Many of the arguments for biodiversity conservation pertain to both red-listed and common species, including organisms of importance for ecosystem functioning and ecosystem services. The different aspects of biodiversity are poorly captured by single measures of species richness of an unspecified part of its components. This problem has several aspects: Should we still emphasize species richness, but acknowledge the different components of richness? Or should we rather question species richness as a useful indicator of biodiversity as well as ecosystem services?

Which of all organism groups and their species richness should be our concern? Any choice between, e.g., birds, vascular plants, bees, earthworms, springtails, amphibians, insects, etc., is fraught with difficulties, implicit value statements and trade-offs between the richness of various taxa. Even simplistic indicators such as "total richness" or "phylogenetic variation" are value statements that favour some organism groups above others, without specification. Furthermore, since organisms respond differently to environmental conditions or human activities, relationships between species richness of different taxa or other biodiversity indicators are unlikely to be strong, and also vary spatially and temporally. Wolters et al. (2006) found an average correlation (r-value) of 0.374 among richness correlations gathered from the literature, with a large variation spanning from strongly negative to strongly positive, the latter being more common than the former. This pattern has been corroborated by e.g. Pearman and Weber (2007) and Ekroos et al. (2013).[20] These results suggest that it is unlikely that conservation efforts based on certain taxa, like butterflies, birds, plants or bees, will result in ubiquitous increases in species richness of many other taxa. There will be trade-offs between focusing on certain groups vs. other groups.

In addition, the diversity of rare or red-listed species is -– by necessity in many cases -– not related to the delivery of most ecosystem services, which are often driven by either biomass (abundance) or strong interactions between common species. For rare species to have measurable effects on ecosystem functioning, they need to be either top predators or ecosystem engineers, be able to become more common under certain ecological conditions, or affect functioning under or following disturbances to the ecosystem. Species can also be rare in fundamentally different ways — having one or combinations of the characteristics

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[20] Janne once suspected that the trend towards positive correlations could be an effect of choosing taxa that were already expected to be correlated, such as plants and insects. Therefore, a student of his instead calculated richness correlations from the residuals from species-area relations, log-log transformed, assuming that these taxa had not been chosen according to this expectation. Surprisingly, this independent data set had a mean r-value of 0.373! (Ström 2006) Available from `https://stud.epsilon.slu.se/12425` or if this doesn't work, by sending a mail to the first author.

small local population size, small geographic range or restricted habitat niche (Rabinowitz 2014). Apart from key top predators or ecosystem engineers, it has been difficult to find evidence that rare species are important for ecosystem functioning[21] (see e.g. Ridder 2008; but also Dee et al. 2019 for an interesting discussion). Placing too much emphasis and policies on conservation of threatened species risks ending up in the bizarre situation that we spend most of our time and resources on rare species of, say, pin lichens or soil mites of negligible value for humans while losing ecosystem service providing species when industrial agriculture and forestry wreak havoc in the production ecosystems around the globe. We should be able to do both, but for different reasons and with a diversity of actions and policies. Unfortunately, species richness measures often include many rare species and are less likely to relate to the delivery of ecosystem services.[22]

In accordance with the above, Birkhofer et al. (2018) found low correlations in species richness of a number of organism groups in south Swedish landscapes – birds, plants, spiders, beetles and hoverflies. They also examined how richness correlated with ecosystem service potentials. Biological pest control, pollination, conservation and yield were correlated with each other, but usually not with the diversity of the organism groups assumed to be responsible for these services. Although for one region only, these results indicate that relations between biodiversity and ecosystem services are complex, probably driven by abundances of species or groups, habitat structures and farming practices that vary over small as well as large scales.

Hence, simple measures of richness are usually not adequate indicators of this elusive thing we call biodiversity, biodiversity-friendliness, or ecosystem services. The research agenda on relations between biodiversity and ecosystem functioning (and services) has been questioned along these lines (e.g. deLaplante and Picasso 2011; Frank 2022).[23] In fact, species richness does not do anything, it is just a usually poor indicator of something that we in fact do not know much about. If it is species that do the job in ecosystems – what we call ecosystem functioning – we need to abandon species richness as a useful concept and instead think about the species and their interactions, i.e. composition of ecological communities and ecosystems (Bengtsson 1998; Gagic et al. 2015).

We should instead focus on how species respond to environmental conditions, interactions between species and how these are affected by human activities, and the effects

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[21] It is possible that when rare species have unique niches, or support functions that may become important under new environmental conditions, they are important for ecosystem functioning -- but evidence for large effects on ecosystem functioning is lacking, maybe because the time scales involved for this to show are longer than most ecological studies.

[22] However, this does not negate the validity of existential arguments for biodiversity, nor the possibility that rare species may be useful for functional ecosystems under novel environmental conditions in the future, i.e. option, insurance or resilience value (see above). Nevertheless, these arguments are based on a possible future value and hence not possible to measure until it's too late, a dilemma for all decision-making.

[23] On a course on the history of ecological ideas, one of the bright students asked Janne "... you have been active in Biodiversity and Ecosystem Services research for 20 years. What's your opinion? Was it a waste of time?". Janne had to ask for a night's grace. He came back the next morning thinking that "it was not a complete waste of time, but we forgot the key question asked by John Lawton 'What do species do in ecosystems?' 1994 and framed the problem as a diversity/species richness question. Which was the wrong framing to study the importance of organisms for ecosystem functioning. So it took us in the wrong direction for a decade or so."

of such interactions on the systems that the species are part of. This is what community ecology has been doing for several decades by studying traits (including functional traits; e.g. Loreau et al. 2001; Lavorel and Garnier 2002; Suding et al. 2008). It is by understanding the complexity of ecological communities that we can understand what species do in ecosystems (Lawton 1994), and which species are important for what we would like ecosystems to do — be it benefits to humans, society or just sustain nature in a state less impacted by humans. A potential and unsolved problem is that communities and ecosystems may be examples "middle number systems" that are too complex to find simple and general patterns in (Lawton 2000). Ecological generalities may be few and often valid only for restricted systems in space and time. Consequently questions and answers need to be anchored in local conditions and are subject to temporal (historical) contingencies.

A consequence of all this is that the question whether we should focus on biodiversity in the farmed areas, or on biodiversity in the non-farmed or less intensively managed landscape elements, is probably the wrong question. This on the surface simple question does not have a simple answer – if any answer at all.[24] Answers will depend on which organism groups or taxa that are studied, how the species are interacting in the local context, and the intensity of land use in different habitat types. In addition, the broad term "landscape" harbours large complexity in itself. A "forest" landscape element can be anything from an insect-rich old-growth southern deciduous forest with a soft edge towards arable land, to a planted monoculture of spruce or fast growing Eucalyptus trees, in which insects usually are few and when abundant mainly a few pest species.[25] In the former case, landscape elements not part of the farming system may contribute overwhelmingly to community composition and biodiversity at the landscape level and potentially influence farmed areas, while in the latter case such elements will be of no or very little consequence compared to a lower intensification and diversification of the farming systems, i.e. how we "choose" to farm the available land to produce food and other things that we "need".[26]

For these reasons, to focus biodiversity policies and research primarily on species richness is narrow-minded, to be blunt, and especially Janne has been guilty of this.[27] Biodiversity policies are supposed to conserve, support and sustain both biodiversity as such and

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[24] Paul Keddy, in his book Competition (Keddy 1989), suggested that some, perhaps many, ecological questions are framed in the wrong way. Referring to Buddhism he suggested that answers could be neither "yes" nor "no", but "mu", implying that the questions are put in the wrong way, cannot have a clear answer and need to be re-framed.

[25] On one hand, most ecologists already know this, but it is still not enough put into practice. Most analyses of landscape retort to simple measures of landscape complexity or heterogeneity that suffer from similar problems as species richness measures. The measures don't catch the complexity of landscapes, their various elements and social-ecological relations very well. Some examples are the landscape measures used in Persson et al. (2010), Birkhofer et al. (2018), and Marja et al. (2022).

[26] These choices and needs do not, of course, have a common "we" – our choices and needs are dependent on the society that we are part of (see below) and who has the power to impose choices and needs on an "us" that is diverse, unequal and often powerless until a social movement hints otherwise or turns the world upside down.

[27] Janne refrains from adding any references to support this claim of guilt; anyone interested can go through most agricultural ecologists' publications and find ample evidence for such intellectual sloppiness.

ecosystem services, the use of biodiversity for human benefits (e.g. IPBES 2019, 2022).[28] As summarised by Emmerson et al. (2016), "focusing only on species richness might not provide sufficient detail regarding the effects of land-use intensification on biodiversity in and around agricultural land. In contrast, in-depth analyses within groups of species with different traits and conservation value would significantly advance our understanding of agriculture related drivers of biodiversity change".

Hence the question raised in (Tscharntke et al. 2021) whether farming system or landscape contributes most to biodiversity is important, but only if we broaden our views. The answers will depend on context, on which organisms the researchers value or are interested in (which is an implicit value judgement that we as scientists sometimes don't want to discuss, but should give more consideration), and on whether we can leave the diversity as richness issue behind and start asking questions about the composition of and interactions in the communities and ecosystems that we are concerned with and worried about. In that process much of the work of Teja provides a foundation from which research can find new directions.

However, if the goal is to change production systems such as agriculture, farming and food production, it is not enough to understand ecology. If we want to transform systems we must understand the complex social-ecological food systems and what maintains them in the present unsustainable state. Which takes us outside the purity of ecology and biodiversity and into the world of interdisciplinarity, a place where they do things differently from what most ecologists are used to.

6.4 The nature of modern agricultural systems

Our social science colleagues working on understanding agricultural systems and landscapes have criticised, in our view rightly so, ecologists as often being overly meticulous when measuring landscapes and diversity, but largely ignorant of what farmers do and can do, and of the implicit assumptions we make about how production systems are shaped. Examples are our views on if and how policies can change behaviour of actors in the food systems, the impact of purely ecological and often top-down ecological advice to policymakers and practitioners, and our assumptions about trade-offs between, for example, food production and biodiversity, or land sparing and land sharing (see above). A basic question that many landscape ecologists, including us, has not addressed very clearly is what it is that drives agricultural systems and food production towards intensification, in particular in the Western world but also globally.

6.4.1 Locked in intensification

A large amount of research on intensification of agricultural and food systems has been performed, largely outside the narrow scope of biodiversity, ecosystem services, and landscape ecology, but anchored in perspectives from sociology or agroecology (Vanloqueren and Baret 2009; Clapp 2015; Kuokkanen et al. 2017; Anderson et al. 2020; Mortensen and Smith

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[28] This has been important for policy ever since the 1992 Rio Convention (CBD) – to *conserve* and *sustainably use* biodiversity.

2020).[29] It is well established that major parts of agricultural policy (including the policy to leave it to the market), farming methods and composition of agricultural landscapes are driven by agrobusinesses and multinational companies, with lobbying connections extending deep into, e.g., EU decision making institutions.[30] This has led to a rigidity or lock-in of modern agricultural and food systems, built on a productivist view of agriculture that perhaps was an appropriate policy in the 1950s after World War II, but is increasingly questioned (e.g. Vanloqueren and Baret 2009; Kuokkanen et al. 2017; Mortensen and Smith 2020; Goldstein et al. 2023). The productivist narrative is emphasizing the necessity of continuing intensification and industrialisation of agriculture, based on increased use of large-scale technology and inputs, such as energy, fertilizers, pesticides and herbicides, to meet a projected increased global demand for more food, usually more meat and processed food, and industrial profitability. It has been contrasted to a sufficiency narrative which argues that such an intensification will undermine the ecosystems that support food production and also generate unacceptable environmental externalities, including exacerbated climate warming (Freibauer et al. 2011; Allaire and Daviron 2020). The sufficiency narrative emphasises a need for large structural changes in farming and food systems, including changes in demand towards more plant foods and less meat consumption in the richer world, a general progress towards less impact on ecosystems, less consumption, and a lower human footprint, especially from the western lifestyle. It could be characterized as a controlled sustainable de-growth of agriculture (Gomiero 2018; Otero et al. 2020; Moranta et al. 2022), but its connection to de-growth remains to be further explored.

The lock-in perspective describes how today's agriculture is following an entrenched path characterized by fossil energy dependent infrastructure, pesticide-herbicide-fertilizer farming and a cognitive technology-dependent trap that — from a social-ecological perspective — impedes transformation to other, more socially, environmentally and ecologically sustainable system configurations (e.g. Mortensen and Smith 2020). While there is a kind of transformation present also in the productivist narrative, the transformations discussed are rooted in a modernity framework that is culturally, technologically and economically determined by the powerful businesses and actors in the present system; actors profiting from certain technological transformations that sustain profits but not much else, and do not threaten the status quo (Patel and Moore 2020; Béné 2022).[31] The power over this

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[29] However, these perspectives have only to a limited extent, if at all, included the knowledge of landscape ecologists in their analyses, which shows how relevant disciplines for agricultural sustainability often have had too little contact with each other.

[30] This can be clearly seen in the discussions on the EU Farm-to-fork and Biodiversity strategies and how they relate to agricultural landscapes, where each take produced increasingly watered down versions of the initially quite radical propositions on agroecology and regenerative agriculture (e.g. Elmqvist et al. 2022); for critical discussion see, e.g. Corporate Europe Observatory (2022-03-17) `https://corporateeurope.org/en/2022/03/agribusiness-lobby-against-eu-farm-fork-strategy-amplified-ukraine-war`, Rudquist G. Bglc eye (2021-09-15) `https://www.su.se/stockholm-university-baltic-sea-centre/web-magazine-baltic-eye/eutrophication/the-eu-farm-to-fork-strategy-what-is-happening-1.606756`, and Askew K. Food Navigator (2023-03-13) `https://www.foodnavigator.com/Article/2023/02/13/Is-Europe-s-Farm-to-Fork-strategy-in-trouble-Political-resistance-is-threatening-to-derail-the-process`) (All accessed in May 2023).

[31] This of course implies that the term economic sustainability needs to be relegated from the pillars of sustainability to one of many tools in our toolbox, as our friend Thomas Hahn has often emphasised in

system is unevenly distributed, with the actions of individual farmers being coerced by powerful agents further up in the food chains. This narrows their choices and how they can transform farming on their piece of land.

Within the productivist narrative the obvious need for some kind of transition to a believed (or hoped for) sustainable food system or society is discussed in different ways. Within the constraints of the present corporate-driven system, we can find those believing that capitalism can be harnessed to do the job to solve the problems it created, such as ecological modernisation (Mol et al. 2014; but see Foster et al. 2010) and ideas similar to Robert Reich's 'saving capitalism' from itself (2015). Others discuss more drastic and radical changes in farming systems and policies. These range from, for example, agroecology as an adaptive approach in pursuit of a more just and sustainable food system (Anderson and Rivera-Ferre 2021), organic agriculture in all its colours from intensified grey to outstanding green (Reganold and Wachter 2016; Seufert and Ramankutty 2017), regenerative agriculture – whatever meaning it has (Giller et al. 2021; Elmqvist et al. 2022) – all the way to more utopian ideas of leaving the imperative of continued growth behind through de-growth, producing food systems that are vaguely formulated (Svenfelt et al. 2019), or leaving the capitalist system for ... yes, for what? The track record of past socialist or communist agriculture warn us that these did not leave the productivist paradigm at all, exacerbating the human-nature conflict rather than finding a solution.

The consequence of this large-scale lock-in is that in order to change current agricultural systems towards more sustainable ones, a broader perspective than a purely biodiversity-friendly landscape one is needed. This entails a more in-depth understanding of the drivers of biodiversity loss and possible ameliorative policies in production landscapes in general –agricultural as well as forestry landscapes. It has been highlighted in the IPBES reports (2019; 2022) as well as by IPCC (2014) that biodiversity loss and climate change have similar underlying drivers, namely the last 50-100 years of increased resource use, a growth and consumption oriented global economy, and intensification of land use. This means that the drivers are to a large extent social, and that solutions are complex and need to be based on analyses and understanding of social-ecological systems.

The concept of lock-in or path dependence implies that the present drivers of biodiversity loss are more or less stuck in the present situation. The powerful actors are likely to have no intention or incentive to change except along the present trajectory, i.e. continuing along an intensification and technological innovation path. It also means that they are unlikely to show much interest in contrasting perspectives on agriculture, neither listening to them nor taking them into consideration when they plan ahead, make or give advice on investments. They are likely to grab any argument for staying on this path, no matter whether these are based on reality and facts or not.

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lectures and conversations. The economic drivers of the globalized food and agriculture systems have the goal to make profits, they do not wish us well, and they are unlikely sustainable socially and environmentally (e.g. Patel and Moore 2020).

6.5 Some possible futures for agricultural biodiversity

Much of the preceding discussion is oriented towards future agricultural systems and landscapes, and how well they might conserve and utilize biodiversity, and ecosystem services related to parts of that biodiversity. Many ecologists, including Teja, seem to assume that there can be a good future for biodiversity, and implicitly that policymakers and agrobusinesses will listen to the advice from landscape and agro-ecologists. We agree that this is desirable, although we have problematized some of the recommendations that seem to emerge from Teja's and others' work. Here we want to end by pointing out that future agricultural production systems can, for better or worse, handle and utilize biodiversity and ecosystem services in very different ways, depending on how society and production is organised and the responses to the climate and biodiversity crises at regional, national or European (continental) levels. The question then becomes which of these systems – if any – best combine biodiversity goals with social and environmental sustainability goals.

The Swedish research program Mistra Food Futures is developing a set of goal-seeking scenarios for Swedish food production that can meet multiple goals by 2045 (Gordon et al. 2022). The goals are related to climate (net zero emissions by 2045, i.e. meeting the Paris agreement of no more than 1.5°C warming), biodiversity (basically, no further reductions in birds and pollinators, and reduced pesticide use) and health (diet according to EAT-Lancet).[32]

Scenarios are meant to open up a discussion about possible futures. However, since scenarios are also about taking power over the future, they also close or hide futures by implicit or explicit selection of which factors and alternative scenarios are included in the discussion. They are not predictions, but possible trajectories into the future, and hence anchored in today's discourses rather than in all possible futures. Scenarios can be based on today's societal structures to protect the status quo and prevent transformations, or emphasize alternatives to today's society and policies. The latter type of transformative scenarios have been characterized as acts of "imagination, love and resistance" and of care toward future generations (Andersson 2018). Therefore, scenarios may say more about today's views of the world than what future generations may think, but still scenarios like these are structured considerations of the future that hopefully include important aspects such as climate change, food systems, limits to resource use as well as the future for biodiversity, a combination that is hitherto quite rare in the present menagerie of scenarios.[33]

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[32] The targets for the goals were pragmatically set to be able to follow indicators for them. For biodiversity in Sweden, birds are monitored by a national program since 1975, pollinators were supposed to get a national monitoring program but this was recently (early 2023) halted by the new right-wing government drastically reducing funding for environmental monitoring. Pesticide use is also monitored nationally. The targets can be questioned but reflect global targets, the state of the art of monitoring and to some degree ecological importance in agriculture. See Gordon et al. (2022).

[33] This paragraph is partly based on a book chapter in Swedish (Bengtsson 2021), available from the first author on request.

Fig. 6.2: Summary of four scenarios for Swedish agriculture 2045, with major factors related to biodiversity goals indicated. For details, see text and Gordon et al. (2022).

Four scenarios were developed (Fig. 6.2). They represent different ways in which a national food system might simultaneously aim to meet the three goals of climate, biodiversity and healthy diets. They can be briefly summarized as:

1. *Food as industry*, in which Swedish agricultural products are marketed globally as "outstandingly sustainably produced", with support from the government and private sector. This implies a special kind of intensified agriculture and larger food industries in Sweden, improvements in productivity and technology, but at the same time less Swedish meat consumption. Thus it requires that Swedish meat and dairy replaces less environmentally friendly production, mainly in other EU member states, which makes it possible to reach climate goals through substitution effects. The health goal is met by lower meat consumption nationally and more plant food. Biodiversity goals are reached by increasing meat and dairy production from semi-natural grasslands, but the intensification of farming systems makes it problematic to enhance diversity and ecosystem services in arable land, reminiscent of a policy that probably will focus on landscape complexity. Whether this qualifies as sustainable production is unclear, and may rely on marketing rather than real biodiversity and ecosystem service friendly farming. This scenario is largely a continuation of present trends in Swedish agriculture, and hence represents a business-as-usual scenario embraced by many (but not all) mainstream food system stakeholders.
2. In *Food as technology*, diet change by technology innovation has transformed food systems. Power belongs to the transnational corporations that produce, process and sell novel foods. New technologies such as artificial meat, microbial proteins, and food printing allow personalized diets, and plant-based products replace "old foods". While

Swedish food processing increases, agricultural production declines, which opens up for reduced agricultural land area, less meat production mainly from semi-natural grasslands, and rewilding at the same time as plant production for the novel foods intensifies. Whether this will lead to land sparing or land sharing landscapes is unclear. National governments have less power over land use, and the idea of rewilding might be usurped as an excuse for more intensive forestry, since climate goals are fulfilled by a combination of less livestock, low-carbon transportation, carbon farming, rewilding and forest growth. Health goals are met with new diets and artificial products, which have to submit to some regulation at the EU level since national governments are weak. The major contribution to biodiversity goals comes from rewilding, grass-fed meat, and regenerative farming on parts of the arable land, all of which contain plenty contradictions that might be resolved by policies and regulations. However, governments and the public have little power in this scenario.

3. *Food as culture* assumes that Swedish and international food systems drastically transform by social movement responses to climate disasters and the biodiversity crisis. These changes are brought about by an emphasis on global and national equity, self-sufficiency and environmental justice, and placing food, farming and nature at the centre of local and regional culture and identity. The transition involves new rural-urban and human-nature interactions, movement to smaller cities around which peri-urban and rural living is supported by social policies. Food and food production is diversifying locally and regionally, less intensive agroecological farming systems are supported by the public and agricultural policies. With the help of technologies such as digitalization, rural jobs and multifunctional landscapes have been created. Climate goals are reached in agricultural landscapes through regenerative farming, agroforestry, less consumption of meat and dairy, which is mainly produced on permanent and semi-natural grasslands that sequester carbon. This diversification of farming, and a general decrease in intensification across whole landscapes, including more permanent biotopes, fulfils ambitious biodiversity goals. In this rather rosy scenario technologies that support better work conditions and environmentally friendly farming are prioritized, but it can also contain elements of de-growth (Svenfelt et al. 2019). It requires that governments and especially public social movements become stronger than today.
4. In the *Food forgotten* scenario, EU-driven climate policies drive European food systems. Food and how it is produced is constrained by the necessity for large-scale climate mitigation. Farming and food industry in Sweden are of little political and social importance. Climate taxes change diets towards less meat and dairy and more plant-based food, and land use focuses on climate mitigation and carbon sequestration. Some agricultural land is converted to bioenergy production. Afforestation and wetland restoration further decreases the area of arable land. Farming likely becomes a kind of intensive regenerative agriculture with large areas of permanent crops, depending on regional and local landscapes. Biodiversity goals are not prioritized but still met, mainly through restoration of wetlands, grasslands and forests. The latter two may have low or medium biodiversity value, but C-sequestration of forests implies longer rotation periods which enhances biodiversity and several ecosystem services (Jonsson et al. 2019), introducing a partial rewilding that increases diversity of forest species which may or may not be regarded to compensate for losses of biodiversity on arable land.

While none of these scenarios may be realized,[34] they show that it is fairly easy to imagine several drastically different agricultural landscapes for biodiversity by 2050, driven by different combinations of governmental policies and regulations, technological change, industry and market forces, and social movements. The biodiversity targets are met in different ways in different scenarios, for example larger areas of grazed grasslands (scenario 1 and 3, and perhaps 4), less intensive farming and new farming systems (3), restoration and rewilding (2, 4; partly dumping biodiversity responsibility on the forest sector). The ensuing uncertainty and local specificity of future landscapes caution against thinking about future biodiversity-friendly landscapes without taking society and its development and relation to ecosystems and nature into account. Although the scenarios suggest that the future is open, the realized future may not be decided by those who understand or care about biodiversity at all. It is up to ecologists and environmentalists to make an active choice to influence how future landscapes will develop as social-ecological systems. At the very least, scenarios like these force us to discuss what kinds of futures that our often unspecified "we" want, and perhaps more importantly which futures that can be considered as clearly undesirable.[35]

6.6 Final comments

We hope to have shown that the questions on farming systems and agricultural landscapes asked by Teja in his research have been important to ask. They have driven a lot of excellent agroecological and landscape research, even though many of the questions remain to be answered. We have highlighted some complexities of farming systems and agricultural landscapes that we believe should be included in future studies of how to transition to biodiversity-friendly production landscapes, and emphasized the importance of expanding our view on landscapes as parts of social-ecological systems.

Important remaining questions concern, for example, the importance of farming practices for biodiversity-based food production, how different local farming practices can be scaled up to agricultural landscapes, and what the landscape-wide ecological effects of such expansion might be. We also need a better understanding of how the qualities of seminatural habitats, grasslands and crop fields affect biodiversity, and how farming practices and landscape management complement each other. Biodiversity studies need to focus more on the species that make up biodiversity, their traits and interactions in food webs, and thus the role of species and community composition for ecosystem functioning, rather than on simplistic measures of taxonomic richness.

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[34] The scenarios can be questioned as they make a number of simplifying assumptions, of which some are important to state: All of them assume continued economic growth, although this is less prominent in Food as culture; they also assume that no rebellion or migration from the global south in response to increased global warming will take place. More scenario-specific assumptions are that: Policies are possible and do the right thing(s); Social movements can make a difference; Novel technologies will fix the climate and sustainability; Technology food will be socially accepted; Electrification of Swedish society is possible (but none considered electrification in the rest of the world).

[35] For food systems, the French Agrimonde scenarios are exemplary in their discussion of scenarios that are clearly unsustainable, hence undesirable, and which futures that may be sustainable (Le Mouel et al. 2018).

Finally, ecologists working in agriculture and other production landscapes should account for and better understand how society, people and ecology interact, primarily through working together with scientists from other disciplines, especially social sciences. By incorporating important social and political drivers in our studies, ecologists can ensure that ecological knowledge is used in social discourses and policies, rather than remaining at the margins of decision-making. Hence Teja's questions will require further work and re-framing, presumably for generations, before they can be answered – we live in exciting but also depressing as well as hopeful times.

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Part II
Pollination in Agroecosystems

Chapter 7

Shaping research on pollinators and pollination between 1983-2023: from bees in the nature reserve Snaakenmoor to pollination deficits of global crop production

Alexandra-Maria Klein & Ingolf Steffan-Dewenter

Abstract Almost 40 years ago Prof. Dr. Teja Tscharntke started contributing to the discussion of the importance of bogs for nature conservation with a faunistic study on bees. Today, both bogs and bees are more threatened than ever by human activities. Bogs and pollinating bees are needed to mitigate extreme climates and food production gaps. In our essay, we describe how Teja shaped pollination research with his innovative ideas and trained pollination ecologists across the globe. He initiated original research in temperate and tropical countries and conducted systematic reviews and meta-analyses to highlight the importance of pollinator diversity to mitigate deficits of global crop production in changing environmental conditions.

7.1 Introduction to the research of Teja Tscharnkte on bees and pollination

Anthropogenic interventions led to the destruction of many ecosystems in our open cultural landscape dominated by agriculture (Poschlod 2017). One ecosystem of high relevance for climate mitigation and biodiversity is the raised bog (Joosten et al. 2017; Wilson et al. 2022). The decline of raised bogs in the open landscape of Germany threatens many organisms including wild-living insects (Vítovcová et al. 2022) and likely also wild bees.

In 1984, Prof. Dr. Teja Tscharntke published his first paper related to landscape-scale bee conservation. Interestingly, his first bee research was conducted in a raised bog. He used pan traps and netting to describe the bee community of the nature reserve "Schnaakenmoor" near Hamburg. The nature reserve consisted at that time of bogs with large dunes providing nesting opportunities for bees. He found 33 bee species with three stenothermic

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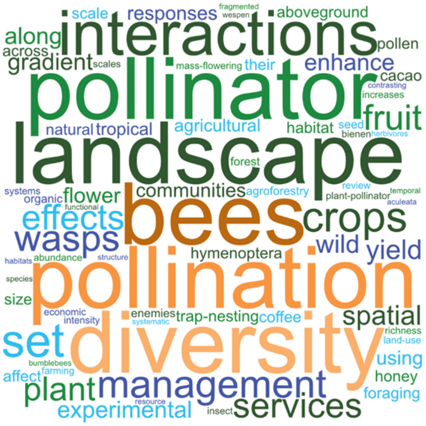

Fig. 7.1: Word cloud generated from titles of the overall 126 publications of Teja Tscharntke in the field of pollination and pollinators until early 2023. The word cloud was generated by WordClouds.com. Shown are all words occurring at least four times. We deleted the following words: and, for, the, their, from, with, but, not, than. Words were used in singular or plural only.

cold-adapted species, *Andrena ruficrus* (Nylander, 1848), *Halictus fratellus* (Pérez, 1903) and *Halictus rufitarsis* (Zetterstedt, 1838), and an Atlantic distributed species, *Andrena angustior* (Kirby, 1802). Hence Teja highlighted almost 40 years ago the importance of low-temperature bogs for biodiversity conservation with a focus on bee pollinators. Looking at our temperatures today and temperature scenarios in the future, Teja was ahead of his time when he called for the conservation of bogs in general and of cold bogs for pollinator conservation in particular.

Overlooking Teja's 126 (out of a total of over 465) publications published until January 2023 and related to bees, pollinators and pollination, we see in a word cloud (Fig. 7.1) that his research of the last 40 years focused on bees among other pollinators, with a strong focus on pollinator diversity and interactions. The word cloud also highlights Teja's early recognition of the importance of the landscape context when evaluating bee communities and their functional interactions with flowering plants. Words like "fruit", "crops" and "yield" indicate the applied nature of his research and his group in an agricultural context. His research in the open landscapes shaped a new area of agroecological research — with a focus on the functional diversity of organisms in agricultural landscapes.

7.2 The early pollinator research of Teja Tscharnkte in Karlsruhe

Teja moved from Hamburg to Karlsruhe in 1985 where he worked as Assistent Professor (Scientific Assistant), where he continued his research on insects and their trophic interactions in Poaceae, with a focus on common reed (*Phragmites australis*) (e.g. Tscharntke 1988, 1989a,b). In line with the main fashion of international ecology – while modern ecology was nearly non-existing in Germany at the time – Teja was interested in insects on plants, their trophic interactions, and drivers of population dynamics. Importantly, his work addressed major ecological concepts of this time such as density dependent population regulation, effects of habitat fragmentation (Tscharntke 1992) and later mechanisms of successional changes (Tscharntke and Greiler 1995). But at this early stage of his career he also laid the ground for various future research directions, including pollination ecology.

His first PhD student, Hans-Joachim (Jogi) Greiler, worked on grass-inhabiting insect communities on set-aside fields as part of Teja's first agroecological project, but was also an enthusiastic faunist. He reassessed the change of a local bee community in an abandoned vineyard in comparison to historical observations of a regional taxonomist from ca. 1900. In Karlsruhe, Teja was the first to offer teaching and practical courses in terrestrial ecology which attracted many students and lead to a lively group of Diploma and later PhD students.

With his typical creativity, Teja explored new topics of which many will even nowadays sound quite familiar. For example reed stems are not only inhabited by gall makers but also used as nesting site by a few specialised bee species such as *Hylaeus pectoralis*. This lead to the idea of using bundles of reed internodes as a standardised nesting resource for bees and wasps to evaluate their diversity and biotic interactions in different habitats (Gathmann et al. 1994; Tscharntke et al. 1998), laying the ground for a still broadly used and highly valuable model system on multi-trophic interactions (Staab et al. 2018). By advertising trap nests for research in agro-ecology and conservation, Teja followed the fascination of bees and wasps by Jean-Henri Fabre (1823-1915), a French scientist, entomologist and novelist of the best-selling book "The Mason-Bees" (Fabre 2001). "Fabre's bee hive" and "Teja's trap nests" were also used as models for "bee hotels" and the reed trap nests by Teja were more attractive than bee hotels made of other materials (von Königslöw et al. 2019) and stimulated different researchers to evaluate different designs of trap nests for wild bee monitoring (Westphal et al. 2008; MacIvor 2017). Trap nests were used in different projects lead by Teja e.g. the Bioteam BMBF project – Evaluation of biological diversity of land-use systems in a mega-diverse region of Ecuador (e.g. Tylianakis et al. 2005), but also in national biodiversity monitoring projects such as MonViA – Monitoring of biological diversity in agricultural landscapes in Germany.

Further projects, comprised e.g. experiments with ant lions and the assessment of bee and wasp communities in sand dunes at different successional stages (Jörg Wesserling 1995, unpublished PhD thesis), experimental placing flowering plants on traffic islands to assess pollinator communities in urban environments, and with Prof. Dr. Ingolf Steffan-Dewenter (today at University of Würzburg) the assessment of butterflies, and bees on set aside fields (Steffan-Dewenter and Tscharntke 1997, 2001).

7.3 Early research on pollinators at the landscape scale in Göttingen

In 1993, Teja moved to Göttingen and established the Agroecology group. He was in the lucky position that ten group members from Karlsruhe decided to join him, although for unknown reasons only male researchers. In the pioneering phase in Göttingen the group laid the basis for much of the spatial ecology research which is nowadays an important part of landscape ecology. One pioneering work at this time was an experimental project on the relationship between bee body size and foraging distances (Gathmann and Tscharntke 2002), already directing to larger landscape scales. At the same time, calcareous grassland in the region were selected as study system, first to assess resource competition between wild bees and honey bees (Steffan-Dewenter and Tscharntke 2000), but later also as an excellent model for research on effects of habitat fragmentation on butterflies and other pollinator taxa (Steffan-Dewenter and Tscharntke 2000). Teja's first publication on plant pollination also used calcareous grassland to investigate the effect of increasing distance from these source habitats on flower visitation and seed set (Steffan-Dewenter and Tscharntke 1999). Teja's break through to what is nowadays known as a landscape approach was first achieved in the area of his core interest at this time, plant-herbivore-antagonist interactions, with a pioneering study on biological pest control in oilseed rape (Thies and Tscharntke 1999). Soon, a similar approach was used to study other functional groups and biotic interactions including pollinators, pollination, and seed predation (Steffan-Dewenter and Tscharntke 2001). A further important step was the parallel consideration of multiple spatial scales to link foraging or dispersal distances of different taxa to landscape structure (Steffan-Dewenter and Tscharntke 2002). Nowadays, pollination ecology at landscape scales is still a lively research area with continuously emerging new aspects and many unsolved questions, underpinning the long-term value of Teja's work for spatial ecology.

7.4 Moving to crop pollination research

The first research of Teja in a tropical region after his expeditions as a student to Peru started in Sulawesi, Indonesia. Teja travelled with Ingolf to Sulawesi for the first time in 1997 and they discussed their potential contribution to a Collaborative Research Centre for an application with the German Science Foundation. They came back with a life-long fascination for tropical ecosystems and with many ideas directing to their core interests in plant-herbivore-antagonist and plant-pollinator interactions, and recognised the huge research gaps in tropical agroecology including pollination of the major cash crops cacao and coffee. Unfortunately, the grant application was rejected in the first round, but Teja engaged a Diploma student to start working in the region on parasitism rates of butterfly pupae along gradients of land-use intensity in cacao and coffee agroforestry systems, an idea stimulated by the many small caterpillar farms in the backyards of the Indonesian smallholders.

Prof. Dr. Alexandra-Maria Klein (now at University of Freiburg) was encouraged by their enthusiasm and aimed to address this topic in her diploma thesis. Unfortunately, she hardly found any parasitoids in the pupae and the caterpillars ate so much that she could not keep up with them to bring enough food to the study sites. So, Teja, Ingolf and Alex came up with the idea that they could observe bees on coffee flowers instead leading to Teja's research era on coffee pollination.

7.5 Coffee pollination

Teja's crop pollination studies started with coffee, showing, on the one hand, that the diversity of solitary bees visiting coffee flowers increased with increasing light intensity in agroforestry systems. On the other hand, social bee diversity on coffee flowers was decreasing with forest distance (Klein et al. 2002). Consequently Teja and colleagues conducted pollination experiments on the two dominant coffee species *Coffea arabica* and *Coffea canephora* and found pollination deficits in both coffee species (Klein et al. 2003c,b,a). They conducted pollination treatments of open pollination, where insects had access to coffee flowers; wind pollination, where insects were excluded by gauze bags (of different diameters as shown in the picture) but pollen could pass when transported by wind; cross pollination, where pollen were transferred by hand from one coffee plant individual to another; self pollination with pollen of the same coffee plant but different flowers; self pollination with pollen from the same flower; and no manipulation to allow for spontaneous selfing as control (Fig. 7.2; Klein et al. 2003a). Initially, developing fruits were then counted in proportion to the number of flowers in the treatments. Like indicated in the literature, *C. canephora* was not able to set fruits with spontaneous selfing or any of the two self-pollination treatments and fruit set with wind pollination was lower than with hand-crossed or open pollination. *Coffea arabica* was able to self-pollinate but highest fruit set was reached in the hand-crossed and open pollination treatments. Hence, both coffee species need hand-cross or insect pollination (Fig. 7.2). This was surprising as only lowland coffee was described to benefit from insect pollination (Free 1993).

In the pollination experiment conducted in Sulawesi, no significant pollination deficit was shown when comparing open versus cross pollination considering all treatments but when comparing the open versus the hand pollination treatment only, *C. canephora* but not *C. arabica* showed significant pollination deficits. Nonetheless, the diversity of bee species was highly correlated with initial fruit set of both coffee species and this was mediated by forest distance (Klein et al. 2003c,b). These coffee studies were one of the first indicating the importance of functional diversity for agriculture. Although the results were most important not only for ecology but also of interest for agronomy, reviewers, and also Teja himself, criticised that initial fruit set can blur potential pollination effects on fruit production and economic yield (Bos et al. 2007). Hence, Teja continued with his coffee pollination research and travelled to Ecuador with his Bioteam project, led by Prof. Dr. Roland Olschewski (now at Swiss Federal Institute for Forest, Snow and Landscape Research WSL Zürich), and showed that bees are not only important for setting fruits but also for coffee bean production at the field scale (Veddeler et al. 2008). After Ecuador he decided to study cocoa pollination when back in Indonesia, maybe because he has a fondness for midges over bees?

In a recent review, Teja showed, with an international team, coffee pollination deficits across the globe, but the negative effect of increasing forest distance on the flower-visiting bee species on coffee was not consistent across countries (Moreaux et al. 2022). Despite this, the coffee pollinator data from Sulawesi revealed that the density of the forest is also an important driver for the coffee pollinator community (Moreaux et al. 2022). We could not refer to all coffee pollination studies of Teja here, but we show that his coffee pollination research spans a publication period of 20 years, meaning more than 20 years of research

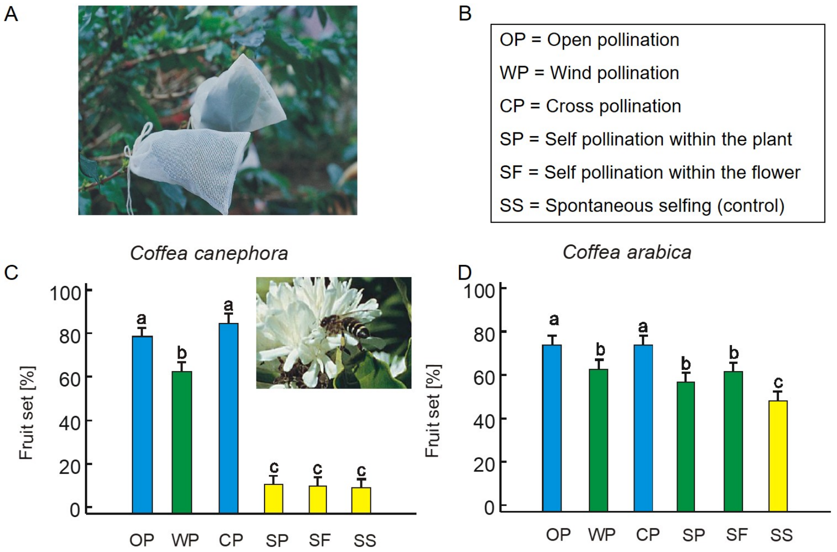

Fig. 7.2: Pollination experiments on lowland (*C. canephora*) and highland coffee (*C. arabica*) were conducted in 2000 and 2001 in Sulawesi, Indonesia. A) shows bags to exclude insects and insects and wind pollination. B) gives the abbreviations of pollination treatments used in C) and D), which present significant differences between pollination treatments using ANOVA on the response variable initial fruit set (Klein et al. 2003a).

on coffee pollination by Teja, his great team, and collaborators from different places of the globe.

In German agricultural landscapes, Teja's group focused on understanding how bee pollination is influenced by agricultural and landscape management using potted radish and mustard plants (Steffan-Dewenter and Tscharntke 1999) and with Prof. Dr. Andrea Holzschuh (now at University of Würzburg) and Prof. Dr. Carsten Dormann (now at University of Freiburg) on the pollination of wild plants (Holzschuh et al. 2011). An important innovation was the consideration of spillover effects between crops and conservation habitats, demonstrating that wild plant populations in fragmented habitats might face reduced reproductive success as a consequence of competition for pollinators (Holzschuh et al. 2011). Later he studied in collaboration with Andrea, Prof. Dr. Yann Clough (today Lund University), Prof. Dr. Catrin Westphal (Teja's successor in Göttingen), among other authors, the role of bees in pollinating strawberries and showed that pollination is not only influencing crop quantity but also quality (Klatt et al. 2014b,a; Wietzke et al. 2018).

This is only a small fraction of Teja's highly influencing crop pollination work. He continued asking several research questions related to crop pollination deficits across the globe with the goal to find landscape management strategies to mitigate crop pollination deficits. Crops of his original pollinator and pollination research included, for example, pumpkin and cucumber in Sulawesi (Hoehn et al. 2008; Motzke et al. 2015), cocoa in Sulawesi and Peru (Toledo-Hernandez et al. 2021; Vansynghel et al. 2022), macadamia in

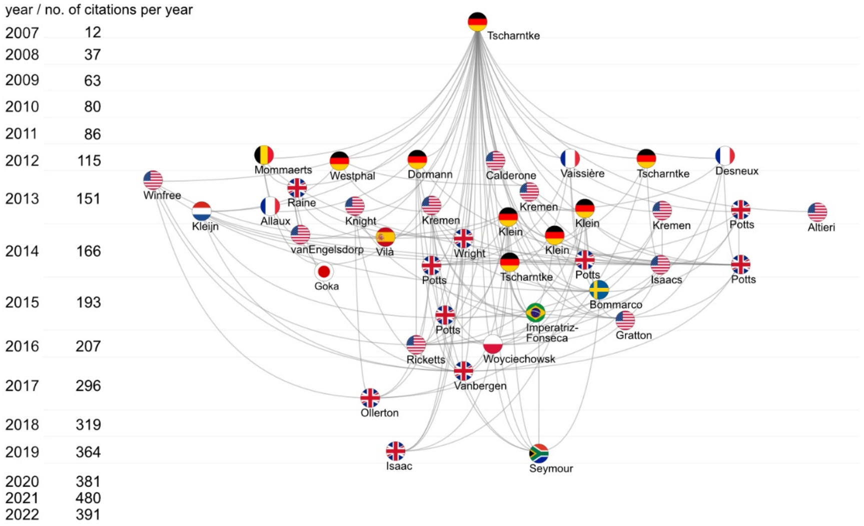

Fig. 7.3: Teja Tscharntke's citation network based on Klein et al. (2007) as his most-cited paper in the field of pollination and pollinators. The network shows the 39 most-cited papers (more than 80 citations) citing the original paper in all years between 2007 and 2022. We used CitNetExplorer for the graphical demonstration based on Web of Science data. Shown are the senior authors (defined as researchers with high contribution in shaping research and conclusions other than Teja) of each paper citing Klein et al. (2007) and their respective countries at time of publication indicated by the flags from Pixabay. On the left-hand side, the publication dates followed by the total numbers of citation for each year are presented.

South Africa (Grass et al. 2018) and oil palm in Sumatra (Li et al. 2022). All these and other original research studies of Teja led to several synthesis projects: for example, Teja and colleagues conducted a meta-analysis and showed pollination deficits in apple, with fruit set deficits being strongest in Asia and less severe in Europe (Olhnuud et al. 2022). In a quantitative review on cocoa, Toledo-Hernandez et al. (2017) showed that although midges (Ceratopognids) are the dominant pollinators, a large diversity of insects including bees, flies, wasps, beetles and especially ants contribute to cocoa pollination. One could argue that insect diversity is therefore crucial for us to get tasty chocolate. To close the circle, Teja returned to Peru, the starting point of his endeavour in the tropics, to study pollination and pest control of fine flavour cacao varieties together with Dr. Bea Maas (now University of Vienna) and Ingolf (Tscharntke et al. 2023).

7.6 Highly cited and internationally influencing pollination research

Teja's research on crop pollination was and still is highly influential for many researchers across the globe. We are illustrating his exceptional visibility to the international community of ecologist by creating a citation network of his most cited paper in the field of pollination (cited 3462 times, 13.04.2023 in Clarivate Web of Science):

> Klein, A.M., Vaissière, B.E., Cane, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London, Series B. 274: 303–313.

This paper showed that most crops we consume and which are important at the global market need pollinators for high production values. It also provides in two supplementary lists information on the reproduction system and most important pollinators per crop. Looking at citations for this paper in Web of Science from December 2022 (Fig. 7.3), papers citing this particular paper were also often highly cited. In Figure 7.3 we show the 39 most-cited papers (more than 80 citations) referring to Teja's global crop pollination review. Researchers recognizing this paper are from Teja's own group such as Alex, Catrin and Carsten (being senior authors of the citing research) and from other countries such as Bernard Vaissière (France), Tiffany Knight and Claire Kremen (USA), Adam Vanbergen, Simon Potts (UK), Riccardo Bommarco (Sweden), Montserat Vilà (Spain), Davin Kleijn (Netherlands), Vera Imperatriz-Fonseca (Brazil), among others. As expected, more researchers from Europe and the USA than from developing countries publish highly cited papers. This will hopefully change in the future as Teja educated many junior researchers from the global south and developed countries to successfully conduct their Diploma (BSc, MSc) and PhD theses and mentored many scientific careers until reaching permanent positions (see also Fig. 7.4). We decided to highlight in this figure the senior authors, and not the first authors, as important people shaping the story and conclusions of the scientific findings in research publications. Teja, in our perspective, is a strong research leader acting during his career as the leading person for the majority of his papers.

7.7 The Agroecology group, conclusions, and the way forward

Teja published 126 papers related to pollinators and pollination until January 2023. We all know that this will continue even when Teja is retired. In Figure 4, we present the first authors involved in Teja's research group focusing on pollination studies. The pictures present 44 researchers, 20 men and 24 women underpinning that Teja, as a pioneer in agroecological pollination research, supported women in science. Most of the first authors are German but ten have different nationalities from Europe but also from other continents, indicating that Teja is not only a biodiversity researcher, he also pushes diversity in the academic community of pollination researchers. Many of Teja's scholars are today professors: Ingolf Steffan-Dewenter, University of Würzburg, Germany; Alexandra-Maria Klein, University of Freiburg, Germany; Katja Poveda, Cornell University, USA; Catrin Westphal, University of Göttingen, Germany; Jason Tylianakis, University of Canterbury,

Achim Gathmann	Federal Office for Consumer Protection
Jörg Wesserling	
Ingolf Steffan-Dewenter	Professor, University of Würzburg
Thomas Alfert	Teacher, Mariengymnasium Bocholt
Alexandra-Maria Klein	Professor, University of Freiburg
Andreas Kruess	Federal Office for Nature Conservation
Katja Poveda	Associate Professor, Cornell University
Catrin Westphal	Professor, University of Göttingen
Jason Tylianakis	Professor, University of Canterbury
Dorthe Veddeler	Research and Transfer Services, Univ. Göttingen
Merijn Bos	Embassy of the Netherlands in Germany
Doreen Gabriel	Researcher, Julius Kühn Institute
Andrea Holzschuh	Professor, University of Würzburg
Anne Ebeling	Scientist, Scientific Coordinator, Univ. of Jena
Patrick Hoehn	
Stephanie Sobek (now Stephanie Sobek-Swant)	Charitable Research Reserve, Canada
Janna Groeneveld	Geoinformation Services
Jochen Fründ	Professor, University of Hamburg
Kirstin Krewenka	Postdoc, University of Hamburg
Susann Parsche	PhD Student, University of Halle
Péter Batáry	Professor, Hungarian Academy of Sciences
Anikó Hostyánszki	Professor, Hungarian Academy of Sciences
Björn Klatt	Postdoc, Lund University
Elke Vockenhuber	Ecotoxicologist, BASF
Iris Motzke (now Iris Kormann)	Director Pro Agricultura, Switzerland
Hella Schlinkert (now Hella Ludwig)	Federal Office for Nature Conservation
Claudia Chumacero de Schawe	Gesellschaft für Nachhaltige Entwicklung
Urs Kormann	Senior Researcher, Swiss Ornithological Institute
Christine Venjakob	Project Manager, BfU Dr. Poppe AG
Manuel Toledo-Hernández	Postdoc, Westlake University
Tatiane Beduschi	ADAMA Deutschland GmbH
Ingo Grass	Professor, University of Hohenheim
Anne-Kathrin Happe	Manager, Biologische Station Kreis Unna
Annika Louise Hass	Postdoc, University of Göttingen
Alexander Wietzke	Local Nature Conservation Authority, Kassel
Kevin Li	Postdoc, University of Michigan
Svenja Bänsch	Project Coordinator, Museum Koenig Bonn
Costanza Geppert	Postdoc, University of Padova
Kristy Udy	Student, University of Göttingen
Arne Wenzel	Postdoc, University of Göttingen
Felix Klaus	Postdoc, Julius Kühn Institute
Felipe Librán-Embid	Postdoc, University of Hannover
Julia Piko	PhD Student, University of Göttingen
Annemarie Wurz	Research Fellow, University of Marburg

Fig. 7.4: List of first authors of all of Teja Tscharntke's 126 papers on pollination and pollinators (until January 2023). First authorship was chosen to show the researchers working in agro-pollination ecology educated and collaborated with Teja. If available, photos of the time when the work was published were selected. Affiliations were assigned to the respective author's job held in early 2023.

New Zealand; Andrea Holzschuh, University of Würzburg, Germany; Jochen Fründ, Professor at University of Hamburg, Germany, Péter Batáry, Hungarian Academy of Sciences, Hungary; Ingo Grass, University of Hohenheim, Germany. This list refers only to the first authors of his pollination publications who worked in Teja's group. There are many more professors raised and educated by Teja not named here.

In summary, during the last nearly forty years, Teja has initiated an extraordinary amount of innovative work on pollinators and plant pollination in agricultural landscapes. He managed extremely successfully a diverse group of researchers from different countries and with an increasingly high share of female researchers. With his group he highlighted the importance of landscape management for pollinator diversity and how this influences crop pollination, production but also on hand pollination (hopefully not) as a potential substitute for insects (Wurz et al. 2021). During the last years Teja moved back to his roots of his student expeditions to Peru and performs ongoing research on cacao pollination and pest control in Peru (e.g. Ocampo-Ariza et al. 2022; Tscharntke et al. 2023; Vansynghel et al. 2022) underpinning that more exiting work from Emeritus Professor Dr. Teja Tscharntke is to be expected in the future.

We are highly grateful to have such a wonderful mentor, colleague and friend. Many thanks Teja for exciting discussions and enjoyable experiences as ecologists in the field, during workshops and field trips and while dancing and talking.

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Chapter 8

Linking flower visitation, seed set, and seed predation of *Primula veris* at multiple spatial scales

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Abstract Reproduction of plant populations in fragmented habitats can suffer from pollination limitation or seed predation, but the interplay and relevant spatial scales of these biotic interactions are little understood. We examined pollination service, reproductive success, and seed predation of *Primula veris* L., a self-incompatible, declining plant species on fragmented remnants of semi-natural habitats in an agricultural landscape in Germany. Mutualistic and antagonistic plant-insect interactions were analysed on differently sized patches of *P. veris* populations on calcareous grassland fragments of differing area that were surrounded by agricultural landscapes of differing complexity. Pollinator abundance was positively influenced by factors at all three different spatial scales: i) by increasing size of *P. veris* patches, ii) by increasing area of calcareous grassland fragments and iii) by increasing landscape diversity around fragments. Seed set was strongly reduced in small populations, presumably because low visitation rates in small patches lead to pollen limitation. Seed predation ranged from 0 to 100% of examined fruits and was most profound in large calcareous grassland fragments and moderately increased in diverse landscapes. In conclusion, the spatial structure of plant populations in fragmented habitats shape plant reproductive success, with pollination functions responding to smaller spatial scales than seed predation. Hence, multiple spatial scales have to be considered when analysing mutualistic and antagonistic relationships of rare plant species. Future conservation management schemes to protect rare plants could benefit from the inclusion of patch to landscape scales.

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8.1 Introduction

Almost 90% of angiosperms existing today are pollinated by animals (Ollerton et al. 2011). Their pollinators are in decline due to anthropogenic factors such as land-use change, agricultural pesticides, and invasive species (Kearns et al. 1998; Potts et al. 2016). At large spatial scales, agricultural land-use change over the past decades resulted in homogeneous landscapes (Kuemmerle et al. 2016), impeding pollinator dispersal and thus colonisation of habitats (Steffan-Dewenter and Tscharntke 2001; Redhead et al. 2018). Within these human-transformed landscapes, habitat loss and fragmentation of formerly common semi-natural habitats is one of the most detrimental consequences of agricultural land-use change (Kuussaari et al. 2009; Bennett and Saunders 2010). Small and isolated habitats with limited availability of food and nesting resources support less diverse pollinator communities at lower densities (Brückmann et al. 2010; Hopfenmüller et al. 2014), potentially disrupting plant-pollinator interactions (Grass et al. 2018). Calcareous grasslands are especially under threat from fragmentation (Poschlod and WallisDeVries 2002) and they are among the habitats with the highest taxonomic diversity in Western Europe (Ellenberg 1996; Krauss et al. 2010). Within habitat fragments it is assumed that plant populations are more likely to go extinct when they occur in small and spatially separated patches (Fischer and Stöcklin 1997). Such small patches of flowering plants might lack ample rewards of nectar and pollen thereby failing to recruit sufficient numbers of resident pollinators (Rathcke 1983).

Fragmented plant populations can thus suffer from pollinator limitation on three different spatial scales: the landscape, habitat and patch scale. Self-incompatible, obligately out-crossing plant species which completely depend on pollinators for sexual reproduction suffer most from pollinator limitation due to fragmentation (Aguilar et al. 2006). Their reproductive success, however, is not only determined by the number of seeds from successfully pollinated flowers, but also antagonistic relationships such as pre-dispersal seed predation (Brody and Mitchell 1997). In this study, we focus on *Primula veris*, a self-incompatible, perennial plant species that is declining in Central Europe due to the loss of nutrient-poor grassland habitat. To account for responses of biotic interactions at multiple spatial scales, we analyse the effects of human land-use acting at different spatial scales, i.e. patch size of plant populations within a habitat, fragment area of calcareous grassland habitats, and habitat diversity of the surrounding landscape, on flower visitation, seed set and seed predation of *P. veris*.

8.2 Materials and Methods

8.2.1 Study species

Primula veris L. (Primulaceae) is an herbaceous perennial hemicryptophyte that occurs on nutrient-poor grasslands and forest edges on calcareous soils in Europe and Asia (Demuth et al. 1999). In calcareous grasslands, *P. veris* often forms a prominent yellow flowering cover in early spring. The flowers of *P. veris* are distylous and allogamous (Wedderburn and Richards 1990), only cross-pollination between the long-styled pin flowers and the short-styled thrum flowers results in seed set. The entomophilous *P. veris* is a generalist with respect to its pollinators, being mostly visited by numerous species from the orders

Hymenoptera, Diptera, Coleoptera and Lepidoptera (Woodell 1960). Most of the reproduction is sexually, but vegetative propagation by rhizomes may occur (Kéry et al. 2000). *Primula veris* is a long-living plant, lasting over 50 years in an adequate habitat (Inghe and Tamm 1988), but disappears when grasslands are left to succession (Lindborg et al. 2005). Because of the fragmentation of its semi-natural habitat, *P. veris* is an endangered species in the study region ('Vorwarnliste': NLWKN 2021).

8.2.2 Study area, landscape and sites

The agricultural landscape of the study region around the city of Göttingen in southern Lower Saxony, Germany, is intensively agriculturally managed with patchily distributed fragments of semi-natural habitats. Calcareous grasslands, a main habitat of *P. veris*, are highly fragmented and cover only about 0.3% of the area. Calcareous grasslands (phytosociological association Gentiano-Koelerietum) represent a very species-rich flora with xero- and thermophilic plants (Ellenberg 1996).

In 2000 and 2005, we selected 16 and 15 calcareous grasslands with *P. veris* populations, respectively, of which eleven grasslands were common to both years resulting in 20 different sites over both years. Calcareous grassland fragments covered a habitat area gradient from 314 to 51 395 m^2. Similarly, fragments were situated in landscapes forming a land-use diversity gradient (Shannon H calculated using percent land cover of arable land, forest, grassland, built-up area, garden land, hedgerows, calcareous grasslands, orchard meadows, fen, plantations, and other habitats) at twelve different spatial scales ranging from 250 to 3000 m radius around the centre of the calcareous grasslands. Because landscape diversity of the twelve different landscape scales correlated significantly with each other, we used only the most significant landscape scale (250 m, H' ranging from 0.09 to 1.45) for further analysis.

All *P. veris* individuals on a calcareous grassland fragment were defined as one population. The total population size on each study site was determined at the end of the flowering period by counting the total number of effective reproductive plants in populations of up to 2,000 individuals. In larger populations, *P. veris* individuals were estimated by determining plant abundance per m^2, multiplied by the populated area. Population size ranged from 411 to c. 100 000 individuals. Within populations, one to four *P. veris* patches per habitat were selected for sampling. A patch was defined as a subpopulation of *P. veris* that was at least 2 m apart from a neighbouring subpopulation. We selected a total of 45 patches in 2000 and 44 patches in 2005, ranging from 0.1–37.0 m^2 (10 to 1 600 individuals) per patch. Patch size and habitat area where not correlated.

8.2.3 Flower visitation observation and seed collection

In each patch, ten plants were randomly chosen and observed twice from April 18th to 29th 2000 and three times from April 14th 2005 to May 3rd in 2005. Observations took place between 0900 and 1730 hours on sunny days with little wind and at least 16°C. All study sites were sampled in a randomized sequence and at different times during the day. The observation time was 15 minutes each, in which we noted all flower visitors as well as the number of inflorescences per plant. Ten additional plants per patch were randomly marked when flower buds first emerged. We collected these plants in July when the seeds had ripened. As a measure of reproductive success ('seed set' hereafter), the number of seeds per plant were counted and divided by the number of non-predated fruits.

Ten further single flowers on five plants in each patch were randomly chosen and their fruits were collected at the end of the season, dried at room temperature in paper bags and analysed for predation by insects ('seed predation' hereafter). When a fruit was predated, usually all seeds were damaged and had turned into crumbs.

8.2.4 Statistical analyses

Both sampling years were analysed separately. In both years, the total population size of *P. veris* individuals was highly correlated with the area of calcareous grassland fragments, and so was the number of plants per patch with the patch area. For further analyses, we therefore used patch area and habitat area for patch and population level analysis, respectively. Because habitat area and landscape diversity were positively correlated in both study years, we ran subsequent analyses with either parameter to infer plausibility. The statistical analyses of the data were carried out using R, Version 4.1.2 (R Development Core Team 2021). All response variables were tested for meeting the assumptions of normality and homoscedasticity, pollinator abundance in 2005 was log-transformed. Area parameters (patch and habitat area) were log-transformed for all analyses to improve homoscedasticity. Predation rate data was unsuitable for parametric analyses (see below).

To analyse flower visitation, seed set and seed predation on the three different spatial scales of patch, habitat, and landscape, we used linear mixed effects models fitted by maximum likelihood in the nlme package (Version 3.1-159, Pinheiro & Bates 2000). The order of fixed effects terms was patch area, habitat area and landscape diversity, while site identity was treated as random factor to account for multiple patches per sites. For predation rates, we subsequently ran non-parametric spearman rank correlation tests with all predictors (patch area, habitat area, and landscape diversity) in each year.

8.3 Results

8.3.1 Pollinator abundance

In 2000, we observed 35 individuals of six bee species (*Osmia bicolor*, *Bombus terrestris*, *Bombus pascuorum*, *Anthophora plumipes*, *Andrena haemorrhoa*, *Apis mellifera*) and bombyliid flies during a total observation time of 1 350 minutes. The low number of flower visitors impeded statistical analysis.

In 2005, we observed altogether 237 individuals from 19 different taxa in a total observation time of 1 980 minutes. Pollinator abundance (number of flower visitors on 10 plants) increased marginally significantly with landscape diversity ($F_{1,12} = 3.78$, $P = 0.076$) and significantly with increasing area of calcareous grassland fragments ($F_{1,12} = 6.76$, $P = 0.023$) and increasing size of *Primula* patches ($F_{1,28} = 10.88$, $P = 0.003$, Fig. 8.1). Habitat area and landscape diversity remained significant when tested with patch area individually.

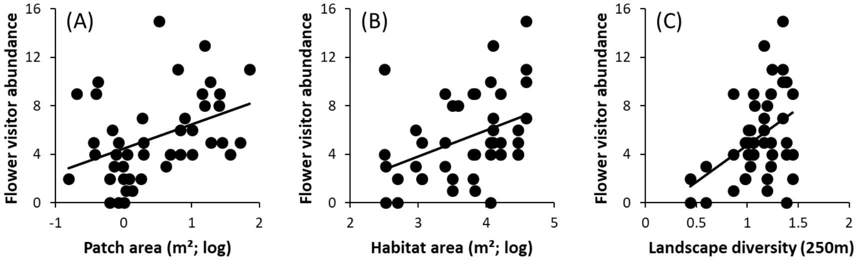

Fig. 8.1: Relation between the number of flower visitors observed over 45 minutes on ten inflorescences and (A) patch area of 44 *Primula veris* patches, (B) area of calcareous grassland fragments, (C) landscape diversity in a 250 m radius around grassland centroids in 2005. Pollinator abundance was log-transformed for analyses.

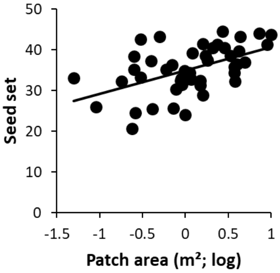

Fig. 8.2: Relation between average number of seeds per fruit and patch size of 45 *Primula veris* patches in 2000.

8.3.2 Seed set

Average seed set per patch in 2000 ranged from 20.7 to 44.5 seeds per fruit and was significantly influenced by patch area ($F_{1,28} = 17.41$, $P < 0.001$). Increasing size of *P. veris* patches lead to an increase in seed set (Fig. 8.2), but habitat area and landscape diversity did not affect seed set per fruit.

Many of the marked *Primula* plants in 2005 were consumed by herbivorous mammals like rabbits, hares, sheep, or goats. Only a low number of patches (N = 20) with adequate sample size (at least 5 fruits) remained and no significant model predicting seed set was found in 2005.

8.3.3 Seed predation

In 2000, predated fruits were found in 11 out of 16 populations and in 27 out of 45 patches. Between 0% and 87.3% of collected fruits per patch were predated by insects. Area of calcareous grassland fragments was the only factor determining the predation rate of *P.*

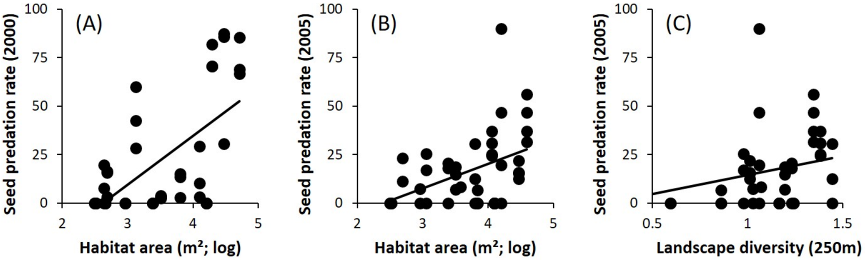

Fig. 8.3: Relation between seed predation rate and habitat area of 16 calcareous grasslands with *Primula veris* populations in 2000 (A) and 15 calcareous grasslands (B) and landscape diversity (C) in 2005.

veris fruits ($S = 6104.2$, $P < 0.001$). Predation rates increased significantly with increasing habitat area (Fig. 8.3).

In 2005, predated fruits were found in 12 out of 15 populations and in 29 out of 44 patches. Predation rates per patch ranged between 0% and 100% of collected fruits and were positively related to landscape diversity ($S = 9425.9$, $P = 0.026$) and habitat area ($S = 7885.2$, $P = 0.003$, Fig. 8.3).

8.4 Discussion

In this study we asked how mutualistic and antagonistic biotic interactions shape the reproductive success of an insect pollinated plant species at different spatial scales. Pollinators were most abundant in large patches of *P. veris*, in large calcareous grassland fragments and in diverse landscapes, thereby responding to all spatial scales related to distinct factors of agricultural land-use change. Seed set, a result of mutualistic plant-pollinator interactions likely benefiting from increased pollinator abundances, responded only at the smallest spatial scale. Antagonistic seed predation rate, in contrast, responded to intermediate and large spatial scales (i.e. area of calcareous grassland fragments and landscape diversity, although there was a degree of intercorrelation among these factors). Plant population dynamics depend on both mutualistic and antagonistic plant-insect interactions and thus require a mechanistic understanding across different spatial scales in order to target conservation management at the most relevant spatial scale. A focus on the population level only would have overlooked the relevance of patch size on seed set, and thus hazards to small subpopulations. A focus on the patch level only would have failed to identify differential rates of seed predation in response to fragment size and the importance of surrounding landscape diversity.

8.4.1 Pollinator abundance

We observed more flower vistors on *P. veris* in those sites that were embedded in a diverse landscape matrix within a radius of 250 m around the calcareous grasslands. A complex landscape in our study region implies the presence of semi-natural grasslands, fallows, orchard meadows, hedgerows, woodlands, and gardens. These habitats provide additional foraging plants and a variety of further resources for bee species and other flower visitors (Steffan-Dewenter and Tscharntke 2002) increasing the abundance and hence the availability of pollinators for the *P. veris* flowers. The amount of semi-natural habitats in the surrounding landscape has been shown to increase bee abundance similarly in canola fields (Morandin et al. 2007) (but see Riedinger et al. 2015) and experimental patches of *Centaurea jacea* L. (Steffan-Dewenter and Tscharntke 2001), respectively. We also found syrphid flies with aphidophagous larvae visiting *P. veris*. These species benefit from the larval food resources provided by arable land (Meyer et al. 2009). Therefore, a landscape comprised of diverse habitats enhances the overall abundance of pollinators.

Primula veris plants received more pollinator visits when situated in larger calcareous grassland habitats than in smaller fragments. Large calcareous grasslands can support large populations of pollinators because they provide ample and diverse pollen and nectar resources in addition to nesting resources and larval food requirements for bees and other pollinators (Jauker et al. 2013). Accordingly, increased habitat area has been associated with increased abundance of wild bees (Steffan-Dewenter 2003) and butterflies (Krauss et al. 2003). In addition to resident pollinators, large calcareous grasslands may further attract pollinators foraging in the surrounding landscape. Size of grassland fragments in our study was highly correlated with the number of total individuals of *P. veris*; this prominent cover of yellow *Primula* flowers in the early spring may be easily detected by pollinators with good dispersal abilities like bumble bees (Westphal et al. 2006).

This attractiveness of *P. veris* flowers also played a role at the smallest spatial scale; the observed number of flower visitors per inflorescence increased with patch size. Large patches of *P. veris* are more attractive to flower visitors because their small-scale abundance in pollen and nectar resources permit sufficient yield for pollinators, leading to extended local foraging bouts (Zimmerman 1981). For instance, it was shown that patches with more flowers of the wild plant, *Lychnis viscaria* L., and oilseed rape, respectively, received higher visitation rates of bumblebees (Mustajärvi et al. 2001) and longer residence time (Cresswell and Osborne 2004). The individual plant may benefit from the attractiveness of larger patches to pollinators by receiving more pollinator visits and hence more conspecific pollen (Sih and Baltus 1987) that will consequently result in higher seed set.

8.4.2 Seed set

We found an increase in seed set with increasing size of the *P. veris* patches. This result concurs with predictions by Kéry et al. (2003) who reported deviations from the equal floral morph ratio (pin vs. thrum flowers) in small *P. veris* populations (fewer than 200 plants). Although total population sizes per habitat exceeded this by far, it corresponds well with our patch scale (10–1600 flowers). Kéry et al. (2003) postulated that the unequal floral morph ratio may have been caused by demographic stochasticity during the fragmentation of previously continuous populations. Because only cross-pollination between the long-styled pin flowers and the short-styled thrum flowers results in seed set, skewed morph ratios might be a possible explanation for the reduced seed set in small populations in addition to overall lower visitation rates.

A reduction in produced seeds may lead to decreased genetic diversity in small patches and compromise the ability of a plant to adapt to a changing environment. This may have detrimental effects on the long-term survival of plants and may increase extinction rates in small patches (Aguilar et al. 2006; Selwood et al. 2015). Because *P. veris* has a life-span of 50 years (Inghe and Tamm 1988) and fragmentation has only become a problem in recent decades, increased rates of extinctions of small populations might be observed in the future (Kuussaari et al. 2009).

8.4.3 Seed predation

In addition to produced seed set, representing the outcome of mutual plant-pollinator relationships, we analysed antagonistic predation rates in *P. veris* across spatial scales. Regular antagonists in *P. veris* are seed predators such as plume (Pterophoridae) and tortricid moths (Tortricidae) (Leimu et al. 2002), of which we observed two species emerging from predated fruits. Spatiotemporal variation in seed predation rates is substantial (Ehrlén 1996; Leimu et al. 2002). In our study, predation rates were consistently related to the area of calcareous grasslands over both study years (and to the larger landscape scale in one year) and we found significantly more predated fruits on larger fragments. *Primula veris*, alluring pollinators with showy yellow flowers covering entire grasslands, is attracting pre-dispersal seed predators at the same time. Overall plant fitness thus depends on increased seed set in large calcareous grasslands counterbalancing the effects of pre-dispersal seed predation (Leimu et al. 2002). Small *P. veris* patches in small habitat fragments are untroubled by seed predation although disadvantaged considering visitation rates and seed set. Small *P. veris* patches in large grassland fragments, however, have reduced seed set and additionally suffer from increased seed predation and are most likely to experience reduced plant fitness over time. Benefiting from increased seed set and decreased predation rates, large *P. veris* patches in small fragments should therefore experience a positive growth rate. These interdependencies of mutualistic and antagonistic relationships acting at different spatial scales warrants further research monitoring the long-time plant fitness of *P. veris* and, in fact, plant species in endangered habitats in general.

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Part III
Biocontrol and Multitrophic Interactions

Chapter 9
The rise, and possible fall, of network ecology

Carsten F. Dormann

Abstract Ecology, much like any other discipline, has its fashions and fads, and each brings its own buzzwords and jargon. "Network ecology" is an example of such a fashion, which has for a few decades imprinted heavily on ecological publications. However, the topics of network ecology are of course much older, as are most of its methods. This invites the question whether network ecology is on a good path to providing different viewpoints and new insights. I here try to outline a somewhat opinionated view of why there is a high risk that this avenue of research may prove to be a cul-de-sac, for two reasons. On the one hand, the word "network" has become an empty buzzword void of specific meaning. On the other, there are six problems that I deem to be "deal breakers" in research on interaction networks: unless they all are resolved, this approach cannot make meaningful contributions. They are: (1) sampling bias; (2) ecological meaning of recorded interactions; (3) data aggregation over individuals; (4) lack of quantitative expectation; and (5) ecologically meaningless indices. Together they lead to the biggest problem (6) confusion in what it all means ecologically. Until these issues are being tackled by improved field and computational research, there seem to be little progress possible in our understanding of assemblages of interacting species under the header of "network ecology".

9.1 Introduction

When many scientists work on a more or less well-defined topic, it is called a "field" of that discipline. In ecology, the prefix "network" has been used, in the same spirit as "landscape" or "animal" or "movement" ecology to define one such field. We can usefully define "network ecology" as a subfield of community ecology, which focusses, largely or exclusively, on *endogenous* processes, i.e. those among its members, rather than on the environment

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(such *exogenous* effects would still be covered in community ecology).[1] And similar to these other examples, it is worth questioning whether the focus of this subfield has contributed to our understanding of ecological topics more widely. Has "landscape ecology" led to myopia with respect to smaller-scale processes? Do principles of "animal ecology" not apply similarly to plants? Are there questions unique to "movement ecology", or only methods? Or, to paraphrase Monty Python: "What has network ecology ever done for us?"

In the end, we study the relationship of organisms to their environment and to each other in order to understand their abundance and distribution (merging the definitions of Haeckel 1866, p. 286, and Andrewartha 1954). Any specific field is to some extent only a means to that end. If network ecology lets us see why a species is here or not, or why one species is common and another is not, why one species has a higher population growth rate or lower mortality than another, great. If, however, it only shows patterns in some indices that do not link back to understanding the ultimate ecological questions, then what's the ecological point?

The question for network ecology is even more relevant, as most topics have already a home in ecology: community ecology, macroecology and food web ecology. (We shy away from questioning the validity of these fields here.) Who interacts with whom is the subject of community ecology, as founded by the seminal books on the topic in 1975 and 1986 (Cody and Diamond 1975; Diamond and Case 1986), but has been followed ever since (Gee and Giller 1991; Lawton 2000; Carson and Schnitzer 2011; McPeek 2017). These books feature loop analyses, interaction matrices, connectance and even nestedness before network ecology was a thing. It is only fair to ask, then, what defines network ecology and whether such a field is progressing the field more than community ecology has done in the last 40 or so years.

The majority of current studies investigate interactions between two guilds, such as pollinators and the flowers they visit, described by a two-mode or bipartite network.[2] However, these can be layered (multiple locations, times) or stacked (tripartite networks). When doing so, they become more like a very selective section of a food web, focussing on what is measurable by a predefined method, or possibly a specific ecological hypothesis involving only this subset of species. When such networks are arranged along gradients (say of altitude or aridity), the exogenous drivers may well dominate community assembly, and community ecology in the wider sense may offer a more comprehensive set of theories and tools (see references cited above).

On the next few pages I want to focus on some known problems in network ecology, which researchers in this field are happy to ignore. I selected those I consider "deal breakers", i.e. so grave that without a solution no progress can be made. Indeed, I would argue that

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[1] This definition is consistent with the way McCann and Gellner (2020) re-interpret "Theoretical Ecology", as well as a non-representative poll among participants of a workshop on networks in 2022.

[2] I write this based on my experience as maintainer of the R-package bipartite (Dormann et al. 2008), which computes a range of network indices, alongside null models and some visualisation, for *bipartite* networks, and may hence have a biased view on the field. What started as a service to the network ecological community has turned into some fruitful and a much larger set of fruitless collaborations. Many questions I received were caused by misunderstanding what a network index may mean, or how it relates to a specific question. Others were naive, assuming that analysing networks invariably will yield interesting answers.

without solutions virtually all previous and current research is void and immaterial, as we have no way of knowing whether it is correct or not. As a theoretical physicist may quip, citing Wolfgang Pauli, network ecology may be "not even wrong". I will start, however, with a reflection of why ecological networks are different to networks in other disciplines, and that this difference matters for the successful application of a network approach.

9.2 Which paths did network ecology open for community ecology?

Claims that network ecology has yielded new insights abound (e.g. Guimarães Jr et al. 2011; Fortin et al. 2012; Bascompte and Jordano 2014; Delmas et al. 2019), but are they correct? That is, are network ecological breakthroughs actually related largely to interactions within a community?

Outside ecology, "network theory" has been applied to power grids, transport connections, metabolic interactions and brain networks, aiming at identifying vulnerable or particularly important parts (e.g. Crucitti et al. 2004; Wang et al. 2018; Guimerà and Amaral 2005; Bullmore and Sporns 2009; Guimerà et al. 2005). In all these cases, the networks exist to achieve a specific goal: provide a steady supply of electricity, connect cities, affect a specific enzyme reaction, or excite neurons belonging to the same task, respectively. It is much less clear, what the "network" in a pollinator-flower network is, what is flowing between nodes, and what actually constitutes the network.

The situation of ecological interaction networks is more similar to the other large group of network studies: social networks. What is the function of the actor-movie network (Peltomäki and Alava 2006) or the supervisory board member-company network (Harris and Helfat 2007)? While we may be able to identify a central actor or CEO, extract power-laws of degrees, in which way does that represent a scientific advance over a classical ordination?

If there are electricity, carbon, consumables flowing in a network, then a shortest path, for example, is a useful information for optimising energy use. In the case of (bipartite) pollination networks, such flux is only between plants connected by the same individual pollinator; pollen isn't deposited, then picked up by another pollinator to be carried over to the next flower and so forth. Similarly, screen time of an actor in one movie does not "flow" to another movie, just because the cast is similar. The analogy occasionally invoked by network ecologists to power grids and brain networks is not obvious, if it exists at all.

If a power grid node is a "hub" then that means many power lines enter and get redistributed. Any fault in that hub affects in an obvious way lower-order power nodes. What, then, is a hub in a pollination network (Olesen et al. 2007)? Will the network fail in whatever it does when a hub-species is lost? No, it will not. A hub pollinator is simply so generalised that it visits flowers that otherwise are predominantly visited by specialists, thereby "connecting" the network graph, but no ecological functions. An attractive flower may well provide resources to many visitors, but that does not mean it "connects" them in any ecologically obvious way.[3] The analogy of a network is simply meaningless. (That

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[3] If anything, it would suggest that pollinators may be competing for this resource, which would stretch the meaning of "connect" beyond recognisability.

is not to say that there aren't keystone or foundation species, but those are not the ones identified by this network approach.)

So, in the following, we audit a few subjectively selected claims of "network-ecological insight", by (a) investigating what is specifically "networky" about that insight, and (b) whether that insight is actually ecological and not merely describing an abstract analogy without representation in ecology (such as the "hub species"). No representative or even comprehensive review is aimed for, but merely an illustration of the point that most "network" texts are full comprised by traditional ecological, non-network research, and/or do not demonstrate that an "endogenous processes only"-approach would approximate well community ecology.

9.2.1 Claim: Network motifs reveal something new

Losapio et al. (2021) stated that "The over-representation of network motifs is positively linked to species diversity globally" (p. 1). The motifs they investigate, in interactions in alpine plant communities, are competition and facilitation among sets of three species. That is, plants may all three compete with each other, some with some but facilitate others, or, at the other end of motifs, all facilitate each other. Since some configuration do not lead to coexistence (e.g. intransitive hierarchies), they find some motifs more often then others.

True to our definition of "network ecology", the scope and approach of this paper is entirely on endogenous interactions. However, there is no detectable element in this paper that warrants or benefits from relabelling competitive interactions as "network analyses". No attempt is being made to explain what is being shared in such a network, or what theoretical expectation would be based in a network-specific theory. Also, no demonstration is given that motifs yield a better description or access to an ecological process than traditional competition/facilitation perspectives.

My point: nothing is gained by using the term "network" in this paper – apart from access to a high-ranking journal.

9.2.2 Claim: Networks more useful for conservation than a focus on species

Harvey et al. (2017) claim that "a shift in focus from species to interaction networks is necessary to achieve pressing conservation management and restoration ecology goals of conserving biodiversity, ecosystem processes and ultimately landscape-scale delivery of ecosystem services" (p. 371). They do not provide quantitative evaluations of studies or experiments as evidence in this commentary piece, rather a narrative based on own previous studies and hand-picked anecdotes.

Most interesting to my point are the arguments they find for arguing that networks are useful. In my reading, all such arguments are based on using "network" as synonym for "analysis of interactions". For example, a study they cite prominently notes that loss of hosts are driving local extirpation of butterflies; no network quantification or theory involved. Of course, the largest driver of species extirpation is loss of habitat, i.e. a non-network cause. A "network approach" would thus definitely be too narrow. Indeed, it seems strange to argue that a focus on endogenous processes (the network approach) is *more* comprehensive than a traditional community approach, which does include exogenous processes.

All of their arguments may be valid, but replacing a narrow "species-centric" approach by one that ignores exogenous drivers (implied by a "network approach") will get conservation biology from the fire into the frying pan.

9.2.3 Claim: Networks reveal community processes across spatial scales

Galiana et al. (2022) report that for interaction networks of various types several characteristics scale as power law with spatial scale, but the number of interactions per species does not.

While this pattern is intriguing, it does not use any network theory to explain it. Post hoc explanations resort to moving from unspecific network jargon into the vague quagmire of complexity, evolutionary adaptations and "factors beyond species richness and number of links" (p. 5).

I read this paper as a description of network topologies without linking them back to processes at population or community level *beyond* that of classical coexistence theory (Grover 1997; McPeek 2022). Also, in their interpretation the authors recourse to exogenous drivers, leaving the network focus that they claim to be behind all patterns observed.

9.2.4 Positive effects of a network focus?

It has been argued that networks make ecologists think of the wider context and system (e.g. Kennerley et al. 2022). If so, this may be more indicative of a too narrow focus in ecological research than of the usefulness of a network angle. Of such a narrowness I find hints only in conservation ecology, where conservation targets are defined (arguably rightly so) by societal preference (furry and feathery; or rarity, but not functional importance); of course here a wider context would be desirable, if legally difficult to implement. Indeed, my selective and prejudiced reading in particular of recent ecological publications with network spin leads me to believe that the term is largely a selling point, without any benefit to current ecological understanding.

One special but in my view well-justified truly network-ecological study is that of Bisanzio et al. (2010). They model the robustness of a network to transfer of pathogens among host species by visiting vectors (following up an idea in Pimm and Lawton 1980). Here, it is clear what flows (the pathogen's spores), why a generalist visitor acts as a hub (as it connects different sets of host species), and why modular networks would reduce spread of the infection (because there it reduces pathogen flow from one subset to another). This is such a special case (a very generalist pathogen that can be transported by all vectors) that it cannot serve as a blueprint for network processes more generally.

With our minds thus critically tuned, let us move on to the core points of this contribution: deal breakers for network ecology.

9.3 Deal-breakers in network ecology

Deal-breaker 1: How we sample networks

The median network study today is of bipartite networks, focussing on a set of species in either guild: hummingbirds and the flowers they visit in selected patches (Tinoco et al. 2017); birds feeding on tree fruits (Dehling et al. 2016); or dung beetles burrowing seeds contained in faeces (Frank et al. 2018).

The problem here is that all these networks represent only **partial and biased samples** of the relevant ecological process. Also bees visit the hummingbird flowers; also mammals feed on tree fruits; and seeds also germinate without being buried by dung beetles first.

If, however, the network does not describe the process in its entirety or at least majority, then what can it tell us about the process? Arguably, if hummingbirds also feed on insects and rotting fruits, what relevance does the identity of the flowers visited has for their ecology? If stingless bees (Meliponini) visit and pollinate the hummingbird flowers, what is the relevance of the hummingbird-flower network to the plants? And so it goes for any and all published interaction networks.

The problem is that if networks are neither complete nor representative of the processes in the community, if they do not describe the most relevant functions for their members (growth, death, reproduction, birth), then what can such a network reveal about nature? Certainly it cannot be used to predict effects of climate change on its members (Sonne et al. 2022), as the interactions represented are not capturing what is relevant for the species concerned.

The standard answer is that networks tell us about the specialisation of its members. Except it does not, if the members do something "on the side" not recorded in the network. One hummingbird may be more specialised than another with respect to a flower available to both, so what? It is not until we have unveiled the consequence of such specialisational anecdotes that we can claim to have contributed a scientific insight. Any living organism is subject to evolutionary pressures (if you pardon such sloppy phrasing), and every organism has preferences in some and less in other facets of its life. What community ecology has been looking for are generalisable principles of what makes communities a recognisable entity, how interactions mould the stability and performance of the community; in which way does it help to know the degree of specialisation of a species in a *partially sampled* set of interactions?

A first step towards resolving this problem is to simulate complex communities and investigate theoretically the effect of partial and biased sampling for getting the presumed function right. A second step, in the field, would be to attempt to design the sampling in such a way that the majority of interactions relevant for that process are indeed covered. Knowing, e.g., the fate of almost all seeds of a tree is inconceivably difficult, but it would tell us whether the network interactions with frugivores are of any relevance.

Deal-breaker 2: What an interaction network contains

A food web describes who eats whom. An interaction network describes who interacts with whom. But **what is that interaction**? And what does binary and weighted information represent?

Several studies have argued and shown that binary networks, in which an interaction is present or not, have little chance of representing the actual specialisation of the participants (Blüthgen et al. 2006; Nielsen and Bascompte 2007; Dormann et al. 2009; Blüthgen 2010). The reasoning is simple: an observed link could mean a single instance or a great many interactions. A species with, say, 4 links could thus be a generalist or an extreme specialist, depending on how many interactions are actually hidden behind a single link (10, 10, 10, 10 vs. 36, 1, 1, 1). It thus seems clear that binary networks are not useful for addressing specialisation-related question, but specialisation is all that networks can provide beyond what standard community ecological procedures already report (species richness, abundances). Most new networks are quantitative, but the majority of recent network reviews still analysed binary networks (e.g. Neff et al., 2021, Galiana et al., 2022, Henriksen et al., 2022, Saravia et al., 2022; but see Luna et al., 2022 (itself criticised by Brimacombe et al., 2022), Sonne et al., 2022).

But even if the network matrix contains quantitative information, what do they represent? A flower visit may lead to pollination and to nectar/pollen consumption, representing a “Schrödinger interaction”, simultaneously positive and negative. Some studies show that indeed such a correlation between number of visits and pollen deposited exist in bee pollination networks (Alarcón 2010; King et al. 2013). The balance of negative and positive effects is particularly important in fruit-frugivore or dung-beetle networks (or in lizard pollination: Correcher et al. 2023), where consumption may destroy seeds, but also improve germination/establishment of those surviving. Typical studies compare gut-passaged seed germination to whole-fruit germination (de Carvalho-Ricardo et al. 2014; Fricke et al. 2019; Rogers et al. 2021), which ignores the effect of seed destruction or deposition at unsuitable sites (but see, e.g., Urrea-Galeano et al. 2019).

A different case are antagonistic systems, such as host-parasite/parasitoid networks. For parasites the problem is the same as for pollinators – the effect of a parasitic interaction on the host is typically unclear –, while for host-parasitoid systems the host must die if the parasitoid develops. Here a quantitative network is actually very informative, as it effectively samples the parasitism rate (Morris et al. 2004, 2014; Gripenberg et al. 2019). Combined with coupled population dynamical models, the network may show whether its structure affects community dynamics and species abundances in line with what network indices may suggest. While the data have been collected, I am not aware of any connection of host-parasitoid network data with population models. Hence the jury is still out, whether any index used to describe the network is meaningful for understanding the resulting species abundances.

The way forward could follow the lead of host-parasitoid studies by quantifying the actual demographic consequences of an interaction. Once such effects are quantified, they can be fed into interaction network models, based for example on coupled differential equations (Drossel et al. 2001; Bastolla et al. 2009; Benadi et al. 2012).

Deal-breaker 3: How we aggregate data

Sampling interactions typically does not allow differentiating between individuals (Quintero et al. 2022). Thus, the number of interactions between plant A and visitor B may reflect the behaviour of one pollinator or frugivore, or the attractiveness of a single flower out of

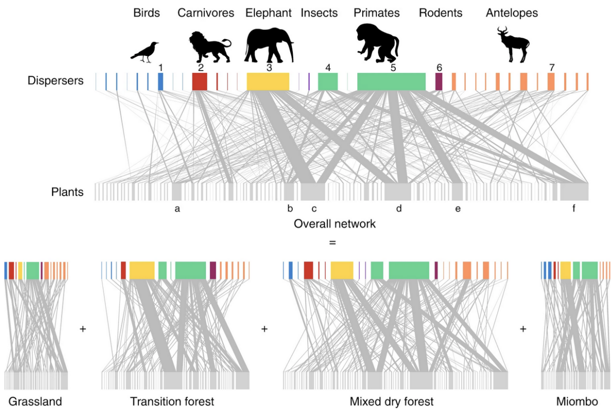

Fig. 9.1: Example of pooling across habitats. "Quantitative seed–dispersal network of the Gorongosa National Park, Mozambique. [...] The aggregated network was obtained by pooling all interactions across the four habitats, and summing their frequencies." (Timóteo et al. 2018, p. 3). Nice graphs, but what do these lines actually mean ecologically, beyond the trivial 'animals carry seeds'?

dozens in the patch. The well-known floral constancy of individual honey bees (Waser 1986; Cakmak and Wells 1994; Hayes and Grüter 2023) is a case in point: the behaviour of each bee is at odds with the generalistic behaviour of the species. Averaging across individuals suggests a very different pollen dilution than knowing about individual's floral constancy. How representative are these data for the interaction studied, if the aggregate information across an unknown (or at least uncommunicated) number of individuals? Also, as data are collected over some time, networks are typically aggregated across hours to days, averaging out any variability that may have existed (Schwarz et al. 2020; CaraDonna et al. 2021). And, occasionally, the same happens in space, when several field sites are used to construct an interaction network (Dáttilo et al. 2019, see also Fig. 9.1).

Network structure is affected by aggregating individuals, samples, sites, but we do not know how (see Arroyo-Correa et al. 2023, for some early ideas). But if we do not know what **happens during aggregation**, we cannot know whether the result reflects interesting ecological patterns or aggregation artefacts.

A first step towards resolving the aggregation problem is to do a sensitivity analysis: aggregate a bit more and a bit less than the focal aggregation level and see how it affects the results. If they are more or less unaffected, then aggregation did not seem to introduce substantial artefacts. If the dataset is particularly rich, analyses at different aggregation levels may even be possible (Schwarz et al. 2020).

A next step would be, again, to explore this issue by simulation, ideally using individual-based simulations, which are then sampled by a virtual ecologists (Zurell et al. 2010) and analysed by different types of aggregation. In the field, attempts should be made to tell between individuals, in order to separate within-species from between-species specialisation.

Deal-breaker 4: What we can expect

Networks are typically described by indices, which quantify some pattern in the data. Many such indices exist, but for most of them **we have no quantitative expectation**. For example, what is a high (or low) value for "linkage density" in a plant-herbivore network?

The absolute value depends a lot on our sampling intensity, on the species richness of the involved guilds, and on their abundances. We can thus compare linkage density between two habitats or treatments, but the actual value is of no practical use. For any single network, however, we need a point of reference. That is where null models come in.

A null model simulates what a network would look like if a specific process was *absent*. In a regression, the null model is the intercept-only model, i.e. a model without predictors. That would also be the go-to approach for networks (Wells and O'Hara 2013), but regrettably such approaches currently cannot accommodate the non-independence of entries in the interaction matrix.

Parametric likelihood of an interaction matrix

There are two avenues towards a solution to this problem, each with its own set of unresolved issues. The first is an (unpublished) way to correctly compute the likelihood of observing an interaction matrix' entries given a probability matrix of the same dimensions *and* fixing marginal totals. This is a bit different from assuming that the matrix is actually the outcome of a multinomial distribution with given per-cell probabilities (as used, e.g., by Vázquez et al. 2009; Benadi et al. 2022). It additionally observes the constraint that species interaction are not independent across rows and columns. One consequence is that once all observed interactions in a column or row are accounted for in the likelihood, this column/row probability must be relocated to the remaining cells per row/column, respectively.[4] In practice, this "Bjorn"-likelihood is only little different from a multinomial likelihood. The sticky point remaining is: where to get the probabilities from in the first place?

Null models

The second avenue is interaction null models, of the same type used in co-occurrence and biogeographical analyses (Gotelli and Graves 1996; Gotelli 2000; Vázquez and Simberloff 2003; Dormann et al. 2009). For example, the Patefield-algorithm often used for quantitative network null models takes the observed abundances as given and assumes all species to interact randomly. Simulated interactions are thus proportional to species abundances, as deduced from the interaction matrix marginal totals.

Other assumptions can be, and have been, made. For example one could choose to keep the number of links in the network constant (Vázquez and Aizen 2003; Vázquez et al. 2007). There are, however, two fundamental problems with modifying the Patefield approach (see also Molina and Stone 2020). First, a null model is not just any simulation algorithm that yields a network. Rather, it has to have two necessary properties, which have been shown for no existing quantitative null model except the Patefield algorithm: (1) full configuration space: the null model algorithm has to be able to find all possible

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[4] A function implementing this algorithm by Björn Reineking is included in the R-package **tapnet**.

configurations of the network that exist; and (2) uniform sampling: when generating simulations, all these configurations must be generated with the same probability. These are extremely stringent conditions, and it is mathematically extremely difficult to prove that they are met (see Carstens 2015, for an example for a binary null model). If either of the conditions is violated, the simulations do not represent what is possible, and they do not represent what is possible fairly, i.e. they are biased.

This is no small matter, and it may be common. When I attempted to construct a null model that maintains marginal sums (like Patefield's) *and* the observed number of links, it all seemed to work nicely. On closer investigation, however, I realised that certain configurations were found by the algorithm much more readily than others, and some were never found. This faulty algorithm can still be examined as `bipartite::swap.web`, but using it would be simply wrong. The null model comparison performed with this null model were too aggressive: it found much stronger deviations between the null and the observations than is correct.

To repeat: using a null model only makes sense if this null model is able to sample the entire space of possible configurations uniformly. Proving this is mathematically difficult, and simulations are infeasible, as the configuration space is typically much too large. So, currently we must consider all non-Patefield algorithms as experimental and provisionally – and the results drawn from them, too.

Abundances: cause or effect of network structure?

Another fundamental problem with formulating an expectation, using null models, is to use the number of interactions we observe per species as its abundance. (I omit here the problem that activity confounds such abundance estimates. The abundance problem is bad enough already.) These "abundances" are potentially a consequence of the interactions in the network. If so, they cannot logically be used as independent estimates of abundance for the null model. This dilemma has been referred to as the "chicken and egg problem" (Fort et al. 2016): if the network structure affects the abundances, then the abundances cannot be used for the null model. While Fort et al. (2016) argue that the chicken-or-egg problem can be solved even with the data at hand, I remain unconvinced until formal simulations have demonstrated that to be the case.

It is unclear when external abundances are independent of network structure, and when the Patefield algorithm can thus still be used. Species in pollination networks typically are much less dependent on interactions for their abundance than host-parasitoid networks, so at that end of the dependence gradient the null model can probably still be useful. Using the Patefield algorithm for host-parasitoid networks "only" tells us whether the observed interactions are surprising given the observed abundances. But it cannot serve as a null model in the sense of "in the absence of specialisation", as abundances are at least to some degree the result of network structure, too.

A different step towards resolving the chick-and-egg problem is to sample abundances in the field independently of the actual network. While that does not remove the circularity of the null model, it at least gives expectations that do not immediately emerge from the network data. A further step would be to collect data over time, so as to be able to represent the population dynamics of the different species involved. With a coupled population dynamic model this system could than be analysed for network configurational effects on species abundances.

Deal-breaker 5: What it means

Network indices abound. Some are plain and general, such as connectance, others are involved and specific to a interaction type, such as the pollination dependence index. Some are based on binary network information, which is problematic for reasons mentioned earlier, others are very ad-hoc attempts to try and extract something meaningful from a network. Very few, if any, network indices have been shown to map to an ecological process or pattern. Only one or two indices have been subject to rigorous simulation or mathematical analysis to investigate their behaviour (Blüthgen et al. 2006; Poisot et al. 2012). As a consequence, the majority of them is affected severely by network dimensions, sampling intensity, degree of lumping species into morphotypes, misidentification and so forth (Nielsen and Bascompte 2007; Dormann et al. 2009; Gibson et al. 2011; Chacoff et al. 2012; Rivera-Hutinel et al. 2012; Fründ et al. 2016; Vizentin-Bugoni et al. 2016; de Aguiar et al. 2019; McLeod et al. 2021).

Many indices have been transferred from other fields of science, such as small world properties, motifs or degree distributions (Vázquez et al. 2005; Olesen et al. 2006; Jácome-Flores et al. 2020). Reading these papers provides **no justification for their purported usefulness in ecology**. What does it mean that a network is robust to extinctions, if the underlying procedures are unrelated to ecology (assuming static interactions as if they were an electricity grid)? What does it mean for the abundance of the species in a network that some motifs of interactions are more common or rare? How can a (truncated) power law of degrees explain abundances of species or traits? How can (lack of) nestedness explain which species dominates in a guild? There is a surprising number of high-ranking publications that I regard as void of ecology, as they are not embedded in an ecologically meaningful concept and which fail to logically relating some "network topological" index to community processes.

To clean this Augean stables of network indices, we must work harder to demonstrate that an index has an ecological meaning. Such demonstration will typically take the form of a simulation study, which as to show that (1) an index does what it claims, and (2) no other ecological cause can affect this index. That is hard! The well-intended and seemingly sound partitioning of β-diversity into nestedness and turnover of Baselga (2010, cited 2453 times) was soon shown to be incorrect and yielding nonsensical results (Almeida-Neto et al. 2012, cited 167 times). To me, this shows that we are not trained in rigorous index development and need to demand a higher standard for any old, new or transferred index applied to interaction networks (one of the points emerging in Brugere et al. 2018).

Deal-breaker 6: Confused minds

Networks can be seen as a third-order pattern (Dormann et al. 2017). The first order is the number of species (two numbers), the second their abundance (two vectors, i.e. $n+m$

units of information).[5] If we can explain a pattern in nature with first-order information, why would we resort to the network matrix ($n \cdot m$ units of information)? Not only does it violate the parsimony principle, it also fosters unclear thinking (also see critique by Brimacombe et al. 2022).

Take, for example, connectance. It is strongly dependent on sampling intensity, and on the number of species observed, and hence connectance is typically a non-linear function of first-order property "number of species observed". It does not represent further information about the network, because it is almost completely explained two levels further down. When we interpret connectance as "forbidden links" (Jordano et al. 2003), we invoke an unproven complicated explanation when a simple one does exactly the same job (Vázquez 2005). Note that this does not argue against the sound idea of implausible interactions, only that connectance cannot possibly be responsible; but lack of matching traits can be.

A striking example of **misconceptions behind networks** is a conceptual figure in Moreno-Mateos et al. (2020), which represents recovery of community properties during secondary forest succession. First, species numbers recover, then species abundances, and then with some temporal delay, "networks". Such a delay implies that there is something that prevents the species to interact as before the disturbance. Why should that be the case? If a species is there, it will interact. Network indices are the direct consequence of interacting species, and species interact as part of there existence. There is no lag between recovery of abundances and "networks". In fact, following the chicken-and-egg arguments, the networks *must* be similar to before the disturbance, otherwise the abundances would be different, too.

To me such mistakes point to a deeper confusion. Networks seem imbued with some near-magical properties that make them the target of much current research, without requiring the scientist to justify *why* a network-ecological approach was taken for a specific question. The added benefit of such an approach, which certainly exists in some cases, should be demonstrated by first failing to explain a pattern with first- and second-order properties of the network.

Furthermore, it is easy to claim some underlying coevolutionary or community ecological cause for a pattern, but very difficult to show (as deconstructed for modularity in Dormann et al. 2017). It is unfortunate that one can simply claim that this or that process underlies a pattern, without proper demonstration. It is, of course, not only network ecology that falls into this trap (see, for example, the many studies which claim that "species distribution models are useful" without ever citing a study that demonstrates, only studies that claim, such usefulness).

9.4 From networks to ecology

The near-trivial equation underlying ecology is $N = B - D + I - E$, describing the number of individuals in the population of a given species as the result of demographic (birth and

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[5] To complicate things a bit more, there is another level between 2 and 3, 2.5 if you like: Do we need to record all interactions together, or could we do species-level observations (e.g. in a cafeteria-experiment) and just place them next to each other? This would also require $n \cdot m$ units of information, but collected in isolation, rather than together. For the following arguments this distinction is not relevant.

death) and dispersal/migration (im- and emigration). Interaction networks, in their typical from, do not quantify the I and E component, in line with their focus on endogenous processes. If they do also not contribute to our understanding of B and D, then what is their point?

The ecologically interesting question is whether, say, specialism increases the number of offspring or reduces mortality; not whether a network has a specific topology. This is not the first time that network ecology has been argued to be disconnected from (community) ecology (Blüthgen 2010). Since then, little has happened with respect to the problems outlined above.

The road ahead will require overcoming substantial obstacles, if network ecology is to contribute to ecology, beyond buzzwords and enthusiasm: clear thinking, dedicated data collection for specific hypotheses, and demonstration of effects of network structure beyond mere claims of relevance.

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Chapter 10
Trophic interactions affecting biodiversity–ecosystem functioning relationships

Bernhard Schmid

Abstract Plant diversity supports ecosystem functions such as plant productivity and carbon capture across a broad range of environmental conditions. However, it is unclear if and how the diversity of other trophic groups, in particular herbivores and their enemies, contribute. Comparative observational and experimental studies in subtropical forests in south-east China revealed that the positive effects of plant diversity were mediated by insect trophic diversity, with plant species richness promoting enemies of herbivores, resulting in increased plant productivity. This top-down control of herbivores in the complex forest ecosystem contrasts with bottom-up controls of herbivores by plant diversity in grassland biodiversity experiments. I suggest that trophic niche partitioning as well as mutualistic niche partitioning can allow for a division of labour that increases the functioning of complex ecosystems. To which extent this involves evolutionary processes at the systems level will have to be assessed in further research.

10.1 Introduction

As life on Earth evolved, the number of different organisms increased and more complex forms evolved (Bonner 1988). An important aspect in the evolution of complex forms was symbiogenesis, the integration of different organisms into single new types of organisms, such as the eucaryotes (Margulis 1993). However, even in the most complex forms of organisms, single individuals cannot do everything alone; therefore, additional functions require groups of individuals to work together, as for example in social insects, where division of labour between different types of individuals allows for the emergence of group strategies (Duarte et al. 2011). Such division of labour has also been postulated as a central feature of interactions among species in ecological communities and ecosystems (van Baalen and Huneman 2014). It implies that underlying evolutionary processes take place, as has indeed been found for evolutionary division of labour via niche differentiation between

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plant species, leading to increased ecosystem functioning in biodiversity experiments (Zuppinger-Dingley et al. 2014; van Moorsel et al. 2021). However, division of labour could also be considered — and may be even more important — between organisms of different trophic groups. For example, the plant as a primary producer lives on inorganic nutrients and converts CO_2 to organic substance using light as energy, yet it cannot decompose itself without the help of microbes, which recycle nutrients from dead plant material to make it available again for new plant growth. In the typical case, multiple trophic groups participate in division of labour to cycle energy and matter within an ecosystem. Plant parts may be consumed by herbivores or pathogens before they are shed off as dead material; and the same applies to herbivores, which may be consumed by predators or parasitoids before dying naturally of old age. Furthermore, these secondary consumers may be eaten by tertiary consumers and so on ("green food web"), until decomposers recycle dead material and may themselves again be eaten by other organisms ("brown food web").

Often when we look at plants, we may not immediately see the herbivores and their influence on plants. This is because we preferentially see the plants that are not eaten, because some herbivores may be hiding as internal feeders (leaf miners, stem miners), because plants are well defended, or because their modular organization can compensate herbivore damage via regrowth (McNaughton 1983; Schmid 1990). Furthermore, herbivores not only have to overcome plant defenses but also are threatened by predators and other enemies, which may reduce their abundance by top-down control as suggested by the "Green World Hypothesis" (Hairston et al. 1960; see also Oksanen et al. 1981). Nevertheless, many common plant species are attacked by a large range of specialized herbivore species that live and feed on them. For example, the common reed, *Phragmites australis*, studied by Teja Tscharntke in his early work, often is attacked by a midge, *Giraudiella inclusa*, that induces the formation of galls in which the larvae survive if the shoot diameter measures at least 6 mm (Tscharntke 1988). In the study region of Central Europe, common reed is also host to further primary and secondary attackers, i.e., insects that eat plant parts or droppings of other insects, or that use the empty galls of the midge or broken stems as nesting sites (Tscharntke 1999). This probably inspired Teja to use dead reed shoots as bee hotels in subsequent research. The example nicely shows that not only multiple trophic levels, but also many species per trophic level can live on a single plant species. With more plant species, the complexity of trophic networks increases further.

The big question, which underpins the more specific question of this chapter about how trophic interactions affect biodiversity–ecosystem functioning relationships, is what determines the number of trophic levels in green and brown food webs and the number of species per trophic level, i.e., the degree of division of labour in an ecosystem. Is this just a consequence of random speciation, colonization, and extinction, combined with environmental filtering as in Hubbell (2001)'s neutral theory of biodiversity, or could there be some sort of ecosystem evolution (Loreau 2010) that shapes trophic networks? Could this lead to the evolution of ecosystems that work better than others, for example randomly assembled ones? Will a greater division of labour and thus greater diversity of species between and within trophic groups lead to higher levels of ecosystem functioning and stability, particularly in environments with broad resource offer and large biotope space (Dimitrakopoulos and Schmid 2004; Jousset et al. 2011)? To study these questions, I here focus on a particular ecosystem function, namely production of aboveground plant biomass.

In the simplest case, where primary producers are only accompanied by decomposers, primary productivity should be greater than if herbivores are added to the system, because the latter will consume living plant material that could be used in photosynthesis. However, as de Mazancourt et al. (1998) have shown, a certain amount of herbivory can optimize plant production under certain circumstances, namely if the proportion of nutrients lost along the herbivore pathway is smaller than the proportion lost through the rest of the ecosystem. To maintain this "certain amount of herbivory", top-down control from carnivores can be one solution. However, until recently we lacked the knowledge to which extent multitrophic interactions can affect primary productivity. In the following, I will report some first empirical evidence for this, obtained in comparative studies and designed experiments about the relationship between biodiversity and productivity.

10.2 Effects of plant diversity on primary productivity and trophic diversity

The relationship between ecosystem species diversity or complexity and ecosystem functioning, including stability, has been controversially discussed for a long time, until over the past two to three decades it became increasingly evident that the relationship is generally positive (Balvanera et al. 2006). One reason for the controversial earlier views was that all natural ecosystems must function somehow, because otherwise they would not exist in the real world. Furthermore, until very recently it was thought that in agriculture the single most productive monoculture would always produce a higher yield than the most productive mixture under intensive management (Harper 1977; Schmid and Schöb 2022). However, studying natural ecosystems may not reveal the underlying causal relationships between diversity or complexity on one side and ecosystem functioning on the other side. To reveal the positive causal relationship diversity → ecosystem functioning it is necessary to disassemble natural ecosystems by removing species experimentally. Such experimental manipulation mimics potential consequences of future extinctions (Schmid and Hector 2004) that currently do not yet occur and thus cannot be studied even with the most careful causal analysis of natural ecosystems (for an example see Dee et al. 2023).

Most large-scale biodiversity–ecosystem functioning (BEF) experiments so far have focused on the relationship between plant species richness and primary productivity (e.g. Hector et al. 1999; Tilman et al. 2006; Weisser et al. 2017; Huang et al. 2018). These experiments showed that primary productivity typically increased linearly with the logarithm of plant species richness up to the richness of the natural ecosystem investigated. The major explanation of this effect was that no single plant species can be so plastic as to extract all available resources from the environment; there would always be some resources left for other plant species. In fact, most experiments found that multiple species partitioned resource uptake among each other, resulting in so-called species complementarity effects or, using a more generic term, division of labour. However, there always remains some doubt as to whether such resource-niche complementarity is sufficient to explain the observed strong effects of plant diversity on productivity or if, in addition, partitioning of enemy-niches (Turnbull et al. 2016) plays a role, with specialized enemies reducing productivity more strongly in plant monocultures than in mixtures.

A further general result of the mentioned large-scale BEF experiments manipulating plant species richness was that with the removal of plant species other trophic groups also suffered a loss of species, for example herbivorous and predatory insects as well as soil and leaf fungi and microbes (see e.g. Weisser et al. 2017). The reduction in richness could be, but was not always, paralleled by a reduction in total abundance of these other trophic groups. For example, one global synthesis found that herbivore abundance was generally reduced by increasing plant species richness, whereas predator and parasitoid abundance was increased (Wan et al. 2020). Overall, effects seem to weaken with the number of trophic links between a group and the primary producers (Balvanera et al. 2006; O'Brien et al. 2017) and generally diversity begets diversity, which is not surprising considering the single plant species mentioned above, common reed, already hosting a large number of specialized insect species.

10.3 Effects of insect trophic diversity on primary productivity

Coming back to the question if a greater diversity of species between and within trophic levels can lead to higher levels of ecosystem functioning and stability, we can more specifically ask how trophic diversity affects the plant diversity–productivity relationship. This is not an easy question. For example, observing herbivores and predators is difficult and time-consuming; and full manipulation of their species richness is difficult under the conditions of a plant BEF experiment. Starting with some thought experiments, one could first reduce predator diversity and abundance and then additionally herbivore diversity and abundance (Fig. 10.1).

Removing predators likely would increase herbivore damage on plants beyond levels beneficial to plant productivity according to the mentioned model of de Mazancourt et al. (1998). Compared with the control treatment shown by dashed lines in Figure 10.1 (specifically Fig. 10.1a), the herbivores may reduce primary productivity by a constant amount (Fig. 10.1b), more strongly at high plant species richness where there is more plant biomass to feed on (Fig. 10.1c), or more strongly at low plant species richness due to accumulation of specialized herbivores as expected with Janzen-Connell effects (Petermann et al. 2008, Fig. 10.1d)). To my knowledge, there have been no attempts so far to selectively exclude predators in field BEF experiments, so we lack good experimental data to test the predictions of the thought experiment. One possible approach are cage experiments where for example herbivores are allowed to graze on BEF-experiment plots in the absence of other insects. This has been done for grasshoppers (Pfisterer et al. 2003; Specht et al. 2008; Deraison et al. 2015), but not for larger groups of herbivores together. It is conceivable that analogues for insect exclusion studies in BEF experiments could be found in the agricultural or biocontrol literature (cf. Brandmeier et al. 2021; Schmid and Schöb 2022).

Removing predators and herbivores together, at least for a particular group of organisms such as insects, would be easier to do. In this case, plant productivity might be higher than in the control — if herbivores were not well controlled by predators in the control (thick solid lines in Fig. 10.1e, f). This was the case in a Swedish grassland BEF experiment,

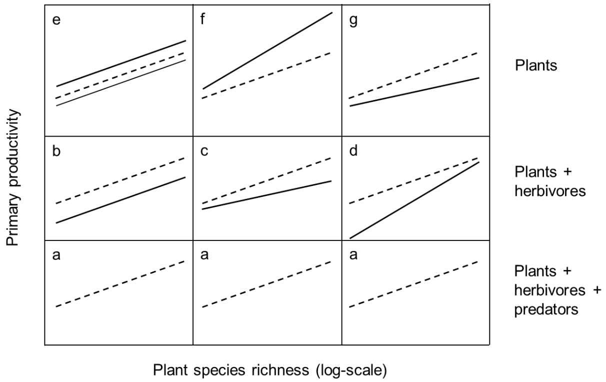

Fig. 10.1: Plant diversity–productivity relationships in typical BEF experiments (dashed lines and repeated panels a indicate control, i.e. no removal of trophic groups). Exclusion of predators is expected to reduce primary productivity (panels b–d). Exclusion of both predators and herbivores may have varied effects (panels e–g). The different scenarios are explained in the text; empirical examples for some of them are also given in the text.

where the exclusion of insects increased primary productivity and the slope of the diversity–productivity relationship as depicted in Fig. 10.1f (Mulder et al. 1999). Such a result is compatible with bottom-up control of insect trophic guilds as observed in another grassland BEF experiment, the Jena Experiment (Scherber et al. 2010, see also Fig. 10.3c). Where herbivores consume not so much of the biomass produced by plants or where they suffer stronger top-down control from predators, it is conceivable that primary productivity in the absence of herbivores and predators is lower than in the control, where both are present together (thin solid line in Fig. 10.1e). Furthermore, this effect could be more pronounced at high plant species richness (thick solid line in Fig. 10.1g). In this case, promotion of multi-trophic diversity by plant diversity would contribute to a strengthening of the plant diversity–productivity relationship, as has been inferred from path analyses in two recent studies (Li et al. 2023; Schuldt et al. 2023) for a subtropical forest ecosystem.

Given the difficulty and scarcity of experimental manipulations of insect trophic diversity in the field, path analysis and structural equation modelling (SEM) — based on observational data of insect species richness or abundance and their correlations with observed or manipulated plant species richness — have been used to derive possible causal relationships mediating the effects of plant species richness on primary productivity via insect trophic diversity (Scherber et al. 2010; Wan et al. 2020; Li et al. 2023; Schuldt et al. 2023). Particularly detailed analyses have recently been done for a large forest BEF experiment in south-east China (BEF-China: Huang et al. 2018). Li et al. (2023) found a weakly positive relationship between herbivore richness or abundance and primary productivity and a strongly positive one between enemy (predator + parasitoid) richness or abundance and primary productivity. I have redrawn these results for herbivore and enemy richness in Fig. 10.2a and b, adjusting productivity for differences between years and focusing on tree richness levels 1–8, using different plotting symbols for these. Higher herbivore and enemy

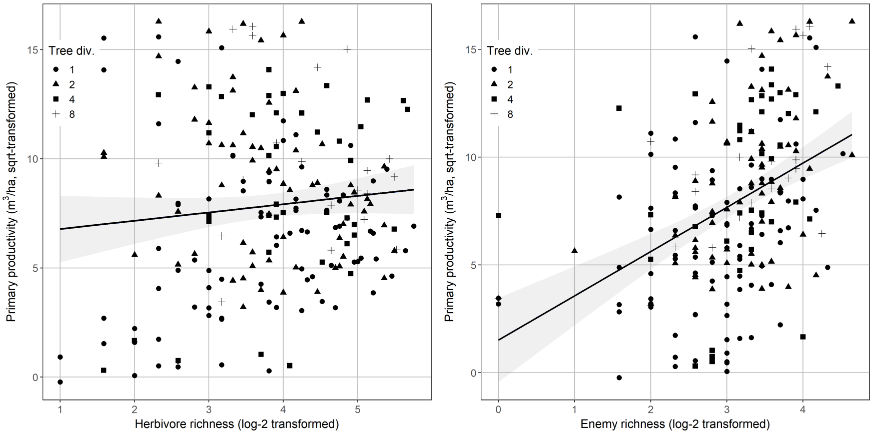

Fig. 10.2: Relationship between primary productivity (stand-level tree volume, adjusted for differences between years) and species richness of insect herbivores (left, $P = 0.14$) and enemies (right, $P < 0.001$) in the BEF-China forest experiment. "Tree div." indicates the number of tree species planted in a square plot of 1/15 ha. The grey bands represent 95% confidence bands around the regression lines. Data are taken from Li et al. (2023).

species richness values come from plots with higher tree species richness, suggesting that the higher trophic level diversity mediates the effect of tree diversity on productivity.

These relationships can be put into a hypothetical causal network using SEMs. The path analysis in Fig. 10.3a was obtained from such modelling using the data presented in Fig. 10.2. Correcting for the multiple dependencies, the direct effect of herbivores on productivity is now significantly negative, as might be expected, yet enemies still have a positive direct and indirect (multiplication of two negative path coefficients) effect on productivity. Tree species richness has a positive direct effect, a negative indirect effect (via herbivores) and positive indirect effects (via enemies or via enemies and herbivores) on productivity. Overall, this suggests that in the subtropical forest in south-east China positive effects of tree diversity on primary productivity are at least partially mediated by insect trophic diversity, a finding also supported by results from plots in the neighbouring natural forest selected according to a comparative study design ensuring equal representation of different tree species richness levels (Schuldt et al. 2023). Results of path analyses using herbivore and enemy abundances were very similar to those using herbivore and enemy richness, yet path coefficients from tree diversity and enemy abundance to herbivore abundance were not significant.

For the Jena Experiment (Weisser et al. 2017), one of the two large grassland biodiversity experiments with extensive insect data (Barnes et al. 2020), a path analysis assuming similar causal relationships as for the BEF-China forest biodiversity experiment (compare Fig. 10.3a and c) is less satisfactory. This was also the case when insect abundances were used instead of insect richness (similar path-analytic results). It appears that in grassland ecosystems bottom-up controls of insect trophic diversity and abundance are stronger than top-down controls (Scherber et al. 2010). This is indicated by the path analysis for the Jena Experiment

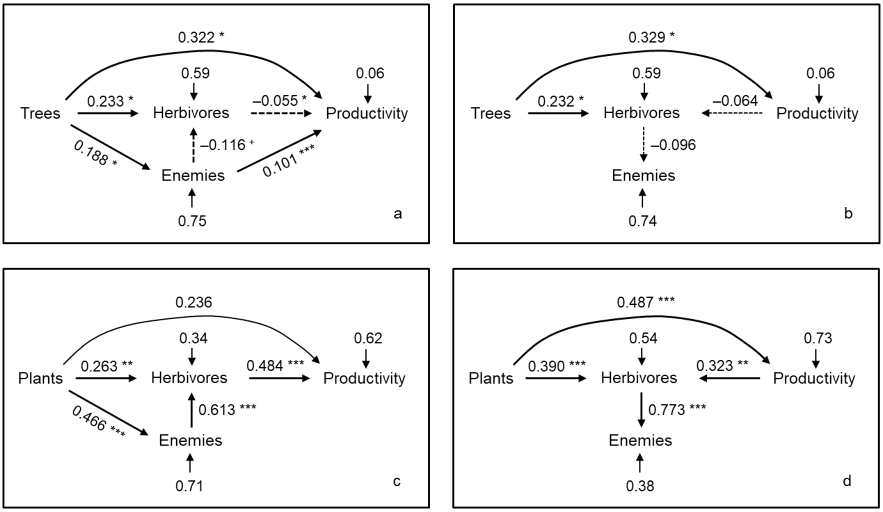

Fig. 10.3: Path analyses relating manipulated plant species richness to aboveground insect species richness of herbivores and enemies and to primary productivity for the BEF-China forest experiment (a, b; data from Li et al. 2023) and the Jena Experiment, a BEF grassland experiment in Germany (c, d; data from Scherber et al. 2010). The first two path analyses (a, b) were calculated using tree richness levels 1, 2, 4, and 8 (data shown in Fig. 10.2), the third (c) and fourth (d) path analyses have been calculated using plant richness levels 1, 8, and 16 (no data available for levels 2 and 4, level 60 excluded). All species richness variables where log-transformed to linearize relationships; productivity was square-root transformed from aboveground stand volume (a, b) or log-transformed from aboveground plant dry mass (c, d) to improve normality of residuals. Numbers indicate standardized path coefficients and residual error variation (for the three dependent variables herbivore richness, enemy richness and primary productivity). $+ P < 0.1$, $^{*} P < 0.05$, $^{**} P < 0.01$, $^{***} P < 0.001$; overall fit for models a, c, and d $P > 0.2$, for model b $P < 0.001$. Plots (a, b) or blocks (c, d) were used as random effects (Scherber 2023).

represented in Fig. 10.1d (and the corresponding analysis with insect abundances), but also by findings in the other large grassland biodiversity experiment in Cedar Creek, Minnesota (Barnes et al. 2020). It should be noted that the path-analytic interpretations rely on the positive (grassland example) vs. negative (forest example) relations between herbivore and enemy richness. Thus, applying bottom-up causation for the BEF-China example results in a very poor model fit (Fig. 10.1b). It is difficult to avoid such dependence between observing data and establishing causal hypotheses in path analysis and SEM. Thus, we still need to find ways to do the manipulative experiments to fully understand the role of insect trophic diversity in mediating plant diversity–productivity relationships.

As mentioned at the beginning of this section, such manipulations should be done for the different trophic groups, e.g. herbivores and enemies, separately, however I do not know of any such experiment in field BEF-studies. In the Swedish grassland experiment mentioned earlier (Mulder et al. 1999) as well as in the Jena Experiment (Weisser et al. 2017) and in a recently published forest experiment within BEF-China (Huang et al. 2022), all aboveground insects were removed together. In the first two cases, as suggested by the results from the Jena Experiment and Cedar Creek (Scherber et al. 2010; Barnes et al. 2020, Fig. 10.3c), enemies probably played a minor role and thus the removal of aboveground insects mostly affected herbivores, revealing a more positive plant diversity–productivity relationship in their absence (Fig. 10.1f; Mulder et al. 1999). However, experimental removal of aboveground insects in the second case did not significantly change the positive plant diversity–productivity relationship (Huang et al. 2022). Perhaps negative effects of herbivores and positive effects of enemies cancelled each other out for the forest experiment; or the study was statistically underpowered to find the overall positive effect of trophic diversity on the tree diversity–productivity relationship suggested by the path analysis shown in Fig. 10.3a.

10.4 Effects of pathogens and mutualists on primary productivity

Besides the moderating effects of herbivore and enemy trophic groups discussed above, other groups of organisms can additionally modify plant diversity–productivity relationships. For convenience I refer to them as pathogens and mutualists, also often it is difficult to assign a species to one of these groups. An example where mutualists probably exceed pathogens are leaf bacteria; their diversity mediated positive effects of tree diversity on primary productivity in a forest biodiversity experiment near Montréal in Canada (Laforest-Lapointe et al. 2017). This conclusion was based on a path analysis of observed leaf bacteria diversity (similar to the path analysis presented in Fig. 10.3a). Again, experimental manipulations of this trophic group remain to be done.

Manipulating soil microbial diversity in plant BEF experiments has been done more frequently (e.g. Schnitzer et al. 2011; Wagg et al. 2011; Luo et al. 2018; Yang et al. 2022). Some of these experiments indicated pathogen-niche complementarity between plant species (Turnbull et al. 2016). That is, the removal of pathogens released plants in monoculture or low diversity from host density-dependent pathogen attack and thus resulted in a flatter plant diversity–productivity relation (Schnitzer et al. 2011; Yang et al. 2022). In other experiments, the presence and diversity of mutualistic mycorrhizal fungi increased resource-niche complementarity between plants and thus increased the slope of the plant diversity–productivity relation (Fig. 10.1g; Wagg et al. 2011; Luo et al. 2018).

Within the BEF-China study we had another sub-experiment in which we used fungicide to remove aboveground leaf fungal communities (Huang et al. 2022). This flattened the plant diversity–productivity relationship compared with the control, suggesting that in the control leaf fungi must have mediated the positive effect of plant diversity on productivity (Fig. 10.4). The slight increase of tree monoculture productivity in fungicide-treated plots could have been due to a removal of pathogenic leaf fungi. However, the reduction of mixture productivities in fungicide treated plots hints towards a positive role of mutualistic fungi in the control treatment at higher tree diversity. Currently, we cannot explain this effect, because we only removed aboveground fungi and left the mycorrhizal fungi undisturbed.

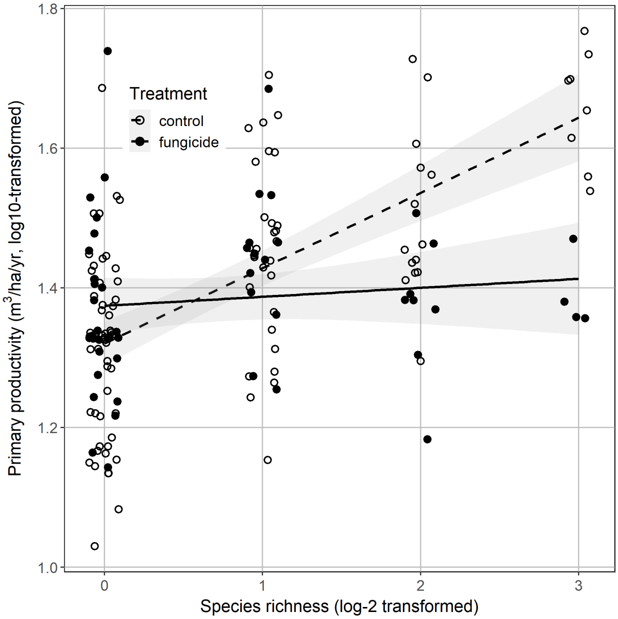

Fig. 10.4: Relationship between primary productivity (yearly increase in stand-level tree volume) and tree species richness (number of tree species planted in a square plot of 1/15 ha) in control and in fungicide-treated subplots in the BEF-China forest experiment. There were two control subplots and one fungicide subplot per plot. Primary productivity was $\log_{10}(y + 10)$-transformed (because some y-values were negative) and then adjusted by adding means for the four tree species richness levels to plot residuals. The slopes of the fitted lines follow the pattern of Fig. 10.1g and are significantly different ($P < 0.001$). The grey bands represent 95% confidence bands around the regression lines. Data are taken from Huang et al. (2022).

Compared with insect herbivores and enemies, for pathogenic or mutualistic microorganisms including fungi, it is more difficult to distinguish richness and abundance, especially if molecular methods must be used for their assessment (Schmid et al. 2021). This is unfortunate, because — at least for pathogenic fungi – richness and abundance and their effects often seem to be negatively correlated, as for example Rottstock et al. (2014) report from the Jena Experiment. In contrast, richness and abundance and their effects were positively correlated in the above-presented examples from BEF-China (Li et al. 2023) and the Jena Experiment (Scherber et al. 2010). It is also difficult to distinguish between effects of microbes that increase plant species complementarity by (i) reducing their interspecific competition via resource-use complementarity (Luo et al. 2018) or (ii) via pathogen-niche complementarity (Schnitzer et al. 2011; Huang et al. 2022), or (iii) that are increasing facilitation between plant species. As molecular methods and annotated data bases further develop, our understanding of the type of interactions with microbial trophic groups will hopefully increase in the near future. In the case of macro-organisms, an example of the latter is the attraction of pollinators by “nurse plants”, thereby increasing the pollination of neighbouring plant species (Losapio et al. 2019, 2021).

10.5 The role of trophic interactions in biodiversity–ecosystem functioning relationships

I presented the above examples as novel evidence for the complex yet often beneficial effects of trophic diversity on plant diversity–productivity relationships. The spectrum of effects observed for insect herbivores and enemies is similar to that observed for microbial pathogens and microbial and pollination mutualists. Often, trophic interactions reduce interspecific apparent competition between plants, thus increasing positive effects of plant diversity on productivity and associated further ecosystem functions such as carbon storage. The observational (Schuldt et al. 2023) and experimental (Huang et al. 2022; Yang et al. 2022; Li et al. 2023) studies carried out in Chinese forests strongly suggest that “trophic-niche partitioning” can contribute to plant diversity effects. This partitioning occurred with respect to insect herbivores and enemies and with respect to fungal pathogens and mutualists. Concluding from additional studies in BEF-China (Luo et al. 2018; Huang et al. 2018), a greater diversity of multiple trophic groups combines to an increased carbon capture in forests with a high tree species richness.

Considering the beneficial effects of trophic diversity in addition to plant diversity on primary productivity and ecosystem functioning more generally (Schuldt et al. 2018) I find it difficult to believe that the degree of division of labour in an ecosystem, both within and between trophic groups, is just a consequence of random processes. If ecosystems with higher trophic diversity have higher ecosystem functioning, they should be the ones that most likely persist for a longer time in nature. And during this time, it is conceivable that interactions among species within and between trophic groups evolve, such as in the classic case of plant–pollinator or plant–mycorrhizal fungi interactions but also in the case of plant–plant interactions as shown for the grassland ecosystems of the Jena Experiment (Zuppinger-Dingley et al. 2014; van Moorsel et al. 2021), where trophic interactions were less beneficial than in the more complex forest ecosystem of BEF-China. Thinking of current microbiome research and the mentioned beneficial effects of leaf bacteria (Laforest-Lapointe et al. 2017) and fungi (Huang et al. 2022), a role of co-evolution in shaping trophic interactions in ecosystems appears even more realistic.

Clearly, there is a long way to go in analysing the role of trophic interactions in biodiversity–ecosystem functioning relationships and in researching the causes for the existence of such highly complicated biological interaction systems. Our current knowledge is still mostly based on observational studies — where it is hard to reveal causality even with the most sophisticated tools (e.g. Dee et al. 2023) — and on complete removal of multiple trophic groups at once. To experimentally study the effects of the total biodiversity in an ecosystem on its functioning requires careful manipulation of trophic diversity at different levels. So far it has mainly been done for primary producers but rarely for insects (but see for example Deraison et al. 2015). This is a good start, but the new results presented in this chapter suggest that many further exciting findings lay ahead. Let’s hope that these can be obtained before the manipulations will be done by unwanted large-scale extinctions across trophic groups due to anthropogenic activities.

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Chapter 11
Multitrophic interactions in agroecosystems: Playing the methods keyboard

Christoph Scherber

Abstract Agroecosystems are complex systems of interacting species, yet it is still common sense to divide these organisms into "beneficials" and "pests". As the number of pesticides available to farmers is decreasing, alternative strategies of manipulating pests and diseases need to be explored. Such manipulation requires knowledge of the network of multitrophic interactions in agroecosystems. Traditional methods such as timed counts, exposure of standardized resources, and various arthropod collection methods are currently used to measure multitrophic interactions. With technological advancements, molecular methods based on analysing the faeces, tissues or gut content of target taxa, or detecting DNA traces have been developed. Additionally, visual and acoustic sensors advance our possibilities to measure biotic interactions and presence of organisms. These approaches have been used to measure insect activity, predation rates, and to reconstruct plant-flower visitor and host-parasitoid networks. To scale up, a solid study design must be implemented, allowing for networks of sensors easily deployable by farmers in the field. If also industry stakeholders become involved and farmers become the next generation of citizen scientists, then real time monitoring of multi-trophic interactions in agro-ecosystems could become a reality.

11.1 Why bother about multitrophic interactions in agroecosystems?

Agroecosystems are complex systems organized in networks of interacting species (Fig. 11.1). While this has been acknowledged in a range of publications (e.g. Altieri 1999; Bohan et al. 2013), it is still common sense to divide organisms in agroecosystems into "beneficials" and "pests" (Karp et al. 2018; Savary et al. 2019, Fig. 11.2a-f), rather than considering the system from a holistic viewpoint. For example, when insecticides are sprayed against a "target pest", the insecticide will never truly only work against that one single target species; it will

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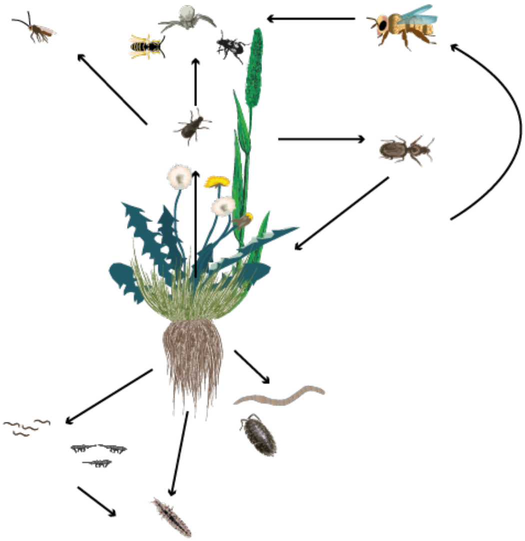

Fig. 11.1: Agroecosystems are organized in complex multi-trophic networks that need to be considered in a holistic way whenever management measures (such as pesticides) are applied. © C.Scherber

indirectly affect also other species, not only insects, but potentially also rather distantly related species (e.g. Douglas et al. 2015). Even worse, combinations of pesticides may make the story even more complex (Rumschlag et al. 2020; Sanchez-Bayo 2011) – in short, yes, it makes sense to invest into studying multitrophic interactions in agroecosystems not only from a purely biological or agroecological viewpoint, but also from a production systems perspective.

Embracing the whole network of interacting species is also important from another point of view: The number of pesticides that farmers are allowed to use on their fields is increasingly getting lower and lower (Handford et al. 2015), and farmers need to find alternative strategies to manipulate pests and diseases on their fields. Replacing pesticide use with biodiversity enhancement strategies, such as on-farm or off-farm biodiversity management, may be a promising alternative to the chemical mace (Thomine et al. 2022). But how can we find out which organisms benefit and which don't from a given biodiversity enhancement approach?

Is it possible to better understand which organisms are beneficial and which aren't? Answering these questions would require a full assessment of feeding interactions or even indirect interactions in agroecosystems. Even for comparatively simple food webs, such as those associated with single crop plant species (e.g. oilseed rape; Fig. 2c-e), this can be challenging. And, overall, for most organisms we simply don't have this information.

Would it not be great to be able to assess full networks of feeding interactions under field conditions and in real time? And, even if species-by-species interactions cannot be

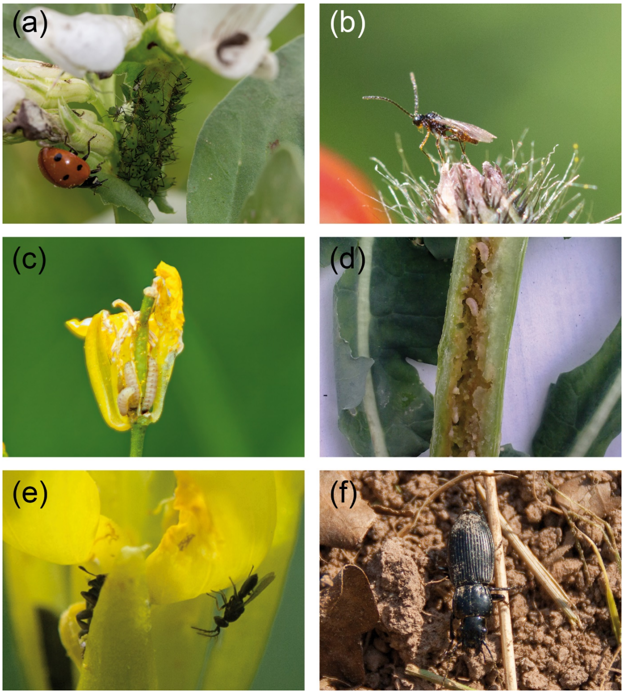

Fig. 11.2: Pests and beneficial organisms in agroecosystems. (a) Green aphids (likely the vetch aphid, *Megoura viciae*) and a ladybird polyphagous predator, *Coccinella septempunctata*, on Faba bean (*Vicia faba*); (b) an aphid parasitoid on an inflorescence of *Hieracium aurantiacum* infected by the Aphid species *Nasonovia pilosellae*; (c) larvae of the rape pollen beetle, *Brassicogethes aeneus*, a pest of oilseed rape, *Brassica rapa*; (d) endophagous herbivores in *Brassica rapa*, the cabbage stem weevil, *Ceutorhynchus napi*; (e) *Tersilochus heterocerus*, parasitoids of rape pollen beetle, *Brassicogethes aeneus*; (f) a polyphagous Carabid beetle, likely *Pterostichus niger*. All images © C.Scherber

assessed, which surrogate measures of trophic interactions and interaction strengths are possible?

In this chapter, I will provide an overview of the range of methods that are currently available to measure multitrophic interactions in agroecosystems. I will also show examples for some of the most novel methods that we have at hand, discuss about how these methods can be scaled up, and finally also draw some conclusions with respect to developing approaches to real time monitoring of multitrophic interactions in agroecosystems.

11.2 Which traditional methods do we have at hand?

Even a single oilseed rape field that essentially consists of just a single crop plant may contain a multitude of different species (Kirk 1992; Fig. 11.2c-e) that interact with each other. For

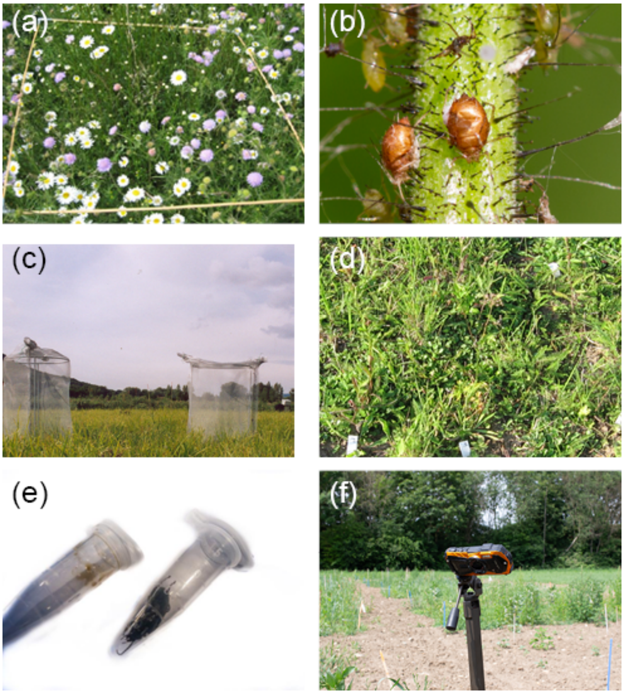

Fig. 11.3: Traditional and modern methods for assessing multitrophic interactions in agroecosystems. (a) Traditional pollinator observation plot; (b) aphid mummies as a sign of parasitism rates; (c) grasshopper cage enclosures; (d) transplanted phytometers; (e) eDNA metabarcoding samples for regurgitate analysis of Carabid beetles; (f) pollinator observation cameras. Fig. a by Christine Venjakob, all other images © C.Scherber

example, many insect species inhabit the stems and flowers, and each of them is parasitized by a specialist parasitoid that is again hyperparasitized by a specialised hyperparasitoid. This applies to any crop plant or cropping system - even a single plant species generally hosts a large range of insect species, all interacting with each other in multitrophic networks.

In some cases, interactions can be observed directly – as has been shown, for example, for plant-herbivore or plant-pollinator interactions. This usually involves timed counts, for example by randomly observing a given unit of space (observation plot: Westphal et al. 2008, Fig. 11.3a) for a given amount of time. The resulting data will usually be waiting times following an exponential distribution (even though they have rarely been analysed taking this fact into account).

Pieces of vegetation can also be exhaustively sampled, e.g. by taking a beating sample or cutting off a given amount of vegetation "biovolume", and then sorting organisms according to on which (host) plant they had been found (Brandmeier et al. 2021).

If the interest lies in measuring process rates (rather than sampling the organisms), a multitude of methods exists for the measurement of herbivory, pathogen infection, predation, parasitism (Fig. 11.3b), hyperparasitism or flower visitation rates (Meyer et al. 2015; Scherber et al. 2010).

Rather than just observing interactions, a much better approach is to perform experimental manipulations, such as using enclosures or exclosures (Fig. 3c), provisioning of food or nesting resources, or transplanting phytometer plants (Clements and Goldsmith 1924; Scherber et al. 2006, Fig. 11.3d) into crop fields or grassland (Table 11.1).

Enclosure cages or fences can be useful for studying particular subcomponents of a multi-trophic system, for example the famous cage experiments by Oswald J. Schmitz 2008. Similarly, predators can be excluded from crop plants, allowing to study indirect effects of predation on herbivore density and crop performance (Thies et al. 2011). Providing artificial food resources, such as sentinel prey can be a useful method to study if particular predators are present in a system (Lovei and Ferrante 2017). The same applies to nesting resources – for example, trap nests (Staab et al. 2018) or artificial sand patches (Gardein et al. 2022) can be deployed to find out about which solitary wild bees inhabit an area. Phytometer plants can be transplanted to grassland or crop fields as a standardized food resource, allowing a multitude of trophic and non-trophic interactions to be studied. An even better approach is to experimentally sow standardized crops of the same variety into fields, as has e.g. been recently done in wheat fields (Raatz et al. 2021).

11.3 Which novel methods do we have at hand?

Technological advancements over the last years have made it possible to think about assessing multitrophic interactions almost in real time (Table 11.2). Broadly, the technological approaches can be classified as (i) molecular methods, such as (e)DNA metabarcoding (Fig. 11.3e) (ii) visual sensors (Fig. 11.4f), such as active vision insect monitoring cameras, (iii) chemical ecology approaches, such as assessments of volatile organic compounds (Fig. 11.4a), (iv) setting out sentinel prey items coupled with camera monitoring (Fig. 11.4b,c), (v) various ways of deploying automatized version of insect traps over longer periods of time (Fig. 11.4d,e) and (vi) acoustic sensors, such as automated devices to record animal sound (Fig. 11.4f).

Certainly the currently most promising technology to study “who is eating whom” is to employ molecular methods based on either analysing whole insect communities (classical DNA metabarcoding) the faeces or gut content of target taxa (Tiede et al. 2020; Tiede et al. 2016, Fig. 11.3e), the tissues of insect hosts such as aphids (Hrcek and Godfray 2015), or by detecting DNA traces of organisms on surfaces such as leaves or flowers (eDNA metabarcoding, Allen et al. 2023; Clare et al. 2021). In a recent study, pollen and animal samples from trap-nesting bees and wasps were also analyzed using DNA metabarcoding (Dürrbaum et al. 2023), allowing to reconstruct pollen-flower visitor and host-parasitoid networks in response to landscape structure.

While analysing environmental DNA is certainly worthwhile, one should not forget that this is a very, very sensitive method, amplifying even single DNA molecules but not “proving” that an interaction has really taken place. Rather, eDNA metabarcoding allows for some first guesses that need to be carefully followed up on by more in-depth observa-

Table 11.1: Manipulation of trophic interactions in agroecosystems using enclosures, exclosures, provisioning of food or nesting resources, and phytometer experiments.

Interaction	**Examples**	**Enclosure fences or cages**	**Exclosure fences or cages**	**Provisioning of food resources**	**Provisioning of nesting resources**	**Phytometer experiments**
Mutualism (+/+)	Plant-pollinator interaction	x	x	x		x
	Seed dispersal by animals		x	x		x
	Aphid-ant mutualism		x			x
Commensalism (o/+)	Phoresy					
	Inquilines in wild bee nests				x	
	Birds and crops; cattle egrets					
	Facilitation - ladybugs and plants	x		x		
	Louse flies on cattle					
Amensalism (o/-)	Allelopathy (crops and weeds					
	Associational resistance					
	Trampling or crushing damage		x			
Predation (+/-)	Herbivory (chewing, sucking, mining)	x		x		x
	True predation - e.g. Carabid beetles	x	x			x
	Parasitism - e.g. aphid infestation, nematodes	x		x		x
	Parasitoidism - e.g. insect parasitoids			x		x
	Contramensalism (resource modification)					
Competition (-/-)	Competition for resources in insects (e.g. nectar, pollen)	x				
	Crop-weed interactions		x			x
Non-trophic interaction	Presence of foundation species					x
	Provision of shelter or shade					x
Tri-trophic interactions	Natural enemies affecting herbivore traits, altering plant-herbivore interactions					
	Plant volatiles altering herbivore-natural enemy interactions					x
	Herbivores altering plant-natural-enemy interactions					x
	Trophic cascades altering plant community composition	x				x
	Bottom-up and top-down effects	x				x

Table 11.2: An overview of trophic interactions in agroecosystems and how they can be measured with a range of modern technological approaches.

		Molecular methods		Optical sensors		Acoustic sensors	Chemical sensors
Interaction	**Examples**	**DNA metabarcoding**	**eDNA metabarcoding**	**Ground-based RGB cameras**	**Remote sensing cameras**	**Microphones**	**Gas chromatography**
Mutualism (+/+)	Plant-pollinator interaction		x	x			
	Seed dispersal by animals			x			
	Aphid-ant mutualism						
Commensalism (o/+)	Phoresy		x				
	Inquilines in wild bee nests	x	x	x			
	Birds and crops; cattle egrets			x	x	x	
	Facilitation - ladybugs and plants	x		x			
	Louse flies on cattle	x					
Amensalism (o/-)	Allelopathy (crops and weeds			x			
	Associational resistance			x			
	Trampling or crushing damage			x	x		
Predation (+/-)	Herbivory (chewing, sucking, mining)						x
	True predation - e.g. Carabid beetles	x	x	x			
	Parasitism - e.g. aphid infestation, nematodes	x	x				
	Parasitoidism - e.g. insect parasitoids	x	x				
	Contramensalism (resource modification)						
Competition (-/-)	Competition for resources in insects (e.g. nectar, pollen)	x	x	x			
	Crop-weed interactions			x	x		
Non-trophic interaction	Presence of foundation species			x			
	Provision of shelter or shade			x			
Tri-trophic interactions	Natural enemies affecting herbivore traits, altering plant-herbivore interactions						
	Plant volatiles altering herbivore-natural enemy interactions						x
	Herbivores altering plant-natural-enemy interactions			x			
	Trophic cascades altering plant community composition				x		
	Bottom-up and top-down effects						

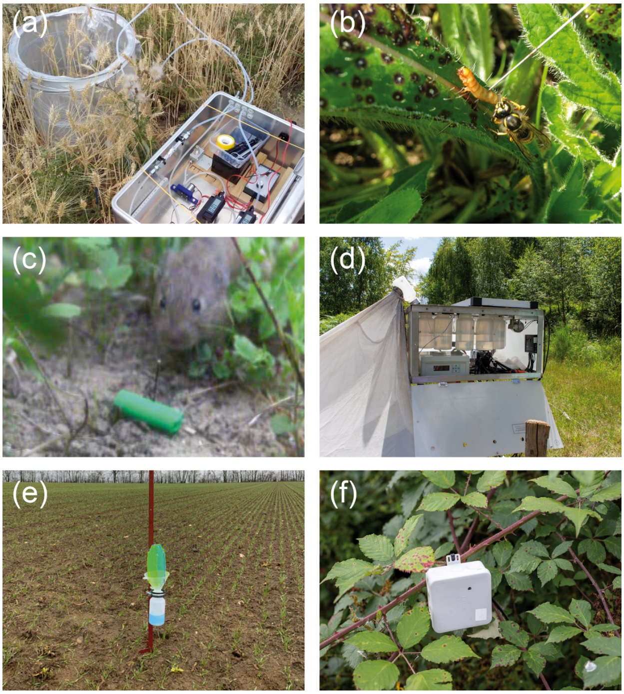

Fig. 11.4: Advanced methods to assess multitrophic interactions in agroecosystems. (a) Measurement of volatile organic compounds emitted in an intercropping trial; (b) deployment of sentinel prey using insect pins; (c) a dummy caterpillar pinned to the ground, photographed with a wildlife camera; (d) an automated Malaise trap with rotating sampling bottles; (e) a modified vane trap used for long-term measurements over the course of several years in collaboration with farmers; (f) an acoustic sensor (AudioMoth®) deployed in a hedgerow. Images c, d by Lionel Hertzog, all other photographs © C.Scherber

tions, such as linking to trait databases (Gossner et al. 2015) or text-mining approaches based on natural language processing (Ma et al. 2019).

Nevertheless, using such approaches can be insightful and open our eyes towards interactions that one would initially never have thought off. For example, in a study by Tiede et al. (2016), for a single Carabid species, interactions with intracellular parasites and extracellular protists were discovered that may be important for Carabid population dynamics and that had so far only rarely been considered. Similarly, investigations into the microbiome of prey or predator taxa may allow novel insights into how feeding preferences emerge at first place; for specialist herbivore insects, for example, the gut microbiome may be an important determinant of host plant specificity (Ma et al. 2021); however, research into the role of microbiomes and insect herbivory is still in its infancy, and there may be complex interactions also with the soil microbiome.

Another approach that has recently been suggested to study multitrophic interactions is to not focus on DNA or its traces, but rather to employ methods that sample the air for organic compounds emitted when trophic interactions are taking place (Fig. 11.4a; Ivaskovic et al. 2021). For example, aphid colonies are known to emit a substance called E-β-Farnesene, an alarm pheromone, when attacked by parasitoids or predators. Such volatile organic compounds (VOCs) can be measured using portable air pumping systems equipped with filters (Kunert et al. 2010). Similarly, a so-called Z-Nose system, which is essentially a portable gas chromatograph, may be deployed (Joachim et al. 2013). Such devices even allow to measure the plant community surrounding a given location without having to send out any botanists to assess the vegetation (Wägele et al. 2022).

On a different and more coarse scale, ask a farmer and he will maybe not want to know the details of volatile organic spectra or trophic interaction networks on his farm; rather, he may just want to know how many non-crop plants, birds or insects are living on his farm, and maybe also if their farm management is biodiversity-friendly. Usually, farmers will not be that much interested in ecosystem services delivered by organisms such as insects, unless their farm is heavily relying e.g. on crop pollination (such as apple orchards). Still, it would be desirable to be able to measure at least some kind of index of insect or arthropod "activity". One of the simplest methods is to deploy artificial prey items, such sentinel prey pinned to the vegetation (Fig. 11.4b) or dummy caterpillars made from plasticine (Fig. 11.4c) and combining such approaches with wildlife cameras to track predators.

Many of the currently developed sensor-based approaches aim at measuring "insect activity" in real time and tracking responses of insects to particular types of farm management such as application of agrochemicals or mechanical weed control. Essentially, these approaches boil down to (i) assessing wing beat frequency (Rydhmer et al. 2022), ideally using infrared-light emitters (light-emitting diodes) and receivers (ii) taking images of insects landing on an artificial of natural resource or hovering in the air (e.g. Geissmann et al. 2022; Pegoraro et al. 2020, Fig. 11.3f) or (iii) using multiple optical sensors, taking images from different angles, to record also insect flight path information (e.g. Straw 2021). A promising approach can be to deploy conventional insect traps such as pan traps, vane traps or Malaise traps (Fig. 11.4d,e), with a combination of optical sensors (infrared and visual spectrum). However, at least at current, all of these approaches suffer from lacking availability of high-quality training data to calibrate image classifiers. Many more image and spectrogram training datasets will need to be made publicly available to increase predictive accuracy of automated insect identification approaches (that usually run via so-called convolutional neural networks).

Acoustic sensors (Fig. 11.4f) currently play a minor role for direct assessments of insect activity (other than easily identified taxa such as crickets or grasshoppers), but recent technological advances appear promising (Ross et al. 2023). Additionally, autonomously operated ultrasonic recording devices can be very important and useful to assess, for example, bat activity and feeding bout frequency (Hill et al. 2018) that may indirectly structure insect communities and affect ecosystem process rates. Similarly, bird nest boxes can be equipped with a range of different sensors (cameras, microphones, and even eDNA sampling of faeces is possible: Verkuil et al. 2022), allowing estimation of predation rates, including major prey taxa and whether these are "pests" or beneficials in agroecosystems.

11.4 How to scale up?

While we now are in the rather luxurious situation that a broad spectrum of sensor technologies is at our fingertips to be deployed in agroecosystems anywhere in the world, there is so far no unifying concept or approach on what to do with the resulting masses of data. Crucially, any study can only be as good as the underlying study design and especially the treatments, their orthogonality and independence, spatial interspersion, and sufficient replication.

Let's say you want to study predation rates in an agricultural field of your choice; let this field be 1 ha in size. Even with the most fine-grained sensor network: What would you be able to conclude from a single field? And even if you knew the predation rate from as many as 100 sampling points in the field: What would your explanatory variable(s) be, other than "only" the latitude and longitude coordinate positions? Even if there would be a single flowering strip at the edge of the field: a sample size of one would not tell us anything.

Thus, any assessment of multi-trophic interactions, no matter whether with "traditional" or "modern" techniques, will require a solid study design right from the start onward. On a landscape scale, typically, something like at least ten fields (ideally 50 or 100) would need to be sampled along gradients established a priori, in order to be able to draw conclusions on effects of particular management interventions (e.g. Scherber et al. 2019; Scherber et al. 2021). If, additionally, different crops are to be compared, the required sample size increases even further.

This is where sensor networks could really make a difference and boost research to new dimensions. For abiotic measurements such as temperature, humidity or even air pollution, such sensor networks already are being built up (yet in a usually unstructured way: Bröring et al. 2012; Kamp et al. 2016). From an agroecosystems perspective, an ideal system will need to be deployable by farmers in their everyday farm management, and these sensors will also need to be easily removable should the farmer want to till the field or apply agroechemicals.

All of these approaches are under way, and they will, eventually, allow upscaling to a landscape, regional, national or even larger spatial scale, provided energy supply is guaranteed by sensors that consume little power and/or can be run using lightweight solar panels. Some of the most fascinating technological frontiers are power harvesting from WiFi signals (Talla et al. 2015) and wind-dispersed tiny sensors (Iyer et al. 2022) that may at least be used to measure environmental conditions at an unprecedented spatial resolution.

11.5 Towards real-time monitoring

An agroecologist's dream could become true, maybe, at some point in the near future: Open your smartphone and watch the pollinators in your apple orchard in real time; watch out for predation or biocontrol efficiency next to your flowering strip. Be able to judge how well your biodiversity-enhancement strategies work. All of this requires farmers that are fascinated by the creatures living in their fields; farmers who love and care for insects. Recent reports on insect declines (Seibold et al. 2019), and reports on declining pollination services (Stanley et al. 2015), may provide a unique chance that the time could indeed be ripe now for a new technological leap that makes farmers the next generation of citizen scientists, knowing not only how much yield they're going to obtain this year, but also how much biodiversity or ecosystem service value was provided on their land. If, then, also the agrochemical and machinery-producing industry would be on board, monitoring multi-trophic interactions in agro-ecosystems could really fly.

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Part IV
Food: Production, Waste and Security

Chapter 12
National yield stability of pollinator-dependent crops is stabilized by crop diversity but threatened by agricultural intensification

Ingo Grass & Oliver Peters

Abstract Growing global population and changing consumption behaviours are increasing demand for food, while climate change and biodiversity loss threaten stable harvests. Future food security requires not only increased production levels, but also better knowledge of yield-stabilizing practices, considering agronomic (e.g., fertilizers), climatic (e.g., temperature and precipitation) and biotic drivers (e.g., crop diversity, pollination dependence of crops). Here, we examined how nitrogen application, proportion of cropland, crop diversity, and climatic instability influence the temporal yield stability of crop production across the world, covering 134 countries, 133 crops and five decades. Thereby, we distinguished between pollinator-dependent and non-pollinator-dependent crops. Yield stability of pollinator-dependent crops was less affected by climatic instability than that of plants not dependent on pollinators. The amount of nitrogen use at national level correlated positively with the yield stability of non-pollinator-dependent crops, but negatively with the yield stability of pollinator-dependent ones. Contrastingly, increasing the diversity of crops grown at country level promoted the yield stability of pollinator-dependent crops more strongly than the yield stability of non-pollinator-dependent crops. Notably, few countries achieved high levels of yield stability and high overall yields, implying that practices to promote yield stability alone will not be sufficient to address world hunger unless they are also accompanied by an increase in overall crop production. In summary, practices related to agricultural intensification can threaten the yield stability of pollinator-dependent crops, while diversification of national crop production benefits the yield stability of pollinator-dependent crops more than that of non-pollinator-dependent crops. Diversifying agriculture and promoting crops that depend on pollinators can help improve food security in countries with low crop diversity, while also increasing yield stability to climate variability.

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12.1 Introduction

Crop yields have significantly increased over the last decades (Foley et al. 2011; FAO 2021b), but stability in yields has not always followed (Iizumi et al. 2014). Stable food production is of great importance to feed a growing world population despite projected increases in climate variations (IPCC 2019), threatening to cause harvest failures (Rosenzweig and Parry 1994). Ensuring national food supply through imports can only partly resolve national food shortages as an increased synchronization of crop failures can be observed globally (Mehrabi and Ramankutty 2019). Therefore, stability-enhancing practices must be evaluated to increase stability of crop production and to avert food shortages without compromising sustainability goals. Reducing the adverse effects of intensive agriculture on the environment is particularly important as most planetary boundaries related to agricultural production are already reached or exceeded (Rockström et al. 2020).

Agricultural intensification drives land and freshwater degradation, biodiversity loss, and loss of ecosystem services such as crop pollination (Foley et al. 2005, 2011). This can negatively affect crop production since globally 70% of the economically most important crops, accounting for one-third of agricultural production, benefit at least to some extent from pollinating animals (Klein et al. 2007). Moreover, pollinator-dependent crops have increased by more than 300% in production volume since the 1960s (Aizen and Harder 2009). Intensive conventional agriculture, with its heavy reliance on mineral fertilizers and chemical crop protection, has been found to reduce pollination in some crops (e.g., oil seed rape, common bean) (Marini et al. 2015; Ramos et al. 2018). Pollinators may also be stressed by climate change and increasing instability of temperature and precipitation, which can negatively impact pollinator populations and crop pollination (Rader et al. 2013).

Yield stabilization has been proposed as a strategy to counteract the aforementioned challenges and to lower the frequency of high yield losses (Lobell et al. 2008). On the national scale, yield stability is influenced by agronomic management (e.g., quantity of mineral fertilizers applied, irrigation practices, national cropland share on land area), precipitation, and temperature stability. Notably, recent studies also highlight the importance of national crop diversity for stabilizing yields (Renard and Tilman 2019; Egli et al. 2021; Mahaut et al. 2021). These studies found strong positive effects of crop diversity on temporal stability of crop yields across decades, with stabilizing effects from crop diversity similar in magnitude to the destabilizing effects of instability in precipitation (Renard and Tilman 2019). However, the aforementioned studies did not investigate whether temporal yield stability and stabilizing practices differ between crops of which yields either dependent on animal pollinators or are independent. Here, we investigated how agronomic, climatic and biotic drivers of yield stability differ between pollinator-dependent and non-pollinator-dependent crops, taking into account the temporal variability of agricultural production in 133 countries from 1961-2010.

12.2 Materials and Methods

12.2.1 Pollinator dependence and caloric yields of crop production

FAOSTAT distinguishes 179 crop commodities (crop species and crop groups) to categorize the world's agricultural production. We divided each of those commodities into three groups: pollinator-dependent, non-pollinator-dependent, and unknown. For this, Klein et al. (2007)'s categorization was primarily used. All crops benefitting from animal pollination were put in the category pollinator-dependent (85 crops). Only crops where the harvested plant parts (e.g., fruit, tuber, root) depend on animal pollination were included in this category. Crops that do not depend on animal pollination or that only benefit indirectly, for example, through seed production or breeding increases, were categorized as non-pollinator-dependent (68 crops). Crop species or crops groups for which no data were available were categorized as unknown (26 crops).

Next, we gathered data on crop yields from FAOSTAT, which provides information about every nation's annual production (tons) and area harvested (ha) for each of the 179 FAO crop commodities. These production data were combined with crop caloric data from the USDA Nutrient Database to calculate the annual caloric production for each crop commodity (kcal ha^{-1} per crop) and country. We only included countries and crop commodities for which annual data in each of the five decades from 1961-2010 were available. This resulted in a final dataset comprising 134 countries and 133 crop commodities (71 pollinator-dependent, 50 non-pollinator-dependent, 12 unknown).

12.2.2 Yield stability

Based on the annual caloric production data described above, we calculated the temporal stability S of national yield as $S = \mu/\sigma$, where μ is the mean national caloric yield of 10 years and σ the year-to-year temporal standard deviation for the decade. We calculated S for each of the five decades from 1961-2010. Afterwards, we removed national yield variation attributable to a temporal trend of increasing crop yield by regressing annual crop yields on year squared for each decade and nation (see Renard and Tilman 2019, for details). We calculated the yield stability for each country and decade based on 1) all crops produced; 2) only pollinator-dependent crops; 3) only non-pollinator-dependent crops.

12.2.3 Predictors of yield stability

As predictors of yield stability, we focused on agronomic, climatic, and biotic drivers. For the agronomy, we assessed the annual amount of mineral fertilizer application, the percentage of land area equipped for irrigation, and the proportion of the land area devoted to cropland in each country (using data from FAO 2021b; Our World In Data 2021). High amounts of fertilizer application, irrigation and land under cropland were interpreted as signals of agricultural intensification and reduced pollinator habitat. For the climatic data, we focused on temperature and precipitation instability. Following Egli et al. (2020), we calculated instability values of precipitation and temperature by dividing their annual means by their annual standard deviations, and afterwards inverting the resulting values (−(mm/SD; °C/SD)). The greater the negative value, the more stable the climate. For the biotic drivers, we assessed the effective crop species diversity of nations, calculated as the exponent of the Shannon diversity of produced crops weighted by their proportional area on the national cropland. We calculated the mean effective crop species diversity for each of for each nation and decade using the full dataset (all crops) and subsets (pollinator-dependent crops only, non-pollinator-dependent crops only).

12.2.4 Statistical analysis

We modelled the temporal yield stability in response to crop diversity, irrigated land, nitrogen fertilizer, cropland proportion and instability in temperature and precipitation. In addition, we included time (i.e., decade) as a factor to account for temporal changes in yield stability. In statistical notation, the model structure read:

$$\text{Yield stability} \sim \text{crop diversity} + \text{irrigation} + \text{nitrogen} + \text{cropland} + \text{time} + \text{temperature instability} + \text{precipitation instability}$$

Using this model structure, we calculated three models, based on the yield stability of 1) all crops produced; 2) only pollinator-dependent crops; 3) only non-pollinator-dependent crops. In three models, we scaled the predictors to zero mean and unit variance, which allows for direct comparisons of effect sizes within and across model results. Yield stability was log-transformed and some predictors square-root transformed (irrigation, nitrogen, cropland) to meet model assumptions of normality and homogeneity of variance.

12.3 Results

This study analyzed temporal trends in yield stability from 1961-2010 across 134 countries growing 133 crop commodities (crop species or crop groups), of which 71 were pollinator-dependent. Over the 50 years' timeframe, maize was the overall most common crop (on average 20.7% of caloric production), while soybean was the most common pollinator-dependent crop, which comprised on average 4.6% of caloric production but increased in recent years (2010: 7.1% of global caloric production).

The country average yield stability for the analyzed time frame was $S = 20.2$ (all crops), while it was $S = 17.7$ for pollinator-dependent and $S = 19.0$ for non-pollinator-dependent crops, respectively. Indonesia had the highest national decadal mean yield stability (1991: $S = 97.1$), followed by Haiti (1961: $S = 92.7$). Across the five decades, Morocco (average from 1961-2010: $S = 4.2$) and Botswana (1961-2010: $S = 5.1$) were the countries with the least stable yields in terms of caloric production. However, high yield stability did not always go along with high levels of overall crop production, i.e., high crop yields (Fig. 12.1). For example, Haiti ranged highest in terms of yield stability in the 1960s and 2000s, yet among the lowest countries in terms of overall crop production (Fig. 12.1). By comparison, yield stability in Germany were comparatively low in both decades, yet caloric yields were much higher. With respect to calories produced from pollinator-dependent crops, Malaysia had the globally highest share because of its great role in palm oil production, making up 77.2% of Malaysia's national caloric production (50-year average). The global average share of caloric production from pollinator-dependent crops increased over the 50 years by circa 2.5%, reaching 16.5% in 2010.

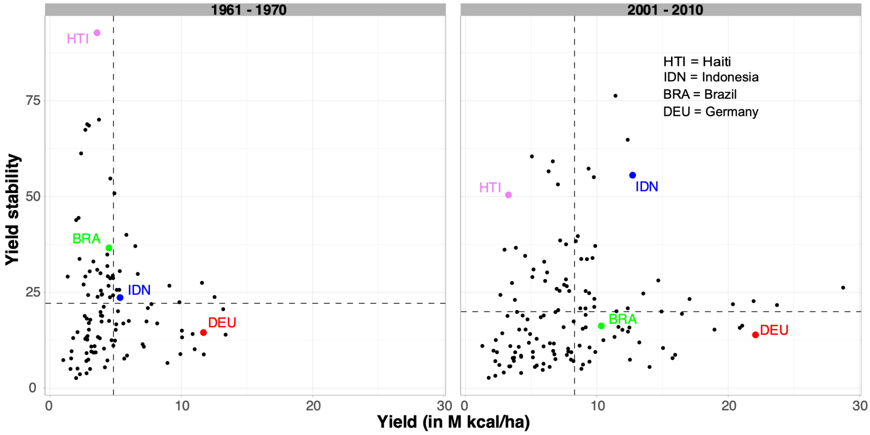

Fig. 12.1: Yield stability and overall crop production do not follow from each. Shown are yield stability (y-axes) and crop yields (x-axes) of countries for the timeframe 1961–1970 (left) and 2001–2010 (right). Black dots indicate the 133 countries included in the study, colored dots indicate Haiti (HTI), Brazil (BRA), Indonesia (IDN) and Germany (DEU). Note that while some countries achieve high yield stability, overall production levels (i.e., crop yields) remain comparatively low (e.g., Haiti). Dotted lines indicate the mean levels for each decade's yield and yield stability.

12.3.1 Drivers of yield stability

Greater crop diversity grown at national level enhanced the temporal yield stability of countries in all cases – that is, for yield stability of all crops produced, yield stability of pollinator-dependent crops, and yield stability of non-pollinator-dependent crops (Fig. 12.2; Table 12.1). Notably, the positive effects of crop diversity were most pronounced when considering yield stability of only pollinator-dependent crops, and least pronounced for non-pollinator-dependent crops (Table 12.1). Equipping arable land with irrigation systems positively affected yield stability of all groups, with the highest stabilizing effect for the non-pollinator-dependent crops (Fig. 12.2). Nitrogen input positively affected yield stability of non-pollinator-dependent crops but negatively affected yield stability of pollinator-dependent crops (Fig. 12.2; Table 12.1). Yield stability of crop production was not affected the share of land devoted to crop production. Similarly, to temporal trends were detected (Table 12.1). Temperature and precipitation instability had strong negative effects on yield stability of all crop groupings considered (Fig. 12.2; Table 12.1). Notably, these destabilizing effects were less pronounced for pollinator-dependent crops and most pronounced when considering non-pollinator-dependent crops or all crops combined (Table 12.1).

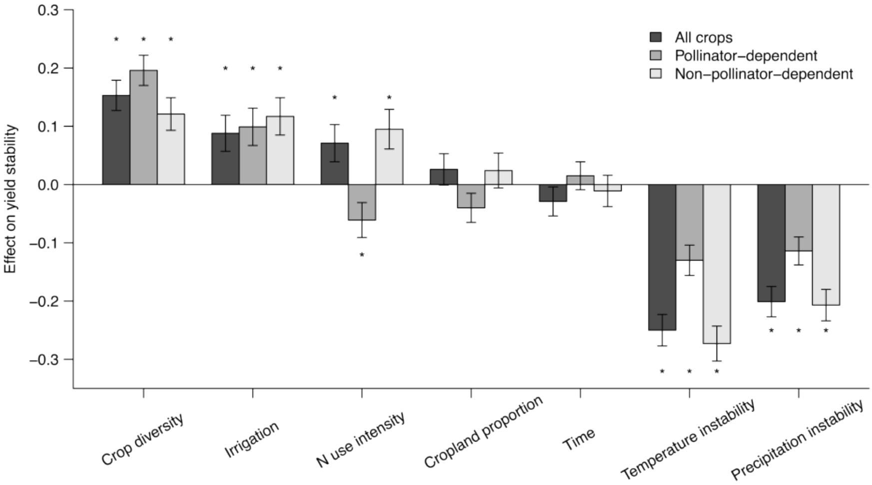

Fig. 12.2: Drivers of national yield stability of crop production across 134 countries. Results from three models are shown, considering the yield stability of either all produced crops within a country across five decades (1961–2010), only pollinator-dependent crops, or only non-pollinator-dependent crops. Shown are standardized regression coefficients of predictors (mean ± 1 standard error). Statistically significant predictions ($p < 0.05$) are indicated with asterisks.

12.4 Discussion

Here we compared the drivers of national yield stability of pollinator-dependent and non-pollinator-dependent crops across 133 countries and five decades from 1961-2010. Crop diversity at country level stabilized yields of both crop groupings, with greater stabilizing effects for pollinator-dependent crops than for non-pollinator-dependent crops. In addition, yield stability of pollinator-dependent crops was less affected by climatic variations in temperature and precipitation. Analysis of agricultural management practices showed that higher nitrogen use stabilized yields of non-pollinator-dependent crops, but negatively affected yield stability of pollinator-dependent ones. Finally, yield stability was often associated with low overall yields, suggesting that stabilizing practices do not necessarily benefit crop production per se.

12.4.1 Crop diversity stabilizes national caloric yields

Overall, the effective crop species diversity at national level exhibited strong positive effects in stabilizing national caloric yields. This stabilizing effect was most pronounced for yields of pollinator-dependent crop, and while still positive, less pronounced for crops of which yields do not depend on animal pollinators.

Our finding that increases in crop diversity lead to greater yield stability confirms previous studies testing the diversity-stability of national crop production (e.g. Doak

Table 12.1: Model coefficients explained variation of models testing effects of crop diversity, irrigation, nitrogen usage, cropland proportion, time and instability in temperature and precipitation on temporal yield stability of 133 countries from 1961-2010, considering a) all crops produced; b) only pollinator-dependent crops; c) only non-pollinator-dependent crops. Statistically significant predictors ($p < 0.05$) are highlighted in boldface type.

	Estimate	Std error	t	p
a) log (yield stability) – all crops				
(Intercept)	2.829	0.024	116.83	**<.0001**
Crop diversity	0.153	0.026	5.942	**<.0001**
sqrt (Irrigation)	0.088	0.031	2.854	**0.004**
sqrt (N use intensity)	0.071	0.032	2.212	**0.027**
sqrt (Cropland proportion)	0.026	0.027	0.945	0.345
Time	−0.029	0.025	−1.135	0.257
Temperature instability	−0.250	0.027	−9.242	**<.0001**
Precipitation instability	−0.201	0.026	−7.787	**<.0001**
$R^2 = 0.317$				
b) log (yield stability) – pollinator-dependent crops				
(Intercept)	2.720	0.023	119.864	**<.0001**
Crop diversity	0.196	0.026	7.450	**<.0001**
sqrt (Irrigation)	0.099	0.032	3.070	**0.002**
sqrt (N use intensity)	−0.061	0.030	−2.028	**0.043**
sqrt (Cropland proportion)	−0.040	0.025	−1.586	0.113
Time	0.015	0.024	0.643	0.521
Temperature instability	−0.130	0.026	−5.08	**<.0001**
Precipitation instability	−0.114	0.024	−4.83	**<.0001**
$R^2 = 0.223$				
c) log (yield stability) – non-pollinator-dependent crops				
(Intercept)	2.717	0.026	105.623	**<.0001**
Crop diversity	0.121	0.028	4.252	**<.0001**
sqrt (Irrigation)	0.117	0.032	3.603	**<.0001**
sqrt (N use intensity)	0.095	0.034	2.784	**0.006**
sqrt (Cropland proportion)	0.024	0.030	0.818	0.414
Time	−0.011	0.027	−0.429	0.668
Temperature instability	−0.273	0.030	−9.188	**<.0001**
Precipitation instability	−0.207	0.027	−7.617	**<.0001**
$R^2 = 0.278$				

et al. 1998; Renard and Tilman 2019; Egli et al. 2021). Renard and Tilman (2019) found that increases in the effective crop species diversity in a country are associated with more stable national yields and lower yield variability, mainly through the portfolio effect. In the context of agricultural production, this portfolio effect implies that when crop diversity is high, losses of some crop species are offset by gains of other species, and thus average yields fluctuate less than when diversity is low (see Tilman et al. 1998; Schindler et al. 2015).

The fact that the effect is stronger for crops that are dependent on pollinators than for crops that are independent of pollinators suggests that greater crop diversity is also beneficial for stabilizing ecosystem services such as pollination. Increased diversity of pollinator-dependent crops could benefit pollinator communities by providing a greater and more diverse range of food sources, contributing to pollinator resilience and the maintenance of pollination services at regional and national scales (Garibaldi et al. 2014). Conversely, pollination-limited crops with a high reliance on animal pollinators are more susceptible to yield losses resulting from a reduction of pollination services (Garibaldi et al. 2011). Losses in crop diversity and homogenization of agricultural landscapes are likely to exacerbate pollinator declines, which may threaten crop pollination.

12.4.2 Threats from agricultural intensification

Increasing the use of mineral nitrogen fertilizer at country level had contrasting effects on yield stability of pollinator-dependent and non-pollinator-dependent crops. While nitrogen fertilization contributed to yield stability of non-pollinator-dependent crops, increasing the amounts of nitrogen applied on fields destabilized yields of crops depending on pollinators, either via decreasing overall stability or increasing yield variation. Overall, nitrogen use stabilized yields across the crop dataset, which can be explained by the proportionally high share of non-pollinator-dependent crops included in the analysis (making up 83.5% of the total global caloric production from 1961-2010). Previous studies found evidence that higher yields from nitrogen fertilization are associated with greater yield variability and weaken yield stability (Renard and Tilman 2019), however, these studies did not consider crop dependence on animal pollination.

Reduced yield stability of pollinator-dependent crops due to nitrogen input might be explained by the share of legume crops in this group. Even though legume crops were present in both groups, they accounted for 35% of caloric production in pollinator-dependent crops but only 1% in non-pollinator-dependent crops (50-year average). Legume yields can be negatively affected by excessive nitrogen fertilization (Lütke-Entrup and Schäfer 2011). In addition, increasing nitrogen fertilization can reduce pollinator visitation, with adverse effects on crop yields of pollinator-dependent crops (Marini et al. 2015; Ramos et al. 2018). The underlying mechanisms are believed to be altered amino acid contents in both pollen and nectar due to nitrogen fertilization, rendering the plants less attractive to pollinators (Hoover et al. 2012). However, without fertilization and on nutrient poor soils, fruit set of pollinator-dependent plants is also low (Ramos et al. 2018), and mineral fertilizers are needed particularly in tropical countries.

The amount of nitrogen use per country can also be seen as a proxy of conventional agricultural intensification, usually accompanied by other aspects like agrochemical use and cropland expansion, which can drive environmental degradation and biodiversity decline (Kehoe et al. 2017; Lanz et al. 2018). Agricultural intensification considerably increased over time as nitrogen use has multiplied 9-fold from 1961 to 2010 (FAO 2016, 2021a). Effects of intensification that accelerate pollinator declines are habitat loss, increased pesticide use, reduced variety of grown crops, increased field sizes, and structural simplification of agricultural landscapes (Tscharntke et al. 2005; Potts et al. 2010). All of these agricultural changes can diminish the numbers of pollinators and may hence destabilize yields of pollinator-dependent crops.

12.4.3 Climate instability

Climate variations account for one-third of global yield variability (Ray et al. 2015). Over the 50-year time frame, climate instabilities in temperature and precipitation exerted a stronger negative impact on yield stability of non-pollinator-dependent crop as compared to pollinator-dependent crops. This indicates that pollinator-dependent crops have more resilient coping mechanisms to climate variability, which may increase their importance of future food security in the climate crisis.

Earlier studies using pollinator exclusion experiments examining stress resistance in crops found that pollinator-dependent crops can compensate for yield from heat or water stress when pollinators are present (Bishop et al. 2016; Raderschall et al. 2021). Compensating measures from animal pollination in stressed plants can result from pollinator-mediated transfer of fertile pollen into flowers with less fertile pollen or promotion of self-pollination in flowers (Bishop et al. 2016). However, studies examining the potential of animal pollination to buffer stresses in plant reproduction and crop yield are still scarce, and to our knowledge, no study so far tested the resilience of pollinator-dependent crops against climate instabilities at the national scale. Our study suggests a growing importance of animal-mediated pollination in a world where agriculture will be increasingly affected by drought, heat stress, and dry seasons (IPCC 2019). Adapting decision-making to protect pollinators and to adapt cropping systems accordingly is of particular importance for countries in the Global South where climate change is expected to significantly impact food security (Knox et al. 2012) and where irrigation systems are less affordable.

12.4.4 High yield stability does not necessarily coincide with high overall yield – country spotlights

Due to the projected increase in caloric needs tied to a growing global population, both yield stability and overall yields need to be considered to achieve food security. However, yield stability and overall yields are not necessarily positively correlated, and huge divergences between the two can exist (Fig. 12.1; Fig. 12.3). In the following, we discuss four countries' yield stabilities and their overall yields and analyse influencing factors of changes between 1961-1970 and 2001-2010.

12.4.5 Haiti

Haiti had the highest average yield stability among all 133 considered countries from 1961-2010 ($S = 60.5$), even though the country's yield stability decreased from $S = 92.7$ (1961-1970) to $S = 50.4$ (2001-2010) over time (Fig. 12.3). During this time, the decadal mean caloric yield also decreased by 9% (to 3.3 M kcal ha^{-1}) (Fig. 12.3). What could be reasons for the high yield stability but overall low crop production of the country? First, Haiti was not able to increase its crop production much during the five decades considered. During the entire study period, the decadal mean caloric production increased by 11% from $3.60 \cdot 10^{12}$ kcal (1960s) to $3.99 \cdot 10^{12}$ kcal (2000s), while the proportion of cropland increased by 19% (to 45% of the overall land area), resulting in an overall decline of calories produced per area (Fig. 12.3). At the same time, Haiti's population grew from ca. 4 million to more than 11 million people from 1961 to 2010, indicating that agricultural production could by far not keep up with population growth. In 1961, sugar cane ($0.86 \cdot 1010^{12}$ kcal) and maize ($0.881 \cdot 10^{12}$ kcal) were the most important crops in terms of calories produced. In contrast, maize ($1.21 \cdot 1010^{12}$ kcal) and cassava ($0.61 \cdot 1010^{12}$ kcal) were the primary crops in 2010. During this time, the share of pollinator-dependent crops increased from 7% to 21%,

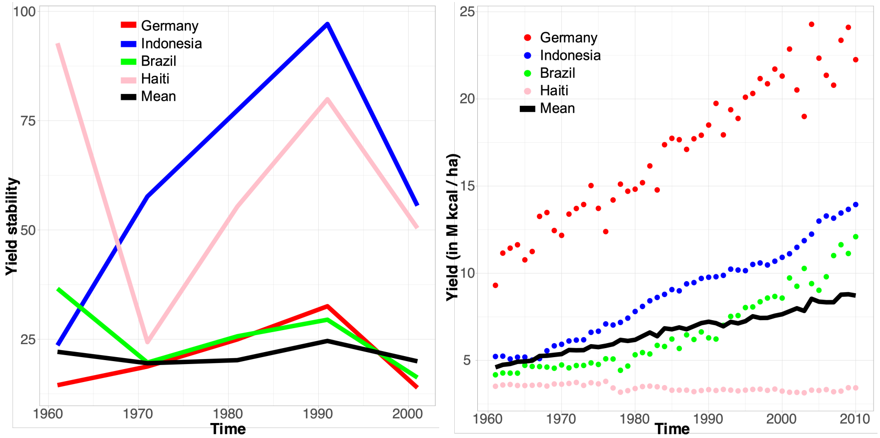

Fig. 12.3: Left: decadal yield stability for selected countries and the whole dataset (mean across 133 countries) across the study period. Right: temporal development of annual national yields and mean yields (all countries).

driven by, amongst others, pigeon peas (2010: 0.24·10^{12} kcal) and mangos (2010: 0.22·10^{12} kcal). Yet, at the same time, Haiti is among the most affected countries by climate change, with high levels of climatic instability, although stability has increased over the five-decade period (temperature instability: −159.8 to −54.6; precipitation instability: −8.8 to −5.9). In addition, Haiti uses very low amounts of nitrogen in both decades (1960s: 0.0001 t ha^{-1}; 2000s: 0.006 t ha^{-1}), indicating that agricultural production experienced relatively little intensification. Hence, Haiti maintained high levels of yield stability, however, with very low overall yields and little increases in crop production over time – a clear demonstration that food security cannot rely on yield stability alone.

12.4.6 Brazil

Brazil increased its caloric yields 2.3-fold from 4.5 M kcal ha^{-1} to 10.3 M kcal ha^{-1} while doubling its area harvested (30.3 M ha to 60.2 M ha) between 1961 and 2010 (Fig. 12.3). However, these increases were accompanied by reduced yield stability (S = 36.6 to S = 16.2). In 2010, three crops (soybean, sugar cane, maize) accounted for 82% of all calories produced (781·10^{12} kcal). Soybean experienced a 97-fold expansion in area, which helped Brazil to increase its share of calories generated from pollinator-dependent crops from 11.6 to 35.8%. During this time, the share of land dedicated to crop production increased from 4.0% to 7.1%. Soybean and pollinator-dependent crops may have been negatively affected by reduced effective crop species diversity (10.5 to 9.2) and increased mineral nitrogen fertilization (0.003 to 0.04 t ha^{-1}), reducing yield stability. From 1961 to 2010, mean temperatures increased but became more stable (−71 to −104), and land equipped with irrigation systems increased to 1.69% of cropland. Overall, yield stability of crop production in Brazil is mainly influenced by fluctuations in yields of the top three crops.

At the same time, overall yields and the amount of land devoted to crop production still increased in recent years, making fluctuations more likely.

12.4.7 Germany

Already high in the 1960s, mean decadal caloric yields in Germany increased 1.8-fold to 22.1 M kcal ha^{-1} by the 2000s. Yield stability, on the other hand, slightly decreased from $S = 14.5$ to $S = 13.9$, falling below the average of the 133 countries considered in this study ($S = 20.8$) (Fig. 12.3). From 1961 to 2010, the proportion of calories from pollinator-dependent crops increased from 2% to 12%, primarily due to increases in oilseed rape production. Wheat cultivation contributed most to caloric production, accounting for 39% of all calories produced in 2010. Because caloric yields of wheat and other crops fluctuated in recent decades (note the increasingly scattered overall yields since 2000 in Fig. 12.3), the decadal yield stability in Germany remained comparatively low. Yield fluctuations might be attributable to high inputs of nitrogen fertilizer (1960s: 0.10 t ha^{-1}; 2000s: 0.14 t ha^{-1}) and low levels of effective crop species diversity (7.7, 7.8). Modest levels of climate stability (temperature: −12.23, −15.4; precipitation: −6.5, −6.7) could also be associated with yield fluctuations. The observation that yield stability decreased in the last decade after having steadily increased over the preceding decades and peaking in the 1990s ($S = 32$) (Fig. 12.3), coincides with trends of increasing precipitation instability affecting Germany's agricultural production. Greater yield stability in Germany could possibly be achieved through higher shares of pollinator-dependent crops that resist climate instabilities and equipping more area for irrigation.

12.4.8 Indonesia

Indonesia increased its caloric yield 2.3-fold between the 1960s and 2000s and almost doubled its yield stability from $S = 23.6$ to $S = 55.6$ (Fig. 12.3), much higher than the global average yield stability in 2001-2010 ($S = 19.9$). Indonesia's high yield stability was achieved despite strong cropland increases, from 14% to 23% of the land area between 1961 and 2010. Increases in overall yields and yield stability were likely due to the country's stable paddy rice and palm oil production. Paddy rice production increased 5.5-fold since 1961 and accounted for 37.1% of the country's calories produced in 2010 ($186 \cdot 10^{12}$ kcal). The second most important crop in terms of calories, oil palm, accounted for 30.8% of caloric production in 2010 ($155 \cdot 10^{12}$ kcal) and experienced a 105-fold increase over the 50-year study period. The oil palm boom also increased strongly increased the share of caloric yield attributable to animal pollination (1960s: 18.4%, 2000s: 39.5%). With its tropical climate, Indonesia had the highest temperature stability of all 133 countries during the 1960s (−354) and, despite an overall decline, a still much a higher stability (−179) as compared to the global average (−61) in the 2000s. At the same time, mineral nitrogen fertilization 13-fold between 1960 and 2010, and the share of land equipped for irrigation increased from 10.1-12.4%. In sum, Indonesia successfully increased both overall yield and yield stability through strong and steady increases in caloric yields across the second half of the 20th century (Fig. 12.3), aided by high temperature stability, and increases in nitrogen use and irrigation.

12.5 Conclusions

Here we studied differences in stabilizing measures of national caloric yield stability of animal pollinator-dependent and non-pollinator-dependent crops globally. Crop diversity at country level stabilized yields of both crop groupings, with greater stabilizing effects for pollinator-dependent crops than for non-pollinator-dependent crops. In addition, yield stability of pollinator-dependent crops was less affected by climatic variations in temperature and precipitation. These findings support the importance of crop diversity, in particular of pollinator-dependent crops, for food security in a world increasingly affected by climate instability. By contrast, agricultural intensification in the form of increased nitrogen use negatively affected yield stability of pollinator-dependent crops. Hence, policies are needed that promote agricultural diversification of crop production at national levels but avoid negative effects of conventional agricultural intensification that are rampant in many countries of the Global North – and which increasingly also threaten biodiversity and ecosystem services in countries developing their agricultural sectors in the Global South. Importantly, we found that yield stability was often associated with low overall yields, suggesting that stabilizing practices do not necessarily benefit food security per se. Diversifying agriculture and promoting crops that depend on pollinators can help improve food security in countries with low crop diversity, while also increasing crop resilience to climate variability.

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Chapter 13

Towards new agricultural practices to mitigate food insecurity in southern Madagascar

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Abstract The south of Madagascar suffers from recurrent droughts with catastrophic effects on the human population and the globally unique biodiversity alike. During these times and shortly thereafter, households from only two out of 24 villages with a total of 374 households achieve food security and most households resort to food resources provided by the remaining forests and fallow land. This poses the question why forest food resources persist and remain available even when agricultural crops fail. The main difference seems to be that the majority of agricultural crops are annual plants that need to be replanted for each growing cycle and do not provide anything if the regular harvest fails, while 48 of 50 forest food resources used by people during times of food shortage are perennial and often woody species that can tolerate prolonged droughts. For improved food security, annual crops could be replaced by, or combined with, perennial crops in various agroforestry systems. These agroforestry systems could be designed to benefit humans and extend the remaining forest habitats for native plants and animals alike.

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13.1 Introduction

Madagascar is known for its exceptionally high endemism and rallying environmental destruction, making it one of the world's most threatened biodiversity hotspots (Myers et al. 2000). Yet, it is also one of the poorest countries in the world with a very poor record of governance and an obvious lack of interest in rural development and nature conservation (Jones et al. 2022). Development projects had little impact lasting beyond the actual project timeframes and the majority of measures of success towards the Millennium Development Goals showed negative trends between 2000 and 2015 (Freudenberger 2010; Waeber et al. 2016). As a result, Madagascar ranks 119th out of 121 countries assessed by the Global Hunger Index in 2022 (Resnick et al. 2022).

The situation is most precarious in the south of Madagascar. The semiarid region is characterized by recurrent droughts, leading to crop failures and hunger crises. In the driest part of the southwest, people cope with the problem by diversifying their sources of income (Hänke and Barkmann 2017; Narvaez and Eberle 2021; Neudert et al. 2015; Noromiarilanto et al. 2016) and clearing natural vegetation (the "dry and spiny forest ecosystem") for agriculture (Brinkmann et al. 2014; Fenn 2003; Zinner et al. 2014). Yet, increasing the area used for standard agriculture does not mitigate the effects of drought and failure of harvest. On the one hand, increasing the agricultural surface leads to a decrease of the area available for livestock, which are often kept as a sign of wealth and as an "insurance option", while also reducing forest cover with negative impacts on Madagascar's unique biodiversity (Nopper et al. 2018; Scott et al. 2006; Heland and Folke 2014). Under drought conditions, people sell livestock and many households resort to the collection of food and other resources in natural forests (Andriamparany et al. 2014; Feldt et al. 2016; Gardner et al. 2016; Hänke and Barkmann 2017). This leads to the discrepancy that natural forests are cleared for agriculture that provide income during years with sufficient rainfall, but people also need resources from these natural forests to survive periods of drought. The need to fall back on non-commercial food also illustrates that the current agricultural systems are insufficient to guarantee the survival of people without external assistance.

Malnutrition is widespread in Madagascar and most prevalent among children (Rakotomanana et al. 2017). Integration of forest resources, including bushmeat, can have a positive effect on human health, though certainly a negative effect on species conservation (Golden et al. 2011, 2019; Manjoazy et al. 2017; Thompson et al. 2023). This leaves us with the discrepancy that the current economic situation and development approach emphasizes the standard agricultural products with high yields in good years, but a high chance of failure in poor years. Thus, it would be desirable to add some kind of agricultural insurance options to the common practice. To this end, we used interviews to collect information on the demography, economic situation, standard agriculture, and utilization of forest resources of households from 24 villages in southern Madagascar (Fig. 13.1). These predictors were then linked to the nutritional state of people. Undoubtedly, data compiled by interviews are hampered by difficulties quantifying the information, but even these data on dietary intake and the nutritional value of food items can help to assess the state of local nutrition in relation to the economic and environmental situation, and derive relevant information on the role of natural food components collected in the forest (Francois 1962).

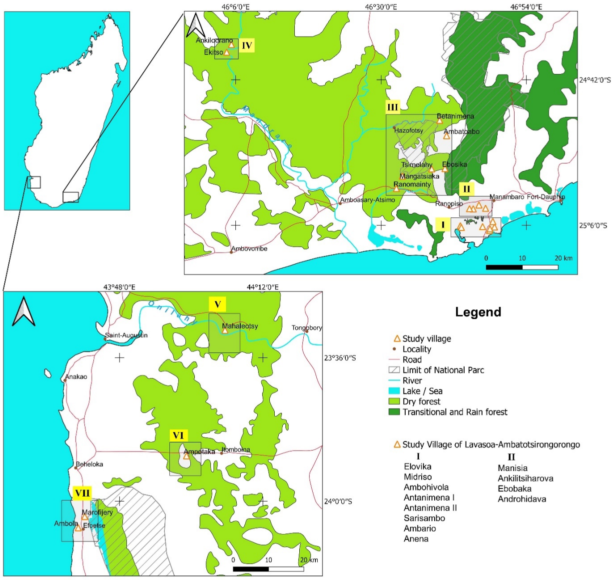


Fig. 13.1: Location of study sites in southern Madagascar. Roman numerals indicate study regions as listed in Table 13.1.

13.2 Study sites

Southern Madagascar is characterized by semi-arid climatic conditions with irregular rainfall averaging less than 600 mm per year (Armstrong and Goodman 2022) and often by years below 300 mm (Kasola et al. 2020). Annual mean temperature is about 24°C (Battistini and Richard-Vindard 1972). The dry season usually lasts 8–9 months, from March to October/November, but locally it may last for several years (Dewar and Wright 1993; Gould et al. 1999; Kasola et al. 2020). The original ecosystem is assigned to the spiny forest ecoregion (Fenn 2003; Moat and Smith 2007), with distinct subtypes of forest distributed in a mosaic-like fashion in relation to edaphic humidity (Andriaharimalala et al. 2011; Ratovonamana et al. 2011).

Cattle herding is the predominant practice in the south. Livestock serves as a sign of wealth but also as insurance for unexpected expenses and crop failure (Feldt et al. 2016; Hänke and Barkmann 2017). Rice cultivation is the most common agricultural practice in the more humid parts of Madagascar, while the dry south used to be dominated by the cultivation of cassava/manioc and sweet potatoes (Francois 1962, "alimentation type féculents":). Apart from the environmental conditions, people are restricted in their behavioural options by a wide range of taboos (referred to as "fady") that can vary locally and even within and between families. These taboos can have severe restrictions on the innovations or consumption of certain types of food, such as using manure for fertilization or eating lemurs, tortoises, or tenrecs (Jaonasy and Birkinshaw 2021; Ruud 1960).

The southwestern study region ranges from the Onilahy River south of Toliara to Tsimanampetsotse National Park (Goodman et al. 2018). Apart from the riverine system of the Onilahy, it mostly covers the sandy plains of the coastal region between the sea and the Mahafaly Plateau. Ethnically, the region is dominated by Vezo along the coast who focus on fishing, and by Mahafaly and Tanalana people, who are primarily known as cattle herders. The latter cultivate mainly cassava, maize, legumes, and sweet potatoes (Brinkmann et al. 2014).

The southeastern study region extends between the Mandrare River and Parcel 2 of Andohahela National Park. Ethnically, the region is dominated by Antandroy. Since the region receives slightly more rain than the south-western study region, people try to cultivate rice, especially along river systems. The southeastern study region includes villages bordering the protected area of Lavasoa-Ambatotsirongorongo in the south. Lavasoa-Ambatotsirongorongo is a transitional forest with distinctly more rain than at the other sites (Goodman et al. 2018).

13.3 Variability of primary production

To illustrate the inter-annual variation of the productivity of the spiny forest ecosystem, we used the southwestern study region as an example. We obtained annual Net Primary Production (NPP) data at 500 m pixel resolution for 2001—2022 from the gap-filled Moderate Resolution Imaging Spectroradiometer (MODIS) MOD17A3HGF product (version 6.1) (Running and Zhao 2021). We extracted all annual NPP values in the study region and calculated an average across the region for each year (Fig. 13.2). The average NPP varied considerably between years, ranging from around 420 g C/m^2/year in drought years to around 700 g C/m^2/year in non-drought years, as the interannual variability in NPP is strongly influenced by droughts in semi-arid ecosystems (Huang et al. 2016). The last three years were characterized by low NPP values. As indicated by the comparison of NPP between 2019 and 2020, NPP does not only show very high fluctuations between years, but also high spatial variations at very small scales (Fig. 13.3).

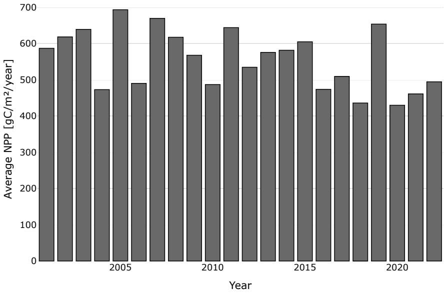


Fig. 13.2: Average annual Net Primary Production (NPP) in the western study region from 2001 to 2022.

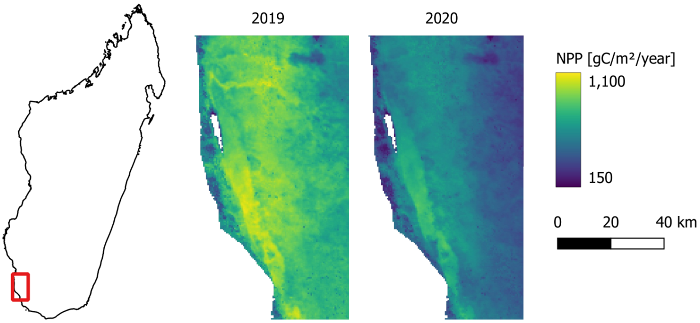


Fig. 13.3: Annual Net Primary Production (NPP) in 2019 and 2020 in the western study region in and around Tsimanampetsotse National Park, southwestern Madagascar.

13.4 Household surveys

In 2021 and 2022 we interviewed 374 households in 24 villages assigned to seven geographic subregions (Fig. 13.1; Table 13.1). Interviews followed a questionnaire developed previously for the spiny region (Andriamparany et al. 2014; Neudert et al. 2015) which has since been applied in other regions of Madagascar (Konersmann et al. 2022). Interviews were run by the Malagasy authors in collaboration with local assistants. Since interviews were completed non-concurrently, they cover different seasons of the year. This caveat may not be relevant for the general questions, but has implications for the analyses of food security.

Table 13.1: Number of households surveyed in 24 villages from seven geographic regions. # = study regions illustrated in Fig. 13.1; "Harvest" indicate whether or not people had been able to harvest crops prior to or during the time of survey; C = cassava (manioc), SP = sweet potatoes, M = maize. Number of people per household are means ± standard deviation and minimum and maximum numbers per household in brackets.

Region	**#**	**Months and year of survey**	**Harvest**	**Number of villages /households**	**Number of people per household**
Southeast					
Lavasoa-Ambatotsirongorongo Sud	I	4, 5 / 2021	None	8 / 92	6.33 ± 2.27 (1 – 14)
Lavasoa-Ambatotsirongorongo Nord	II	4, 5 / 2021	None	4 / 46	5.96 ± 2.87 (2 – 13)
Andohahela	III	6 / 2021	C, SP	6 / 59	5.05 ± 2.18 (1 – 11)
Ebelo	IV	6 / 2021	C, SP	2 / 20	5.35 ± 2.21 (2 – 20)
Southwest					
Amoron'i Onilahy	V	8 / 2022	C, SP, M	1 / 41	5.80 ± 3.33 (1 – 18)
Ampotaka	VI	7 / 2022	C, SP	1 / 37	5.73 ± 2.93 (1 – 13)
Tsimanampetsotse	VII	7, 8 / 2022	C, SP	2 / 79	6.82 ± 2.90 (2 – 15)

13.5 Demography

The seven regions show similar demographic structure with a very large proportion of children and young people (Fig. 13.4). The reduction of age cohorts towards adulthood in the driest regions (Ebelo, Tsimanampetsotse and Ampotaka indicates high child mortality. In most regions, the sudden drop around the age of 20 might reflect emigration of young adults to larger towns and/or cities. Reasons for the demographic structure were not part of the questionnaire. For the compilation of the demography people were simply asked for their age. Thus, the older ages, especially in the southwestern regions, are to be considered personal perceptions of the people interviewed rather than documented ages.

13.6 Agricultural activities

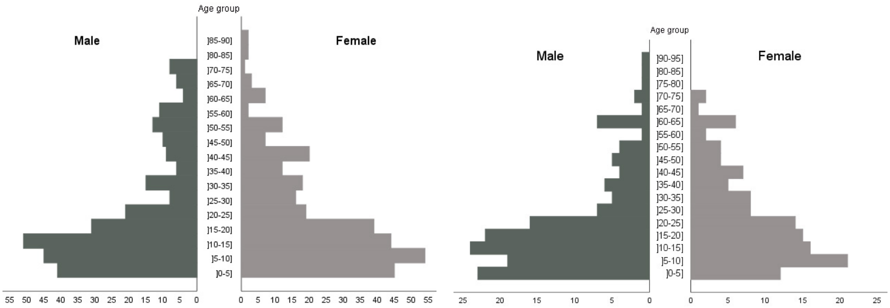
As already described by Francois (1962) during colonial times, manioc and sweet potatoes are still grown most often. Rice and maize are grown at sites where rivers allow irrigation or have a high groundwater table due to their proximity to rivers (e.g., Andohahela, Ebelo, Amoron'I Onilahy). At Andohahela, creeks are more seasonal than the rivers Mandrare and Onilahy in the other two regions. Due to the lack of rain in Andohahela, rice paddies were not cultivated in the year of survey (2021) and had not been cultivated since 2017. In years of drought, holding rice paddies available in expectation of rain reduces the available arable land that could have been used for other crops, especially those more adapted to dry conditions.

Elsewhere, maize is planted in years assumed to have enough rain. Due to the high unpredictability, this also bears high risk of complete crop failure and the lack of seeds for planting after repeated failure of growth. Sorghum would be better suited for dry conditions, but currently appears to be regionally restricted to the southwest. The region of Tsimanampetsotse contrasts from others as a much smaller proportion of households' plant crops. The low proportions are due to ethnic differences. Though the two villages surveyed in Tsimanampetsotse (Ambola and Marofijery) are adjacent to each other, Ambola is a fishing village inhabited by Vezo who do not practice agriculture, while Marofijery is an agricultural village that only recently increased fishing efforts because agricultural harvests have become too unreliable.

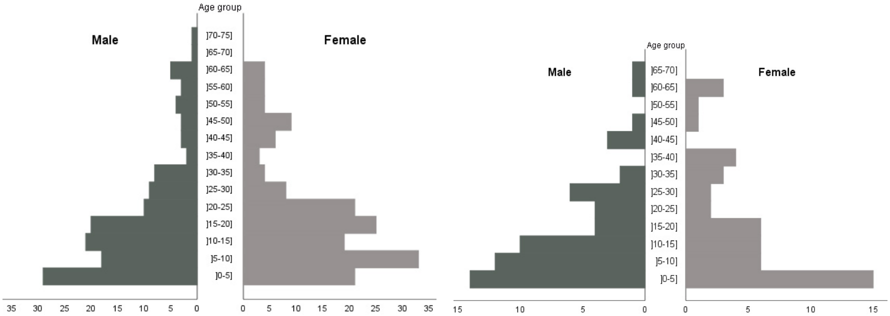
13.7 Food security

Our measures of food security represent the interview days and therefore should be considered a snapshot in time, while all other data represent the situation over the full annual cycle. Thus, these measures should be taken with caution and only as an indication of the situation.

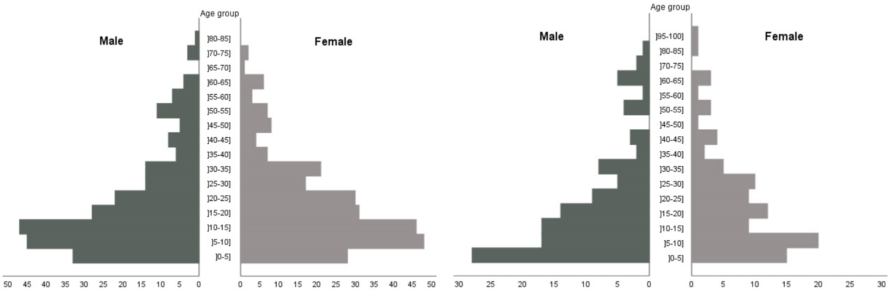
In "normal years", the months of April and May represent the end of the lean season without regular harvests. June and July are the months when manioc and sweet potatoes are harvested. Rice can be harvested in May, November and December. Thus, the southeastern sites had been surveyed during the lean times of the year at the end of a drought that had



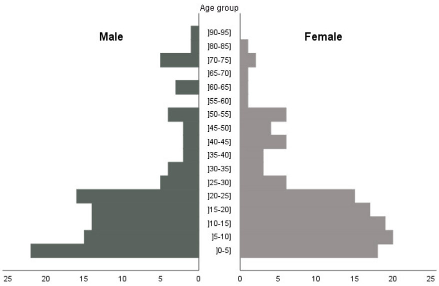
Lavasoa - Ambatotsirongorongo Sud (N=582) Lavasoa - Ambatotsirongorongo Nord (N=274)



Andohahela (N=298) Ebelo (N=107)



Tsimanampetsotse (N=507) Ampotaka (N=212)



Amoron'i Onilahy (N=233)

Fig. 13.4: Age structure of the human population in seven regions with a total of 24 villages and 374 households of southern Madagascar. N indicates the number of people recorded.

Table 13.2: Percentage of households with different agricultural activities in the study regions. Sample size as indicated in Table 13.1.

Region	Lavasoa-Ambato-tsirongo-rongo Sud	Lavasoa-Ambato-tsirongo-rongo Nord	Andohahela	Ebelo	Amoron'i Onilahy	Ampotaka	Tsimanam-petsotse
Agriculture							
Manioc	89.1	91.3	59.3	60.0	65.9	78.4	34.2
Sweet potatoes	91.3	97.8	47.5	40.0	63.4	8.1	32.9
Rice	62.0	73.9	52.5	0.0	0.0	0.0	0.0
Maize	5.4	8.7	20.3	90.0	73.2	24.3	24.1
Sorghum	0.0	0.0	0.0	0.0	31.7	51.4	21.5
Beans	10.9	6.5	5.1	10.0	48.8	91.9	39.2
Fruit	15.2	13.0	3.4	55.0	43.9	29.7	10.1
Vegetable	16.3	10.9	15.3	55.0	56.1	18.9	11.4
Others	3.3	4.3	0.0	5.0	10.0	10.8	1.3
Livestock							
Cattle	22.8	26.1	18.6	30.0	9.8	5.4	7.6
Sheep	0.0	2.2	1.7	15.0	2.4	10.8	11.4
Goats	0.0	0.0	18.6	30.0	22.0	16.2	13.9
Pigs	7.6	13.0	1.7	0.0	0.0	0.0	0.0
Poultry	48.9	39.1	25.4	5.0	24.4	59.5	63.3

lasted from 2017 to 2021. The southwestern sites had been surveyed after the harvest of manioc and sweet potatoes (Table 13.1).

The nutritional status of households was assessed by three different measures. First, we calculated the caloric intake in kcal per day and person. This measure is based on the quantity of food cooked per day. The caloric values of different food items from the region follow those assigned by Francois (1962). The Household Dietary Diversity Score (HDDS) adds a qualitative component to the measure of caloric intake. It is a simple addition of 12 food groups that are consumed by members of a household per day. These groups are: cereals, roots/tubers, vegetables, fruits, meat/poultry/offal, eggs, fish/seafood, pulses/legumes/nuts, milk/milk products, oil/fat, sugar/honey, and miscellaneous (Swindale and Bilinsky 2006). The Food Consumption Score (FCS) reflects the diversity of food consumed based on only eight categories: cereals, tubers and roots, pulses, vegetables, fruit, meat and fish, milk and other dairy, sugar, oil. As a further development of the HDDS, these categories are weighed differently according to their nutritive value. The weighted consumption of the different categories is summed, resulting in a FCS score that can be used as a measure of food security. Food security is considered to be acceptable above a daily intake of ≥ 2100 kcal or FCS ≥ 5 (Huang et al. 2015). For HDDS no definite threshold was defined as the perception of security varies widely in relation to the environmental situation (Hoddinott and Yohannes 2002). Though the three measures are highly correlated (all with $p < 0.001$), they reflect different strategies to satisfy nutritional needs, as the same caloric intake can be reached either by relying on a staple food source or by combining many different food types (Fig. 13.5).

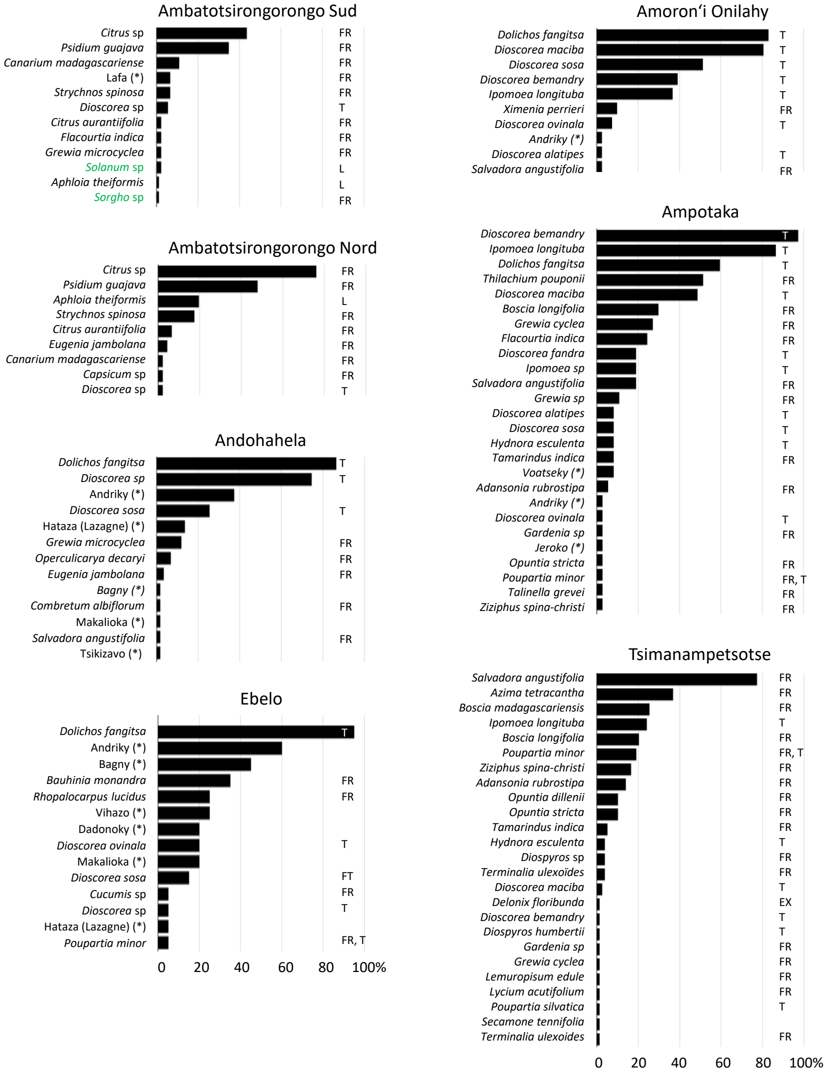


Fig. 13.5: Percentage of households collecting edible plant resources from forests; * vernacular names; annuals written in green; parts consumed: EX = exudates, FR = fruit, L = leaves, T = tubers.

Food security was most precarious in the driest regions, i.e., Ebelo, Andohahela, Ampotaka, and Tsimanampetsotse. This is reflected in the average caloric intake as well as in the HDDS and FCS categories. Ebelo was in the center of the food crisis in 2021, recognized globally. Here, 100% of households fell in the lowest FCS category (Table 13.3). Only Amoron'I Onilahy achieved acceptable food security according to FCS indices, but did not achieve satisfying caloric intakes (Fig. 13.6).

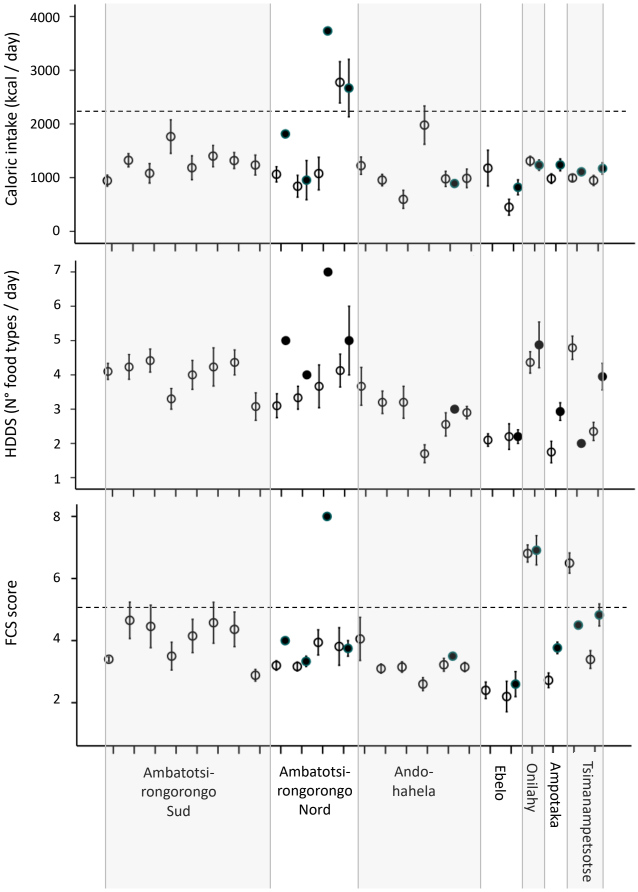


Fig. 13.6: Nutritional and food security measures for 24 villages of the seven regions. Values are means ± standard errors. White circles indicate households without fishing or hunting. Filled circles indicate households with fishing or hunting. The dashed lines indicate the threshold for acceptable food security (Huang et al. 2015). They should be considered as indications rather than absolute thresholds. HDDS (Household Dietary Diversity Score) = number of different types of food consumed per day; FCS (Food Consumption Score) = weighted consumption of different types of food, allowing for defining a score for food security.

Table 13.3: Measures of nutrition and food security. Values for the southeastern regions are based on one day of records. Measures for the southwestern sites were based on 7 survey days. To be comparable with the southeastern sites, Household Dietary Diversity Score (HDDS) was used only from the first day of survey and Food Consumption Scores (FCS) was standardized to a single survey day. Values for caloric intake and HDDS are means ± standard deviations; for FCS the percentage of households that fall into one of the categories: poor food security ($\text{FCS} \leq 3$); borderline ($3 < \text{FCS} \leq 5$); acceptable ($\text{FCS} > 5$).

Region	Lavasoa-Ambatotsirongorongo Sud	Lavasoa-Ambatotsirongorongo Nord	Andohahela	Ebelo	Amoron'i Onilahy	Ampotaka	Tsimanampetsotse
Caloric intake [kcal]	1283 ± 654	1443 ± 1093	1117 ± 740	907 ± 814	1297 ± 464	1183 ± 545	1030 ± 390
HDDS	4.0 ± 1.4	3.7 ± 1.4	2.9 ± 1.3	2.2 ± 0.6	4.5 ± 1.8	2.7 ± 1.4	3.9 ± 2.0
FCS: Poor	33.7%	43.5%	57.6%	100.0%	2.4%	37.8%	17.7%
FCS: borderline	50.0%	50.0%	39.0%	0.0%	7.3%	56.8%	35.4%
FCS: acceptable	16.3%	6.5%	3.4%	0.0%	90.2%	5.4%	46.8%

13.8 Utilization of forest resources

13.8.1 Type of natural food resources collected

Vegetable resources collected in natural forests include leaves from two plant species, fruits from approximately 34 species, seeds and exudates from one species, and tubers and roots from 14 species. Since some species were listed only by their vernacular names and were not physically available at the time of the household survey, species identity and growth forms were not known for all plant species.

The regions differ markedly in the types of food collected from forests. In the areas with most rain (Lavasoa-Ambatotsirongorongo), people collect mainly fruits from the forest. These can be fruits from native trees (*Strychnos spinosa*, *Flacourtia indica* [Indian plum] or *Canarium madagascariensis*) or introduced species that have invaded forests, such as Citrus fruits and *Psidium guajava* (Guava). In most other regions, tubers are collected by most households. These include several species of wild yam and storage organs of other plants. Fruits are also collected, but they come from a larger variety of species than at the more mesic sites (Fig. 13.5).

Of the known plant resources collected for consumption outside the agricultural fields, all but two stem from perennial plant species, with the vast majority belonging to woody plants (Table 13.4). Only sorghum growing as feral crop and leaves of an unknown species are from annual plants. This is in marked contrast to the commercial and standard crops grown in fields which are mostly annual species needing to be replanted after harvest. Commercial annual plants have higher yields when harvests are good, but under southern Madagascar conditions, their cultivation bears a high risk of complete failure and thus this practice is not sustainable for achieving food security independent from international aid programs. This risk could be mitigated by shifting cultivation towards perennial plants.

Table 13.4: Type of natural food resources collected in forests. The total number of species is higher than the species with known growth forms because not all plant species recorded with their vernacular names could be identified. *Poupartia minor* is listed for fruits and storage organs.

	Fruits	Seeds	Leaves	Exudates	Tubers/Roots	Total
Tree	20	1		1	2	22
Tree / Shrub	11		1		1	13
Cactus	2					2
Herb / Shrub	1	1	1			3
Herb / Vine					10	10
Parasite					1	1
Number of species	34	1	2	1	14	51

13.8.2 Hunting and fishing

Protein can be a limiting factor in agricultural systems with low food security. Livestock is not affordable for many households (Neudert et al. 2015) and poultry suffer very high mortality due to the lack of vaccination against cholera and Newcastle disease, though vaccine options may be available soon (Annapragada et al. 2019). Fishing is a viable option to improve protein supply, as is the alternative, hunting (Golden et al. 2019, 2011).

Hunting and fishing are mutually exclusive options for the households in southern Madagascar. Of 373 households, 250 neither fish nor hunt, 52 fish but do not hunt, 70 hunt but do not fish, and only 1 is both fishing and hunting. Hunting traditions also vary between villages. Hunting was reported only from households in 10 of the 24 villages surveyed. Guinea Fowl (*Numida meleagris*) was hunted most frequently (Table 13.5). The various species of Coua (*Coua* spp.) also seem to be taken frequently. Fodies (*Foudia madagascariensis*) are small passerine birds that can occur in large numbers in ripening sorghum fields. Though, except for Guineafowl, bird hunting does not seem rewardable as the small birds weigh only about 10 – 20 g and go up to about 100 g for large passerine species (Table 13.4), Fodies and other small birds are not only hunted to protect fields but also serve as actual food for people (Randriamiharisoa et al. 2015).

Insects are consumed as snacks or during mass occurrences (locusts; crickets in bean fields), but not specifically searched for. Therefore, people might not have listed insects as part of their "hunting" practices. Nevertheless, insect farming might become an accepted option in some areas where insects are already part of the human diet and food for insects is available year-round (Borgerson et al. 2021; Fisher and Hugel 2022).

Bats are collected in large numbers at their roosting sites in caves of Tsimanampetsotse (S. Reher, pers. comm.), but not in the other regions. This might be due to the lack of caves as roosting sites where bats can be encountered in large numbers and be caught easily. Tenrecs (*Setifer setosus* and *Tenrec ecaudatus*) are hunted routinely during the wet season. Lemurs seem to be hunted only in Lavasoa-Ambatotsirongorongo. In some villages, lemur hunting is taboo, while in others, lemur hunters simply may not have told, because lemur hunting is prohibited by law. Bushpigs (*Potamochoerus larvatus*) are most rewardable, but require special equipment and skills. Despite the often small prey, analyses of variance with "village" as random factor and "hunting/fishing" as fixed factor, revealed highly significant improvements of the caloric intake, HDDS and FCS in households that practice either fishing or hunting (Table 13.5, Fig. 13.6). These resources thus contribute substantially to diet, and due to their contribution to a more diverse diet, probably also improve human health (Golden et al. 2011; Swindale and Bilinsky 2006).

Table 13.5: Number of households hunting different species. People in Lavasoa-Ambatotsirongo Sud (I) do not hunt and therefore this region was omitted from the table.Bodymass according to Faliarivola et al. (2022) and Soarimalala and Goodman (2011).

	Bodymass [g]	II	III	IV	V	VI	VII
Insects							
Apis mellifera - Honey bee							1
Birds							
Centropus toulou - Madagascar Coucal	170				1	1	3
Coracopsis spp. - Vasa parrots	245-560				1	1	
Coua spp. - various *Coua* species	100-400			1		19	10
Foudia madagascariensis - Madagascar Red Fody	16				1	1	1
Erempoterix hova - Madagascar Lark	18				1	1	1
Neomixis spp. - Jery	7			1	1	2	
Newtonia brunneicauda - Common Newtonia	10					1	
Numida meleagris - Helmeted Guineafowl	1350	3	1	1	6	17	11
Oena capensis - Namaqua Dove	38				1		
Pterocles personatus - Madagascar Sandgrouse	360						1
Nesoenas picturata - Madagascar Turtle Dove	184			3		2	2
Turnix nigricollis - Madagascar Buttonquail	64			2	3	4	3
Eggs					1	1	
Mammals							
Bats, several species	30–60						1
Setifer setosus - Greater Hedgehog Tenrec	250				2	5	11
Tenrec ecaudatus - Common Tenrec	560					2	9
Lemur catta - Ring-Tailed Lemur	2200	2					
Potamochoerus larvatus - Bushpig	50,000	2				5	5

Table 13.6: Effects of hunting or fishing on measures of nutrition and food security. Values are F values based on ANOVA with "Village" as random variable and "Hunting/Fishing" as fixed factor.

	Fishing or hunting	Village
Caloric intake	9.55^{**}	3.44^{*}
HDDS	12.67^{***}	3.57^{*}
FCS	13.05^{***}	6.56^{**}

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$

13.9 Lessons learned

The dry regions of southern Madagascar are subject to recurrent droughts. In previous times, these droughts were reflected in the human demographic structure by an increased death rate of young children and the lack of children born during these years (Jolly 2004). Though today the devastating effects of droughts are mitigated by development programs, large portions of this region's human population cannot survive without international aid. During periods of food shortage, natural forests provide fallback food resources (Thompson et al. 2023), but the persistent use of these resources is not sustainable and highly destructive (Brinkmann et al. 2014; Zinner et al. 2014).

There are many obstacles hindering regional development, ranging from traditions, economic constraints, poor governance, and even crime (Goetter 2016; Hänke and Barkmann 2017). Many of these obstacles are difficult to overcome, but the traditional use of forest products may provide concepts for new approaches. For the time being, most crops planted are annual plants, and their cultivation resembles a gamble for rain which is lost too often. In contrast to standard crops, most (if not, all) fallback plant resources are perennial. Thus, the logical consequence would be to shift agricultural production from annual to perennial plants. Increasing the emphasis on perennial plants may not only be beneficial for humans, but would have great potential for improving the conservation for endemic animal species. There are a large number of fruit trees and other utilitarian trees that are of value for people and are being used by native animals alike (Gérard et al. 2015; Konersmann et al. 2022; Rafidison et al. 2020; Steffens 2020). These trees could be planted as buffer zones, corridors or hedges. They could provide income and food for people, livestock and native animals and could also serve as support for planting native yam.

While the potential of local knowledge, wild plant foods and agroforestry is being widely recognized (e.g. Andriamparany et al. 2014; Blanco and Carriere 2016; Grass et al. 2019; Moore et al. 2022; Rahman et al. 2017; Wurz et al. 2022), these concepts have not found their way towards large scale implementation in the south of Madagascar. Implementation would require some thoughts about long-term sustainability and is a matter of perspective (Jones et al. 2022). Options are either to extend the exploitation of wild resources into protected areas and bring areas under community-based management decision. This does not seem to work sustainably and so far has resulted in rapid forest degradation in most cases (Gardner et al. 2018; Rafanoharana et al. 2023). Alternatively, plantations of perennial food resources should be extended within the present agricultural areas, combining income for people with biodiversity conservation.

Given that food security will be difficult to achieve under these harsh ambient conditions, it might be worth considering alternative forms of income that substitute or complement the agricultural practices. On the marine side, algae farming seems to be a viable option in the southwest (Ateweberhan et al. 2015). On the terrestrial site, production of high-quality oil from *Opuntia* seeds for cosmetics/pharmaceutical industry could be options that add economic value to "weeds" and can provide additional income by processing the goods (Hänke et al. 2018).

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Chapter 14

Rural livelihoods and biodiversity in Afrotropical agroforestry systems and oil palm plantations

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Abstract West African forested landscapes are characterized by social and economic complexities, but face a number of challenges including over-exploitation of natural resources and habitat degradation, and, more recently, an emerging wave of industrial oil palm development. This study aimed to address some of the apparent knowledge gaps on land use and its effects on biodiversity and rural livelihood in an Afrotropical forest biodiversity hotspot in Southwest Cameroon. We describe both socio-economic conditions of rural households as well as biodiversity indicators in a traditional agroforestry matrix, an industrial oil palm plantation and a national park, in order to explore the potential compromise between human livelihoods and forest conservation. We interviewed 118 households in 12 settlements equally distributed across the three landscapes, using standardized questionnaires on income generation and expenditures. We further systematically sampled birds in 432 sample points around those 12 settlements. We also surveyed large mammals across the agroforestry matrix and different protected areas along 638 km line transects. We found slight differences in total income between park and surrounding villages, though higher income from forest products was generated in the national park compared to the agroforestry matrix, whereas self-employment and wage labour were more important in the agroforestry matrix. However, plantation households spend significantly more time on generating a similar income than households in the national park and agroforestry matrix. Although plantation households were nearly 40% smaller than those in agroforestry and national park, their expenditures were significantly higher, nearly twice as high for food alone. Bird species richness was overall similar in national park and agroforestry matrix, but dropped by ca. 30% in oil palm plantations with true forest species mainly lacking.

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All diurnal primates, including chimpanzees, as well as ungulates and forest elephants were still present in the agricultural matrix, but had lower encounter rates there compared to the national park. Our results highlight that heterogeneous agroforestry matrices in West Africa can assure more diversified and sufficient livelihoods than wage labour in industrial oil palm plantations and might thus represent a more sustainable future for rural households. The biodiversity data suggests that a sustainable coexistence between wildlife and people in these agroforestry matrices may be achieved when agricultural production is smallholder-based, diversified and maintains substantial proportions of forests. Moreover, such a landscape will certainly also be permeable for large mammals and maintain connectivity between protected areas.

14.1 Introduction

Rising global demand for edible oils and biofuels led to a rapidly growing market of palm oil in the last decades (Laurance et al. 2010). Due to the wide application possibilities of palm oil and high yield potentials, oil palms *Elaeis guineensis* are the most extensively cultivated oil crops in the world. As a consequence of the expansion of palm oil cultivation in the tropics, rural agroforestry and natural forest ecosystems facing a substantial threat caused by land use change (Laurance et al. 2010; Dislich et al. 2017). During the last decades, large parts of forested landscapes in Southeast Asia were converted into palm oil plantations (Wilcove and Koh 2010). Subsequently, the oil palm industry started to emerge rapidly in the Amazon and tropical Africa (e.g. Wilcove and Koh 2010; Feintrenie 2014; Linder and Palkovitz 2016) at a time in which most of that region was already facing a severe transformation process from forest-dominated landscapes with rural agroforestry to more intensified forestry and agricultural cultivation (Norris et al. 2010). The adoption of oil palm production has the potential for both stabilizing income in barely developed regions as well as undermining land rights and impoverish local communities (e.g. Feintrenie 2014; Qaim et al. 2020; Sibhatu 2023). Oil palm production may have positive effects on household income and nutrition, if implemented by smallholder farmers (Euler et al. 2017; Tabe-Ojong et al. 2022). Since forest-related livelihoods are characterized by social-ecological complexities and traditional agroforestry systems can provide a variety of ecosystem services and products to local people (Mbile et al. 2005; Vega et al. 2013), effects of large-scale land-use change for industrial oil palm production may be profound. Employment in industrial plantations may yield low and inconstantly paid labour wages (Rist et al. 2010) and deprive local communities of a heterogeneous environment and the products therein, which may have constituted a substantial share of total household incomes before forest conversion (Sheil et al. 2006; Pfund et al. 2011). It has been suggested that in some regions in West and Central Africa forest resources can contribute up to 50% to rural household income (Mbile et al. 2005; Endamana et al. 2019). However, knowledge on the extent and role of monetary as well as non-monetary values of forest resources in the context of land use change in tropical Africa remains – particularly in the presence of an emerging oil palm wave – incredibly poor (Dislich et al. 2017).

The expansion of oil palm cultivation area and its associated infrastructure were also key drivers of land use change and forest displacement, as observed in Southeast Asia (e.g. Turner and Foster 2009; Wilcove and Koh 2010) and, thus, increased habitat fragmentation (DeFries et al. 2005; Laurance et al. 2010) and reduced ecosystem functioning (Dislich et al. 2017). The conversion of forest to oil palm plantations enhances the current tropical biodiversity crisis due to the limited conservation and biodiversity value of oil palm plantations (Fitzherbert et al. 2008). Homogeneous oil palm plantations do not serve as suitable habitats for large mammals, as shown in Southeast Asia (Maddox et al. 2007), and they contain lower numbers of bird species and abundance compared to primary forest (Azhar et al. 2011; Kupsch et al. 2019). In addition, community compositions of most species groups change severely, with a few generalist or even invasive species becoming dominant in abundance (e.g. Danielsen et al. 2009; Kupsch et al. 2019).

Although there is a growing body of studies on oil palm plantations and their socio-economic and ecological effects, those mainly focus on Southeast Asia. Detailed knowledge on socio-economic effect and species-specific responses to conversion from forest to large-scale oil palm cultivation in tropical Africa is still poor but much needed in to evaluate environmental impacts and inform development and conservation policy makers. In addition, there is an urgent need to address the social and ecological complexities of Afrotropical landscapes (Norris et al. 2010). This study aims to address this research gap by providing a systematic assessment of livelihood and biodiversity indicators in a rural multi-land use landscape in Southwest Cameroon. In particular, we want to identify and describe differences in income generation as well as expenditure patterns between households in a protected area, its surroundings dominated by traditional agroforestry and an industrial oil palm plantation. In order to assess the biodiversity of the landscape systems in which human livelihoods are generated, we also systematically document the large mammal fauna as well as the bird communities.

14.2 Methods

14.2.1 Study area

This research took place in Ndian Division, Southwest Cameroon, around its divisional capital Mundemba. The study area (Fig. 14.1) is located between 4°57'N to 5°10'N and 8°44'E to 9°7'E and between 50 and 800 m a.s.l. The climate is generally humid with annual rainfall averaging above 5,000 mm and characterized by distinct dry and rainy seasons, peaking from December to February and June to September, respectively (Etta et al. 2022). The study area is dominated by an intact and diverse lowland rainforest, which is reputedly one of the oldest and richest of its kind in Africa, and located within the biodiversity hotspot of the Gulf of Guinea forests (Darwall et al. 2015). The area encompasses Korup National Park (KNP), which has a total size of 126,000 ha and contains five villages (Mbile et al. 2005), of which one, the northeastern Bareka Batanga, has been recently abandoned. The area around the park is dominated by rural smallholder agroforestry. This agroforestry matrix (hereafter abbreviated AFM) contains large sections of primary and secondary forests at different stages as well as farmland, which is characterized by small-scale shifting cultivation for annual food crops or perennial cash crops, mainly cocoa. Besides farming, inhabitants of the villages in KNP and AFM rely on fishing, hunting, trapping and gathering non-timber forest products (NTFPs: Mbile et al. 2005). Many inhabitants of

Korup area are culturally, socially and economically connected to their neighbours in Nigeria (MINEF 2002). Most settlements are remote and rather hard to access. In and around KNP hundreds of kilometres of food paths can be found, linking villages inside and outside the park.

In the southeast of KNP in the proximity of Mundemba, a number of small to medium-sized (100 – 5, 800 ha) oil palm estates can be found, of which the largest is represented by the industrial plantation of PAMOL Plantations Plc. The public sector company PAMOL Plantations Plc. is partly owned by the state after establishment in 1960 (Konings 1986). Besides Ndian estate, PAMOL produces palm oil products in Lobe and Ekondo Nene, both located in the Southwest Region, for sale on the local and export markets. PAMOL employs a mix of permanent and casual workers, totaling 2,683 in Ndian estate in 2014. In addition to monthly salaries, PAMOL uses an incentive-based reward system (PAMOL 2014), which allows encouraged workers to earn above minimum wages, especially during peak harvest season. PAMOL Ndian estate contains eight settlements, in which mainly migrated workers and their families live. Housing, electricity, primary school access as well as basic health care are provided free by the company.

14.2.2 Definitions and categories

Smallholders

There are several characteristics of small farms or smallholders, e.g. total farm size (<2 ha: C'saki and Haan 2003), production orientation (mainly in-kind staple food, Hazell et al. 2007) or limited resources of land capital, skills and labour (Dixon et al. 2003). However, since this study focused on income structures, we use the term 'smallholder' for those rural households making their living mainly from subsistence and cash-crop farming, forestry and fishery activities, while these can be complemented with non-farm activities.

Households

We use households as our sampling units, which might either be a single economically independent person or a group making common provision for food or other essentials for living, in which intense social and economic interdependencies occur (Ellis 2000). It differs from the term 'family', which refers to any kind of kinship relation and sometimes spreading over different households. At the same time, a household may also include non-family members.

Income

We focus our study on household income flows, since their composition represents the main visible product of livelihood status and structure (Ellis 2000). Since households in rural Southwest Cameroon highly depend on forest products and stable farming for self-consumption (Mbile et al. 2005), our total income measure comprises both cash and in-kind components. We valued self-consumption according to the amount of cash income that could have been generated through selling the same good at the local market. We consider a set of income generating activities: farming, rearing, gathering NTFPs, fishing, hunting and trapping, employment including self-employment and other income sources such as support from non-household members (e.g. monetary donations or food provided by relatives). Total annual net income is composed of gross cash or in-kind income from an activity minus particular input expenses, such as fertilizer, wage labour, transportation of goods for farming, nets, hooks and lines for fishing or guns, batteries, bullets for hunting and building material for keeping cattle.

Expenditure

Since income as a measure alone cannot reflect the ability of households to buffer their standards of living through saving and borrowing (C'saki and Haan 2003), we also collected data on household expenditure as a measure of well-being. In addition, detailed expenditure data gives us an impression on the social and economic needs of households in its particular environment. We collected expenditure data within different categories: food, consumer goods, clothing, luxury goods, housing, education, health, transportation and other (including any contributions to church, village or relatives). In addition, for food and consumer goods, we differentiated between basic (indispensable for living), diversified (not essential, e.g. food that is not grown in the region) and dispensable items (not common, usually processed and expensive).

14.2.3 Questionnaire data collection

We conducted fieldwork from March to April 2015 in twelve villages in three landscape types of the Korup region, namely Bera, Erat, Ikenge and Esukutan in KNP, Fabe, Ikondo kondo I, Lipenja I and Mokango/Massaka in AFM, and Center A, Ikassa, Makeke and Mana settlements in OPP. The selection of sample settlements was based on willingness to collaborate, settlement size, spacing between each other and accessibility. We performed a preliminary interview survey in a village south of Mundemba to test the methodology and questionnaire for final modifications. We conducted ten household interviews in each of the settlements, except for Bera, where the village household number was only eight in total, summing up to a total of 118 households. Several days before the interviews started the community chiefs and camp officials were informed about the project to obtain their consent and give time for them to prepare full household lists. The day of arrival at a study location, households were randomly drawn from that list and appointments for interviews made with household heads and, if applicable their spouses. Since in rural households women and men usually do not contribute to the total income in the same way (Ruíz Pérez et al. 2002), the survey team consisted of a women and a men group with each one researcher and local assistant, enabling us to gather income data gender-related and pool them afterwards. Interviews took between 1 and 2 hours and were conducted in the houses of the respondents in English, and – with the help of the local assistants – in Pidgin English, as well as occasionally in Korup and Oroko languages.

During interviews we used a standardized questionnaire, which included four sections: (1) general household characteristics, (2) household income from income generating activities, (3) personal time budget and (4) household expenditures. To determine who counts as a household member, a minimum of 3 months of continuous presence before the interview was set. Income and expenditure data were collected for the last twelve months. For all income types, we requested the quantity of all harvested crops, gathered NTFPs, caught

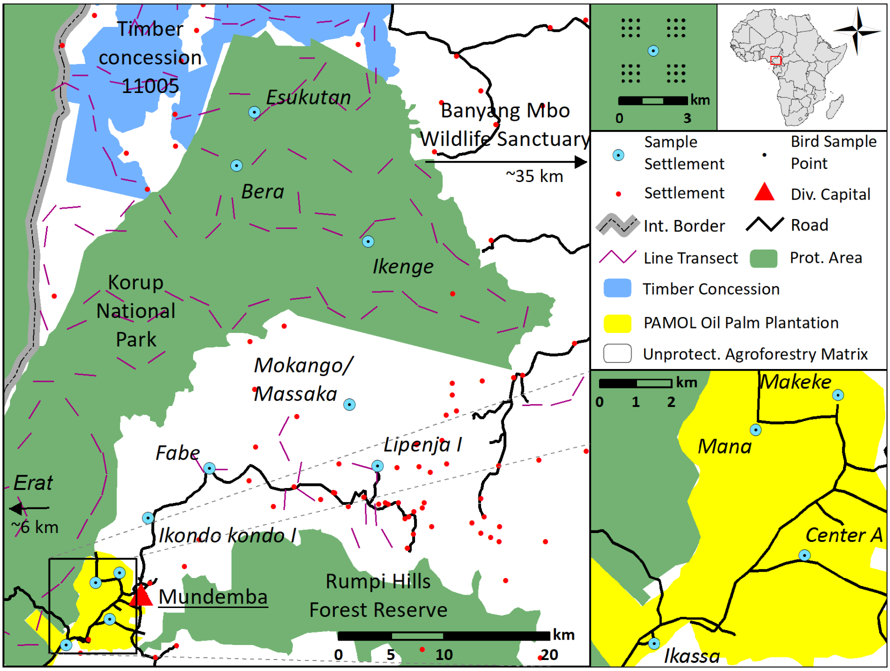

Fig. 14.1: Map of the study area in Southwest Cameroon and an illustration of the study design at settlement level.

fish and trapped or hunted animals, as well as the proportion of self-consumed and sold quantities. Data of income and expenditures were recorded in CFA-Franc (FCFA, Franc de la Coopération Financière en Afrique Centrale; fixed exchange rate 656 FCFA = 1 €). We requested a detailed overview on time spent for the daily activities for each day of a week, in addition, we asked for changes in the personal time budget during the course of a year. Since women spend more time for reproductive activities than men (Fonjong 2004), we also asked for activities such as housework (i.e. cooking, washing and cleaning). During interviews, we used checklists of income types, farm and forest products and expenditure items to enhance interviews and ensure completeness.

We reviewed all gathered interview sheets during the survey and revisited households if data were unclear, inaccurate or incomplete. We revised or eliminated interview sheets when the total cash income exceeded 150% of total expenditures and vice versa, or the interviewee did obviously withhold information, such as income from poaching activities. If so, we randomly drew another household from the list provided by village authorities. However, since we already built a trustful cooperation in all villages during field research stays in previous years, those cases were seldom.

14.2.4 Bird surveys

Between June 2013 and June 2014, we systematically sampled bird communities around the same twelve villages in KNP, AFM and OPP, which have been surveyed for livelihood (Fig. 14.1). We used the centre of each settlement to define the midpoint of a grid consisting of nine 1 km × 1 km blocks (Fig. 14.1). Of these nine blocks, the four extreme corner blocks were sampled, resulting in 48 sampled blocks in twelve sample sites. We placed nine sample points within each sample block, spaced 333 m each (Fig. 14.1). We surveyed 432 sample points across the whole study area. For more information on the bird survey methodology, please see Kupsch et al. (2019).

14.2.5 Large mammal surveys

We sampled large mammals and hunting signs along line transects (Buckland et al. 2001) in Korup National Park (1 260 km^2) and the neighbouring protected area Banyang Mbo Wildlife Sanctuary (640 km^2) as well as the adjacent agroforestry matrix and a forest concession (800 km^2, concession no. 11005) between April 2013 and March 2014 (Fig. 14.1). The survey area of the unprotected agroforestry matrix was defined by a former proposed oil palm concession (735 km^2), which has, however, never been realized (for more details see Kupsch et al. 2014), and contains three of the four surveyed AFM villages (Fabe, Lipenja I and Mokango/Massaka). We overlaid grids of 4 km × 4 km and 3 km × 3 km cell size and randomly placed one transect of 2 km and 1.5 km length, respectively. Transects were cut with a minimum of disturbance, and survey teams followed the transect cutters earliest one day later. In the agroforestry matrix, we repeated the transect walks, whereas in the remaining sites transects were surveyed once. The total survey amounted up to $L = 638.5$ km and $n = 321$ (see Table 14.4 for site-specific survey effort).

14.2.6 Data analysis

We tested for differences in household income and expenditure measures, bird guild richness and mammal relative abundance between survey sites using the Kruskal-Wallis test with multiple Dunn test (Benjamini and Hochberg 1995) as post hoc with the **dunn.test** package (Dinno 2017) in R version 4.3.1 (R Core Team 2020).

14.3 Results

14.3.1 Human livelihoods

Even though the number of respondents as well as household gender structures were similar between surveyed landscapes households in the plantation settlement supported significantly lower number of household members compared to the national park and the agroforestry matrix (Table 14.1; Kruskal-Wallis $\chi^2 = 15.47$, $p < 0.001$). Respondents in the oil palm plantation were often migrants from other parts of Anglophone Cameroon or Nigeria, and held higher educational degrees than people in the agroforestry matrix and the national park.

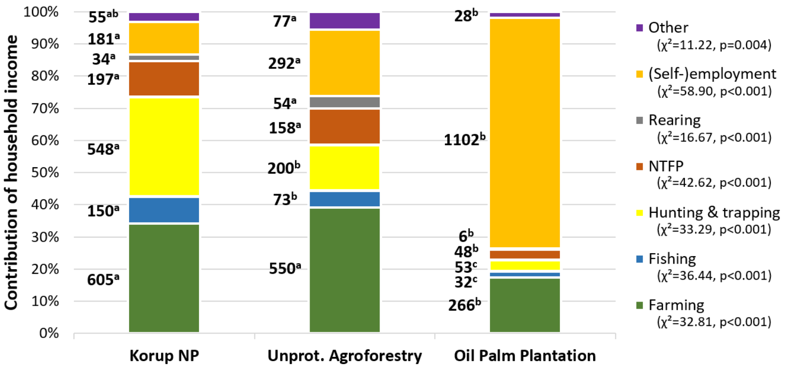

Fig. 14.2: Contribution of income generating activities to annual household income in three landscape types as percentage and in 1,000 FCFA as well as results of Kruskal-Wallis tests on differences between landscape types. Significance levels as derived from Dunn post hoc tests are indicated as superscripts.

Table 14.1: Overview on the interviewed households.

Landscape Location	No. interv.	No. ±SE HH members	**Household gender structure** F	M	MF	MFF	FF	No. respon. (M/F)
Korup National Park	38	4.7 ± 0.4	4 (11%)	8 (21%)	23 (64%)	2 (5%)	–	64 (34/30)
Bera	8	3.1 ± 1.1	1	4	3	–	–	11 (7/4)
Erat	10	5.5 ± 0.7	2	2	5	–	–	15 (8/7)
Esukutan	10	4.5 ± 0.8	–	2	6	2	–	19 (10/9)
Ikenge	10	5.5 ± 0.6			9			19 (9/10)
Agroforestry	40	5.1 ± 0.4	12 (30%)	5 (13%)	20 (50%)	2 (5%)	1 (3%)	64 (27/37)
Ikondo k. I	10	4.3 ± 0.7	4	1	5	–	–	15 (6/9)
Fabe	10	3.5 ± 0.5	4	3	3	–	–	13 (6/7)
Lipenja I	10	6.7 ± 0.8	3		5	1	1	17 (6/11)
Mok./Mas.	10	6.0 ± 0.7	1	1	7	1	–	19 (9/10)
Oil-palm plantation	40	3.1 ± 0.4	8 (20%)	12 (30%)	17 (43%)	3 (8%)	–	60 (32/28)
Center A	10	2.1 ± 0.5	4	4	2	–	–	12 (6/6)
Ikassa	10	2.5 ± 0.8	2	4	3	1	–	14 (8/6)
Makeke	10	4.2 ± 1.1	3		7	–	–	17 (10/7)
Mana	10	3.7 ± 0.9	2	1	5	2	–	17 (8/9)

Mean total annual household income was highest in national park villages and lowest in the agroforestry matrix. However, differences were not significant (Table 14.1). Whereas households in the national park and agroforestry matrix spent between 70 and 80 minutes to generate 1,000 FCFA (= 1.52 €), households in the oil palm plantation need significantly more time (>2 h). Due to the dominant proportion of salaries from wage labour in the oil palm plantation (Fig. 14.2), total cash income was highest and in-kind income was lowest, compared to national park and agroforestry matrix (Table 14.2). (Self-)employment was more important in agroforestry matrix than in national park. The most important income type in national park and agroforestry matrix was farming, though income from hunting and poaching was nearly as high as farming in national park, which is mainly attributed to extraordinary high hunting activities in the village Ikenge. Consequently, the total share of all forest related income types significantly increased from oil palm plantation over agroforestry to national park. The least importance of all income activities in all landscape types was livestock rearing.

Table 14.2: Selected annual household income and expenditure parameters in twelve settlements and three landscape types in 2015 (1,000 FCFA = 1.52 €), as well as the results of Kruskal-Wallis tests on differences between landscape types. Column-wise significance levels as derived from Dunn post hoc tests are indicated as superscripts.

Landscape	**Mean annual income ± SE**			Hours / 1,000	**Mean annual expend. ± SE**	
Location	Total HH	In-kind only	Forest prod.*	FCFA ±SE	Total HH	Food
Korup National Park	1,651 ± 132	530 ± 45^{a}	893 ± 111^{a}	1.2 ± 0.1^{a}	$1{,}072 \pm 96^{ab}$	198 ± 20^{a}
Bera	1,343 ± 318	411 ± 113	531 ± 192	1.5 ± 0.3	890 ± 223	170 ± 38
Erat	1,288 ± 170	400 ± 50	761 ± 217	1.3 ± 0.2	907 ± 154	245 ± 50
Esukutan	1,486 ± 184	569 ± 86	678 ± 115	1.1 ± 0.1	932 ± 134	120 ± 25
Ikenge	2,488 ± 206	739 ± 74	1,600 ± 183	1.0 ± 0.2	1,559 ± 191	256 ± 32
Agroforestry	1,373 ± 113	457 ± 31^{a}	443 ± 70^{b}	1.3 ± 0.1^{a}	994 ± 113^{a}	237 ± 16^{a}
Ikondo k. I	1,069 ± 114	520 ± 55	492 ± 114	1.4 ± 0.1	587 ± 52	179 ± 21
Fabe	1,550 ± 229	522 ± 62	452 ± 141	1.3 ± 0.2	1,020 ± 167	261 ± 30
Lipenja I	1,532 ± 300	307 ± 36	268 ± 62	1.5 ± 0.2	1,393 ± 355	321 ± 37
Mok./Mas.	1,340 ± 223	478 ± 70	558 ± 207	1.1 ± 0.2	975 ± 167	188 ± 23
Oil palm plant.	1,420 ± 126	172 ± 26^{b}	134 ± 43^{c}	2.1 ± 0.2^{b}	$1{,}335 \pm 93^{b}$	403 ± 21^{b}
Center A	1,413 ± 208	196 ± 42	143 ± 62	2.4 ± 0.5	1,344 ± 162	349 ± 37
Ikassa	1,389 ± 394	130 ± 61	101 ± 92	2.4 ± 0.5	1,400 ± 262	414 ± 53
Makeke	1,418 ± 206	119 ± 31	59 ± 32	1.8 ± 0.4	1,355 ± 195	428 ± 40
Mana	1,462 ± 188	244 ± 67	232 ± 130	1.6 ± 0.2	1,242 ± 130	421 ± 40
Kruskal-Wallis χ^2	3.52	47.58	49.80	14.26	9.64	42.91
Kruskal-Wallis p	0.173	<0.001	<0.001	<0.001	0.008	<0.001

*This figure of forest products includes all non-farm, non-employment and non-rearing income types (NTPFs, hunting, fishing).

The most important food crops were banana, plantain and cassava (Table 14.1). Moreover, nearly half of the income generated from the latter was in cash. Cocoa was the most important cash crop in all landscape types. Whereas most households in agroforestry and national park were engaged in red oil processing, only plantation households sold considerable amounts of palm oil or their raw bunches. We found that nearly all households in agroforestry and national park as well as 70% of the households in oil palm plantation were engaged in NTFP gathering. Whereas the latter occasionally collected snails for consumption within the plantation area, bush mango (*Irvingia* spp.) and njangsa (*Ricinodendron heudelotii*) in particular contributed strongly to agroforestry and national park households. We listed 36 species (grouped for smaller species, such as mongooses or gallinaceous birds) being targeted by households of all three landscapes, with porcupines and cane rates being the most relevant in-kind and duikers the most relevant cash income sources, respectively. However, only few households in the oil palm plantation were engaged in hunting and trapping, and if so, they were mainly professional hunters, who live in household of plantation workers but gather income from hunting in the nearby Korup National Park.

Table 14.3: Mean net annual income and proportion of engaged households for the two common cash crops, the top six food crops, the top six hunted wildlife species and the top six gathered non-timber forest products in three landscape types in 1,000 FCFA (=1.52 €).

	KNP		**AFM**		**OPP**		**Total**	
Type	HH [%]	mean ± SE	HH [%]	mean ± SE	HH [%]	mean ± SE	HH [%]	mean ± SE
Cash crops								
Cocoa	63	203±42	65	139±37	13	29±24	47	122±21
Palm oil	66	28±6	50	-14±18	15	99±56	43	38±4
Food crops								
Cassava	87	92±23	90	95±23	60	32±12	79	72±13
Plantain	97	79±9	100	70±6	53	26±7	83	58±5
Banana	97	56±7	100	73±9	50	13±4	82	47±4
Cocoyam	68	16±4	83	28±5	58	9±3	69	18±2
Palm wine	58	39±8	35	25±8	-	-	31	21±5
Corn	89	13±2	88	19±3	78	13±2	85	15±1
Hunted species								
Brush-t. porcupine	76	94±17	58	47±14	10	5±4	48	48±8
Blue duiker	68	94±19	48	31±13	10	6±5	42	43±8
Ogilby's duiker	61	76±18	38	18±6	10	13±11	36	35±8
Greater cane rat	71	40±9	58	18±5	13	5±2	47	20±4
Tree pangolin	40	27±10	33	8±4	5	1±1	25	12±3
Red river hog	37	23±6	18	12±7	3	-	19	11±3
NTFP								
Bush mango	95	91±11	78	61±9	20	9±5	64	53±6
Njangsa	58	27±6	65	31±6	5	0±0	43	19±3
Snails	50	8±2	50	11±4	55	31±12	52	17±4
Bitter kola	47	13±3	48	13±4	13	4±2	36	10±2
Country onion	26	8±3	20	19±11	5	1±1	17	9±4
Bitter mango	32	19±5	5	2±1	-	-	12	7±2

Total mean annual expenditures were highest in plantation settlements and lowest in the agroforestry matrix (Table 14.2). Herein, the proportion of food expenditures decreased significantly from oil palm to agroforestry and national park. Plantation households in oil palm plantation spent more money on diverse and dispensable food and consumption goods than households in agroforestry and national park. Moreover, there was a significantly higher alcohol consumption in oil palm but also national park compared to agroforestry (Kruskal-Wallis $\chi^2 = 8.31$, $p = 0.04$). Overall transport expenses were similar between landscape types, but households in agroforestry undertook mainly short and regular trips compared to oil palm and national park. Expenditures for education, health and other purposes, such as the support of relatives, did not differ between sites. Since many households along the main road were engaged in building new structures, expenditures on housing were (though not significantly) in agroforestry. Workers of the palm oil plantation use settlement houses free of charge, but some invest in new housing structures in their villages of origin.

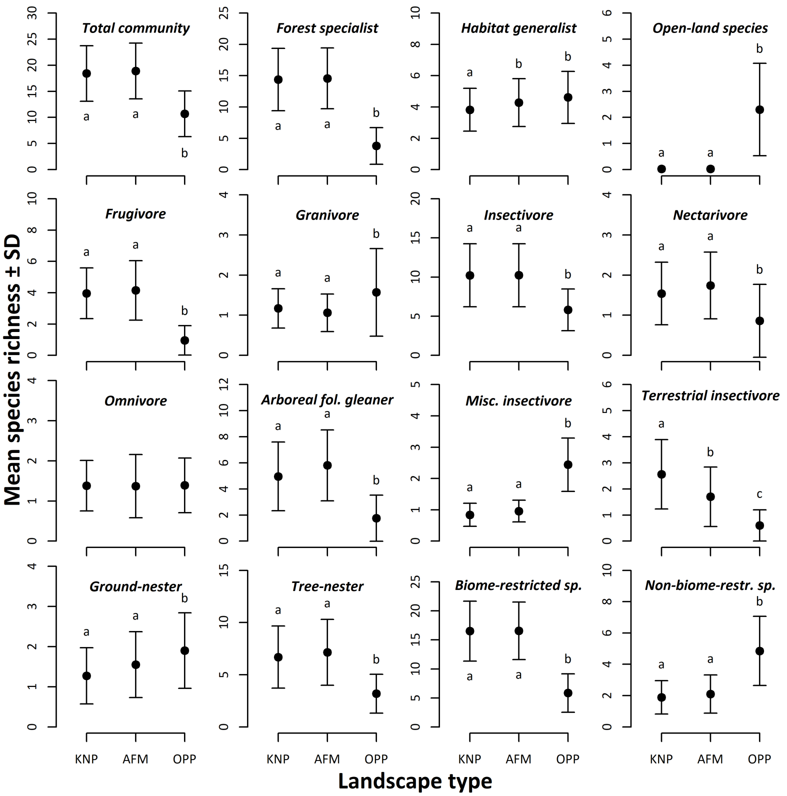

Fig. 14.3: Mean species richness and standard deviation at sample-block level (1 km^2) of bird guilds in Korup National Park (KNP), unprotected agroforestry matrix (AFM) and oil palm plantation (OPP). Differences in significance levels as derived from Dunn post hoc tests (following Kruskal-Wallis tests) are indicated with different letters.

14.3.2 Bird communities

We recorded a total of 6,883 bird encounters and 198 bird species along 432 sampling points (for full species list see Kupsch et al. 2019). With the exception of some groups (bush nest builders, carnivorous and omnivorous feeders), we found significant differences in species richness between land use types (Fig. 14.3). Total species richness was similar between the national park and agroforestry landscape but significantly decreased (by ca. 30%) in the oil palm plantation. Guilds, which are an elemental part of native forest bird communities, show a similar pattern, e.g. frugivores, arboreal foliage gleaners or tree nest builders. Consequently, species that are no endemics to the Guineo-Congolian forest biome as well as open-land species are significantly more prominent in the plantation area compared to national park and agroforestry.

Table 14.4: Mean encounter rates (with standard errors; all signs) of large mammal species and hunting signs in four sampled landscapes in 2013 and 2014 as well as the results of Kruskal-Wallis tests on differences between landscape types. Significance levels as derived from Dunn post hoc tests are indicated as superscripts.

Species & signs	**IUCN status***	**Korup NP** *n* **= 88;** *L* **= 176 km**	**Banyang Mbo WS** *n* **= 83;** *L* **= 124.5 km**	**Timber concession 11005** *n* **= 104;** *L* **= 156 km**	**Unprotected AFM** *n* **= 46;** *L* **= 182 km**	**Kruskal-Wallis test**	
		Mean encounter rate [enc./km] ± standard error				χ^2	p
Primates							
Pan troglodytes ellioti	EN decr	0.107 ± 0.029^{a}	0.176 ± 0.059^{a}	0.025 ± 0.012^{a}	0.027 ± 0.013^{a}	8.01	0.046
Mandrillus leucophaeus	EN decr	0.022 ± 0.013	0.056 ± 0.032	0.038 ± 0.017	0.016 ± 0.012	0.29	0.962
Piliocolobus preussi	CR decr	0.005 ± 0.005	0.024 ± 0.013	0.012 ± 0.009	*	2.54	0.469
Cercocebus torquatus	VU decr	0.051 ± 0.021^{a}	**	0.006 ± 0.006^{b}	0.010 ± 0.010^{ab}	12.21	0.007
Cercopithecus pogonias	VU decr	0.056 ± 0.018^{a}	-	0.038 ± 0.017^{a}	0.021 ± 0.013^{a}	8.88	0.030
Cercopithecus erythrotis	VU decr	0.238 ± 0.037^{a}	0.176 ± 0.044^{ab}	0.064 ± 0.019^{b}	0.016 ± 0.009^{b}	25.69	<0.001
Cercopithecus nictitans	LC decr	0.448 ± 0.049^{a}	0.273 ± 0.053^{b}	0.307 ± 0.048^{ab}	0.157 ± 0.029^{b}	13.55	0.004
Cercopithecus mona	LC unkn	0.295 ± 0.039^{a}	0.248 ± 0.048^{ab}	0.134 ± 0.032^{b}	0.086 ± 0.022^{b}	15.57	0.001
Proboscidea							
Loxodonta africana cyclotis	EN decr	1.375 ± 0.245^{a}	1.799 ± 0.282^{a}	0.250 ± 0.081^{b}	0.092 ± 0.044^{b}	48.11	<0.001
Bovidae							
Cephalophus ogilbyi, *Cephalophus dorsalis****	VU decr NT decr	3.090 ± 0.194^{b}	5.453 ± 0.468^{a}	3.416 ± 0.203^{b}	2.190 ± 0.272^{c}	32.52	<0.001
Philantomba monticola	LC decr	3.000 ± 0.229^{a}	2.538 ± 0.239^{a}	2.820 ± 0.229^{a}	1.010 ± 0.148^{b}	38.58	<0.001
Cephalophus silvicultor	NT decr	0.250 ± 0.061^{a}	0.112 ± 0.040^{bc}	0.121 ± 0.035^{ab}	0.016 ± 0.009^{bc}	11.94	0.008
Syncerus caffer nanus	LC decr	0.079 ± 0.026^{a}	0.008 ± 0.008^{b}	0.019 ± 0.014^{b}	0.027 ± 0.013^{ab}	12.42	0.006
Tragelaphus spekii	LC decr	0.107 ± 0.033^{a}	-	0.019 ± 0.010^{b}	0.010 ± 0.010^{b}	19.92	<0.001
Tragelaphus scriptus	LC stab	0.011 ± 0.007	0.024 ± 0.017	-	-	3.55	0.314
Tragulidae							
Hyemoschus aquaticus	LC decr	0.318 ± 0.051^{a}	0.120 ± 0.048^{b}	0.397 ± 0.073^{a}	0.092 ± 0.027^{b}	20.52	<0.001
Cetartiodactyla							
Potamochoerus porcus	LC decr	1.193 ± 0.119^{b}	2.401 ± 0.272^{a}	1.096 ± 0.110^{b}	1.065 ± 0.145^{b}	20.31	<0.001
Pholidota							
Phataginus tetradactyla, *Phataginus tricuspis****	VU decr VU decr	0.289 ± 0.039^{a}	0.152 ± 0.043^{b}	0.500 ± 0.079^{a}	0.402 ± 0.060^{a}	26.05	<0.001

*IUCN (2023); **presence confirmed by survey; ***difficult to distinguish by indirect signs in the field.

14.3.3 Large mammals

Almost all mammal species were detected in each of the protected areas as well as in the agroforestry matrix (Table 14.4). While some rarer primate species (chimpanzee, drill, mangabey) showed low encounter rates in all sites, most ungulate and guenon species were found being significantly more abundant in the protected areas compared to the agroforestry matrix. On the contrary, we encountered most pangolin signs in timber concessions, however, not significantly more than in the agroforestry matrix and in Korup National Park. Elephants were significantly more abundant in protected areas.

14.4 Discussion

14.4.1 Socio-economic complexities of rural livelihoods in Southwest Cameroon

In accordance with previous research (Mbile et al. 2005; Endamana et al. 2019), our results highlight the importance of forest products in rural communities in West African forest-dominated landscapes. The contribution of forest products to total household income in Korup National Park (KNP) and the adjacent unprotected agroforestry matrix (AFM) amounted up to 54% and 33%, respectively. Certainly, revenues from hunting represent a considerable proportion of these numbers. When subtracting those, we still yield 31% and 22% of forest-related components in total incomes in KNP and AFM, respectively. However, zero hunting in traditional hunting communities as those in the Korup region is no realistic scenario. Conservation management should rather aim to promote sustainable hunting schemes (Bennett et al. 2007), which could allow a limited offtake of smaller and faster producing species, such as blue duiker, greater cane rat and porcupine. Already in our sample the proportion of these species in total hunting income made up more than 50% in the AFM.

In the plantation settlements (OPP), forest resources played a minor role (< 10%), although hunting still occurred, mainly in the adjacent forests of KNP. The same accounts for the in-kind component of total household income. Though more than 90% of the households in OPP were engaged in farming, most of the food crops were grown in small plots inside the workers camp and, thus, yielded very limited income. Unsurprisingly, the greatest share of the total plantation household income came from employment and contract work. However, our findings demonstrate that, on the one hand, the total household income in OPP is still smaller compared to KNP and, on the other hand, the cash component can hardly cover the total household expenditures. The latter is mainly due to the fact that compared to households in KNP and AFM, plantation workers had to buy most of their food items instead of growing them. As a result, plantation households spent twice as much on food items as KNP households, which where even 50% larger in size. As already observed in Southeast Asia, this might lead to social insecurity and indebtedness (Rist et al. 2010).

Households with access to roads have a greater potential to increase their income through small business or trading activities, but also better marketing options for farm and forest products (Warr 2008; Hine et al. 2014; Spey et al. 2019). In nearly all interviewed communities, smallholders started investing oil palm production in sections of their farms (see negative net income from oil palm in Table 14.2), because they can sell oil palm nuts or locally processed red oil on the regional market of Mundemba. Like this, the agroforestry households will benefit from the oil palm development, which would be in line with findings of Euler et al. (2017) and Tabe-Ojong et al. (2022). We also found that income from (self-)employment was 50% higher in AFM households, which profited from road access, compared to those in KNP. Particularly women seemed to benefit from opening up minor businesses and selling food in their villages; their total income was 25% higher in AFM than in KNP and OPP. However, although the studied oil palm estate is located in the direct proximity to the divisional capital Mundemba and its >5,000 inhabitants, the plantation households generated even less income through trading than households in KNP. This might result from differences in household time budgets. Compared to village household in AFM and KNP, plantation households spent significantly more time for income generation activities, mainly wage labour.

What remains is the good predictability of monthly incoming salaries in plantation households versus the strong seasonality of cocoa, the main cash crop in AFM and KNP. A number of respondents in households that depend on farming complained about lacking funds to cover the input expenses (mainly for fungicides) in the beginning of the planting season. However, our results suggest that this is less of a problem stemming from low income in AFM and KNP than a matter of household budget management over the course of the year. We believe this could be addressed by trainings provided by development projects, such as the Programme for the Sustainable Management of Natural Resources, an ongoing bilateral German-Cameroonian development cooperation in Southwest Cameroon.

Our findings also suggest negative indirect ecological effects through the employment practices of the palm oil company. A large number of persons working in in the plantation were coming from other regions of Cameroon and Nigeria. We observed that many migrants held higher school degrees than locals and were often recruited for leading positions with higher salaries. As it has already been suggested for forest concessions (Poulsen et al. 2009; Lescuyer et al. 2012), this increases the pressure on adjacent forests from poaching – in our case Korup National Park – because higher salaries may create a higher demand for bushmeat. In addition, we observed that workers, which migrated from larger towns or cities, such as Bamenda, without traditional rights on village land, used their income surplusses to invest in land for private oil palm cultivation, which might increase forest conversion around Mundemba and along the roads to Toko and Ekondo titi. The fact that the palm oil company buys in oil palm bunches to utilize the capacities of their central mill enhances this development.

While our research represents a regional case study and generalizations should, thus, made with caution, however, to our knowledge this study was the first attempt to compare livelihoods in plantation and agroforestry systems in West Africa. Our results suggest that compared to village households in traditional agroforestry landscapes – which may include smallholder oil palm farming – and national park, plantation households pay a considerably high prize for the benefit of receiving monthly salaries through employment. To put it simply, compared to agroforestry and national park, households in the oil palm plantation work longer for similar or even lower total incomes, while spending more money on living.

14.4.2 Ecological values of studied landscape types

We found that populations of conservation relevant mammals were mainly concentrated to protected areas. Therefore, our results are in line with findings from other parts of West and Central Africa (e.g. Blake et al. 2007; Remis and Jost Robinson 2012), highlighting the importance of protected areas for large mammal conservation. In our study, this is particularly true for flagship species, such as chimpanzee and elephant, which only showed a few encounters outside but close to protected areas. On the other hand, we could not detect significant or only slight differences between sites for encounter rates of the threatened primate species, such as red colobus, drill, crowned monkey and red-capped mangabey. Generally, very little is known about the conservation value of heterogeneous matrices dominated by smallholder agroforestry for large mammals. The fact that we recorded nearly all large mammal species also outside protected areas, suggests that habitat quality requirements for wildlife can be met in rural agroforestry systems in Southwest Cameroon. Therefore, they seem to serve as suitable habitats and in the same time maintain habitat connectivity even for species, which seem to depend on mature forest. Kupsch et al. (2019) demonstrated that the landscapes of Korup National Park and its surrounding agroforestry matrix may reach similar forest cover rates. The results of our bird surveys indicate that those two landscape types can harbour similar forest bird assemblages, whereas only the large-scale agro-industrial estates differ significantly. Bird diversity and composition was significantly lower inside than outside the plantation area, which mainly hold generalist and widespread species. In particular, species with forest-specific ecological niches, such as terrestrial insectivores or ant-followers (Ocampo-Ariza et al. 2019) can hardly be found in the studied plantation area. In fact, the only bird species of conservation importance, which we regularly observed inside the plantation area, was the African Grey Parrot. Parrots probably benefit from year-round supply with palm nuts, but were never observed roosting in the plantation area, indicating that their activity is limited to an opportunistic foraging behaviour (Dueker et al. 2020).

14.5 Overall Conclusions

Our study confirms that the Korup region with its multiple use landscapes including protected areas and a traditional Afrotropical agroforestry matrix has the potential to combine high ecological and socio-economic values. The large and remote protected areas, however, require attention in regard to management efficiency, including law enforcement to regulate bushmeat hunting and trade as well as continued responsibility and funding from the international community (e.g. Tranquilli et al. 2014) Investments in biodiversity conservation may also generate benefits for rural livelihoods if they follow strategies that are adapted to the demands of people living in the focal area (Belcher et al. 2005; Chazdon et al. 2009). Therefore, land managers, scientists, politicians and indigenous people need to collaborate in research and co-design programs and policies to promote both development and conservation (Adams et al. 2004; Chazdon et al. 2009). The traditional agroforestry landscape with its high biodiversity values is characterized by smallholder farming, and requires systematic support of smallholder structures, including financing, training and promotion of organization networks and land use planning to continue to play its role for human livelihoods and biodiversity. The most important conclusion is that large-scale agro-industry with its negative effects on biodiversity does provide little livelihood benefits, at least as implemented during the time of the study. Therefore, it seems unlikely that industrial plantations may serve as a sustainable land use model for the benefit of the people and ecosystems in Central and West Africa.

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Chapter 15

Connecting agricultural diversification, landscapes, and pollination to food security in China

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Abstract China is the second-most populous country in the world and has been implementing several strategies related to food security and rural development. A key strategy is farmland consolidation whereby small-scale farms are aggregated into large and simplified landscapes. Yet, agroecological principles such as agricultural diversification, widely recognized as a way forward for sustainable practices, have not been fully integrated into this strategy. In this chapter, we highlight how Prof. Teja Tscharntke's work on agricultural diversification, landscape ecology and pollination services has been crucial and shaping some of the thinking around sustainable food production in China. After an overview of food security issues in China, we discuss how diversified farming systems may help to overcome these issues and ought to be incentivized for farmers. As a majority of crops produced in China are dependent on insect pollination, we argue that policy-makers should adapt existing policies to maintain ecosystem services to increase crop yield and quality. Moving forward, we suggest that Chinese agricultural policies incorporate the results from agroecology research to ensure food security in sustainable production systems. Science and technology are critical to reduce environmental impacts and to improve the livelihoods of rural farmers.

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15.1 Introduction

The world is currently facing the twin challenge to providing enough nutritious food for an increasing human population while reducing agricultural impacts on the environment, people, and climate (Willett et al. 2019). Ironically, these agriculture related impacts may hamper the ability of our food systems to increase and in many cases even maintain yields (Ortiz-Bobea et al. 2021). Much attention has hence, been given to the global food systems transformation through agroecology and diversification (Tamburini et al. 2020; Wanger et al. 2020). In China, the world's second-most populous country and a major agricultural producer of maize, wheat, potato and rice, has successfully implemented sustainable development programs related to agriculture (Bryan et al. 2018). Sustainable agriculture to reach national food security targets has come to the forefront and is now anchored in the major agriculture-related policies (He et al. 2022; Central Committee of the Communist Party of China and State Council of China 2023). A key strategy for sustainable agricultural production in China is the 'well-facilitated farmland construction' or WFFC approach, whereby small-scale farms are consolidated into large and simplified productions areas. The WFFC approach has been shown to maximize mechanization and to reduce fertilizer inputs (Duan et al. 2021), suggesting a viable option for sustainable farming. However, decades of agroecological research on size and diversification effects at the farm and landscape scales suggest that WFFC may miss long-term environmental benefits, critical for China's food security (He et al. 2022).

Landscape-level agroecology was pioneered by Prof. Teja Tscharntke in Goettingen, Germany (Kruess and Tscharntke 1994; Tscharntke et al. 2005). Prof. Tscharntke's famous Agroecology group has shown the benefits of small and diverse farms in diverse landscapes for ecosystem services such as pollination, biological pest control and yields (e.g. Batáry et al. 2017; Hass et al. 2018; Tscharntke 2012; Tscharntke et al. 2021) amongst other topics. His work has inspired colleagues across Europe, the US, and in recent years also Chinese scholars (orange circle Fig. 15.1), where a landscape perspective on agroecology is still in its infancy (e.g. Liu et al. 2014; Tscharntke 2016; Wu et al. 2019; Gong et al. 2022; He et al. 2022). In this chapter, we focus on the role of agricultural diversification, landscapes, and pollination for food security in China, building on Prof Tscharntke's work. After an overview of food security issues in China, we focus on diversification and pollination related matters both at the farm and landscape scale. We close with an outlook of what is next in the field of landscape agroecology in China.

15.2 China's food security - sustainable agriculture is a challenge

As the second-most populated country in the world, China faces a serious food security issue, whereby the country feeds approximately 20% of the world's population based on 7% of the world's farmlands (Cui and Shoemaker 2018). Over the past 50 years, agriculture productivity in China has grown steadily at an average annual growth rate of 4.6% (National Bureau of Statistics of China 2015). Nonetheless, farmland production is under great pressure, because China is the world's largest producer of a variety of crops, including wheat, maize and potato. In addition, China has about 200 million agricultural holdings

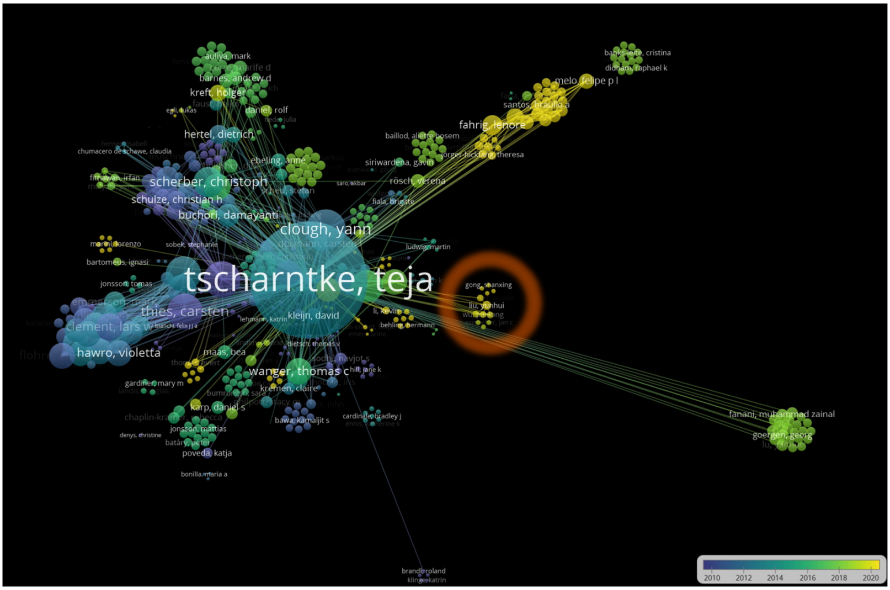

Fig. 15.1: Bibliographic network of Prof Teja Tscharntke. Node size represents average publications per year and edges being document total link strength. The orange circle represents Prof. Tscharntke's influence in China. Data is sourced with the keyword "teja tscharntke" from the EU Research API, author doubletons removed, and visualized with `vosviewer.com`.

(i.e., an economic agricultural unit that operates the land), which account for the 35% of world's total. A global farm size estimation showed that China has more than 70% of fields being < 0.64 ha (Lesiv et al. 2019) and field sizes of these smallholder farmers are smaller than worlds' average smallholder farm size of 2 ha (Tscharntke 2012). This means that supply fluctuations in these crops will have strong domestic but also global food security implications.

Agricultural inputs pose a substantial challenge to sustainable food production in China. The annual nitrogen application is on average more than four times higher than globally (305 kg per ha in China and 74 kg globally), but nitrogen use efficiency (nitrogen use / harvested product) is only 60% (0.25 in China and 0.42 globally (Cui et al. 2018; Zhang et al. 2015). From the 1950s to the beginning of the 21st century, annual pesticide production in China has increased from 500 tons to 929,000 tons (National Ministry of Agriculture 2004). Although the government is trying to control pesticide use and reduce pesticide residues in agricultural products, pesticides are still often overused (Xu et al. 2008). One reasons is that Chinese smallholder farmers sometimes have poor knowledge about agroecosystems (Pan et al. 2021; Xu et al. 2008) and intend to reduce the risk of pest pressure with excessive, yet unprofitable pesticide use in some cases (Zou et al. 2020). The overuse of chemical fertilizers and pesticides has led to major environmental problems such as water and soil pollution as well as food safety issues, calling for an effective implementation of China's sustainable agriculture strategies.

The Chinese government has made great efforts to incentivize and implement environmentally friendly management practices to increase yields while reducing pesticide and fertilizer related pollution. For instance, from 2005 to 2015 more than 20 million farmers adopted practices such as the integrated soil–crop system management (ISSM) program and increased average yields of maize, rice and wheat production by more than 10%, with nitrogen use decrease by 14.7–18.1% (Cui et al. 2018). In 2015, the Chinese Ministry of Agriculture and Rural Affairs established action plans with the goal of 0% growth in fertilizer and pesticide use by 2020 compared to a 2013 baseline, with the achieved amount of reductions varying from between regions (Cui et al. 2021). However, the use of these environmental friendly practices is often associated with yield trade-offs (Rosa-Schleich et al. 2019). Thus, ensuring food security and achieving sustainable agriculture is moving in the right direction, but remains a challenge in China (Huang and Yang 2017). Prof. Tscharntke advanced research that shows how diversified organic and conventional farming systems can promote yields, biodiversity, and ecosystem services without chemical fertilizers and pesticides (e.g. Gong et al. 2022; Tscharntke et al. 2021). In the next section, we explore the link between agricultural diversification and food security challenges in China.

15.3 Agricultural diversification and food security in China

Agricultural diversification is an underlying agroecological principle that focusses on intentionally incorporating functional biodiversity into cropping systems to regenerate biotic interactions for yield-supporting ecosystem services, such as soil fertility, pollination, and pest control (Kremen et al. 2012). Diversification practices include, but are not limited to, crop rotation, intercropping, non-crop diversification like flower strip, integrated crop-animal systems like rice-fish system, and agroforestry. A global synthesis, which Prof. Tscharntke co-authored, showed that biodiversity integration within food production systems help to increase pollination services as well as biological pest control (Dainese et al. 2019). As first and second generation disciples from Prof. Tscharntke's group, we conducted a global meta-analysis on diversification effects on rice production, showing that diversification can enhance sustainability and resilience in Chinese and global production (He et al. 2023, for examples of rice diversification and WFFC in China see Fig. 15.2). Specifically, on-farm diversification of rice paddies leads to higher yields at lower pest loads and reduced pesticide use compared to non-diversified rice paddies in south China (Gurr et al. 2016). Rice- animal integrated systems, which are traditional and common practices in China, have potential for global warming mitigation (Sun et al. 2021). In north China, long-term field experiments showed that grain yields increased on average by 22% in intercropped wheat/maize systems compared to matched monocultures and had greater year-to-year yield stability (Li et al. 2021). Thus, diversification in China's cropping systems may benefit yields, yield stability and the environment.

To meet the increasing demand for its large population, China keeps seeking to increase its food production. Well-facilitated farmland consolidation is expected to expand grain output and strengthen national food security. China is implementing WFFC since 2009

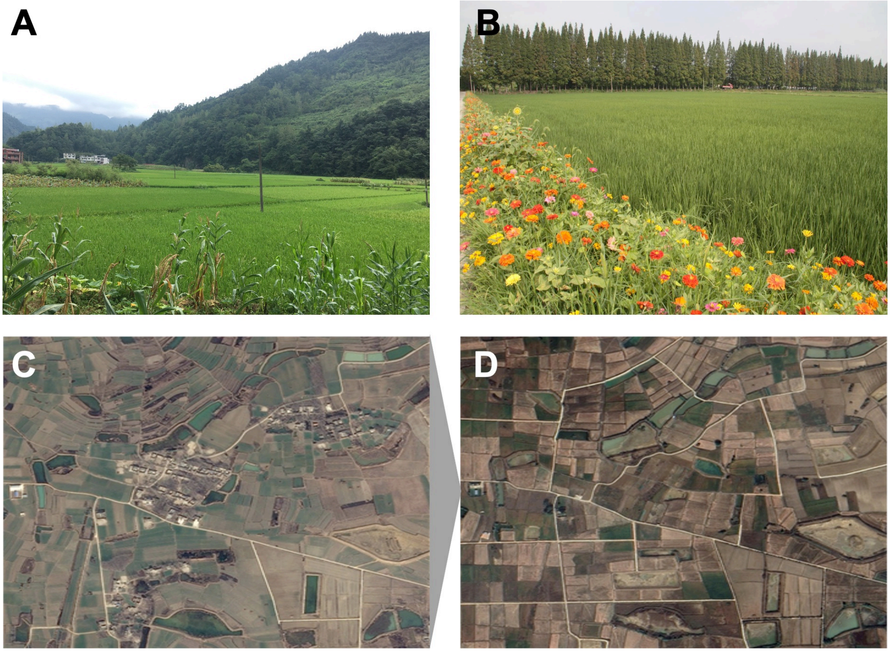

Fig. 15.2: Examples of rice diversification (A: rice-corn intercropping; B: non-crop diversification with *Zinnia elegans*) and the progression of WFFC in Anhui province from 2015 to 2019 (C and D). Image credits: Xueqing He (A), Zengrong Zhu (B), Google Earth Pro (C & D).

and on approximately 53 million hectares by 2020, with a target of 72 million hectares by 2030 (Ministry of Agriculture and Rural Affairs of the People's Republic of China 2021). The existing WFFC focuses on improving land productivity by consolidating small into large fields, increasing soil fertility, and improving accessibility and irrigation, but with limited consideration of diversification. WFFC does not fully capitalize on the multiple benefits associated with small fields as well as semi-natural habitats within agricultural landscapes as shown by Prof. Tscharntke's group (e.g. Grass et al. 2019; Tscharntke et al. 2022). By increasing field size and reducing semi-nature habitats, WFFC increases the uniformity in agriculture landscapes, which will reduce biodiversity and further jeopardize ecosystem services like pollination (Shi et al. 2021; He et al. 2022). However, the newly issued WFFC plan has emphasized ecological conservation and environmental protection (Ministry of Agriculture and Rural Affairs of the People's Republic of China 2021).

China has originally high diversity in crops, livestock, and agricultural landscapes, because of its long history in agriculture and great variation in natural conditions. As in other parts of the world, agricultural expansion and intensification has led to simplified agricultural landscape and caused biodiversity loss (Liu et al. 2013). Multiple global syntheses, which Prof. Tscharntke has contributed to, showed that agricultural diversification practices, such as crop rotation and intercropping, organic amendment, and soil inoculation increase biodiversity and enhance the delivery of several supporting and regulating ecosystem services crucial to crop health and yield (Kleijn et al. 2009; Rosa-Schleich et al. 2019). A global meta-analysis on the effect of field size on yields and agrobiodiversity found that smaller fields enhance yields and biodiversity, suggesting that large fields will not suffice in providing food security (Ricciardi et al. 2021). Moreover, maintaining semi-natural habitat in the well-facilitated farmland areas maintains pollinator abundance (Shi et al. 2021). Recently, He et al. (2022) suggested to integrate agricultural diversification and farm size consideration in China's major policies at national and provincial level, which would strongly leverage the potential of well-facilitated farmland to ensure food security in China.

15.4 Pollination and food security in China

Over the years, Prof. Tscharntke has contributed vastly to our understanding on the role of insect pollination in crop yield and eventually food security (e.g. Hass et al. 2018; Kleijn et al. 2009; Olhnuud et al. 2022; Senapathi et al. 2021). Animal pollinators provide more than a third of global food production (Klein et al. 2007), and other organisms also provide various important ecological services, such as pest control, decomposition and biological nitrogen fixation. In China, insect pollination is of great importance to food security and particularly critical for diverse and high quality foods like fruits and vegetables (Ouyang et al. 2019). For example, one study also co-authored by Prof. Tscharntke showed that insect pollination of apples – a globally important fruit crop with dominant production in China – contributed to a 57% and 25 t/ha increase in fruit set and yield, respectively (Wu et al. 2021). Overall, there are 107 main cultivated crops in China, including 24 food crops (including staple crops, cereals, and legumes), 41 fruit crops, 23 vegetable crops and 19 cash crops (Table 15.1). Food crops are generally not dependent on insect pollination with only two exceptions of buckwheat and broad bean, while fruit crops are strongly associated with insect pollination, including 20 high pollination dependent crops and 9 moderately dependent crops, and one crop with extreme dependence on insect pollination. Among 23 vegetables, 5 and 2 of them are extremely and moderately dependent on pollination, respectively. In addition, 11 of 19 commercial crops are with moderate to extreme dependence. With the improvement of human living standards, demand for these animal-pollinated fruit and vegetable crops are increasing in recent years. As FAO data shows, the total harvest area of 18 fruit crops and 3 vegetable crops, which are moderate or highly pollination dependent, increased by 45.3% and 14.6% respectively during the period from 2001 to 2021 (FAO 2021, Fig. 15.3). On the other hand, with the increasing concern about sustainable development, decreasing utilization of fertilizers have become a long-time national green agricultural policy, that raise the demand to develop new approaches for higher productivity. As one very important factor to modify yields of fruits and vegetables, pollination is becoming an even more critical measure to ensure food security in China.

Table 15.1: Main cultivated crops in China and their insect pollination dependence grade (*sensu* Ouyang et al. 2019).

	Dependence on animal-mediated pollination				
Crop category	Extreme	High	Moderate	Low	No
Staple Food (staple, cereal, and legumes)		Buckwheat	broad bean	Beans, Pigeon peas, Kidney bean, cow peas	Rice, wheat, maize, sorghum, barley, millet, oats, rye, quinoa, chick peas, lentils, lupins, peas
Fruits	Kiwifruit	Apples, Pears, Quinces, Peach, Almonds, Apricot, Cherry, Sour cherry, Plum, Jujube, Persimmons, Cranberry, Blueberry, Raspberry, Tangerine, Tangelo, Grapefruit, Mango, Avocado, Cashewapple	Strawberry Gooseberry Figs, Currants, Orange, Lemon, Lime, Coconuts	Grapes, Litchis, Longans, Arecanuts, Papayas	Dates
Vegetable	Cucumber, Muskmelons, Pumpkin, Watermelons, Other melons, Cocoa beans, Alfalfa	Kolanuts	Eggplant, Ocra	Chili, Pepper, Tomato	Spinach, Peppermint
Other			Cotton, Sesame seed, Soybeans, Sunflower seed, Mustard seed, rapeseed, Seed cotton, Coffee	Groundnuts, Linseed, Oil palm fruit, Safflower seed	Olives, Sugar beet, Sugarcane, Tea

Note: The pollinator dependence of crop (D) were evaluated based on the proportion of yield increase by insect pollination in open pollination, that is $D = \frac{\text{yield}_{\text{open}} - \text{yield}_{\text{closed}}}{\text{yield}_{\text{open}}}$. When $D = 0$, $0 < D < 10\%$, $10\% \leq D < 40\%$, $40\% \leq D < 90\%$, $90\% \leq D \leq 100\%$, the pollination dependence are defined as independence, low dependence, median dependence, high dependence, extreme dependence, respectively.

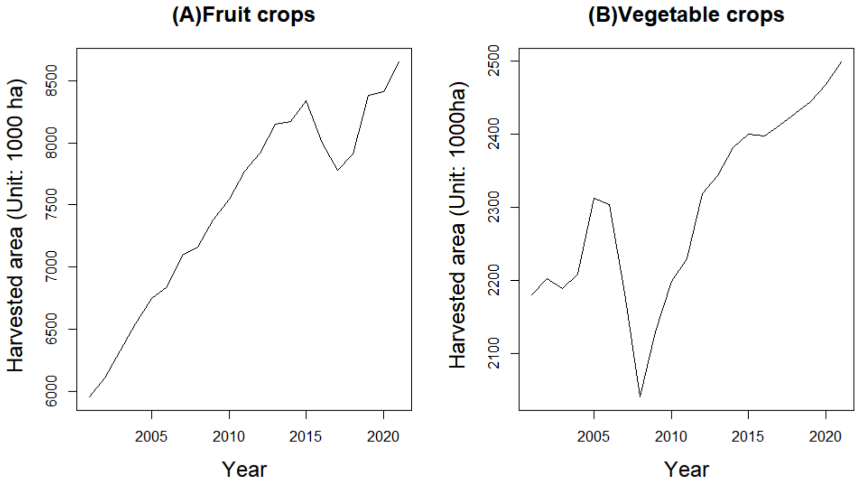

Fig. 15.3: The harvested area of (A) fruit crops and (B) vegetable crops which have moderate, high or extreme pollination dependence in China from 2001 to 2021 (FAO 2021).

15.5 Outlook

China's current strategy for agricultural sustainability and self-sufficient food production must address an increasing future demand for food diversity and quality and the decreasing resource availability. China has drawn a red line policy to protect the quality of its 120 million hectares of arable land (SCIO 2019). Moreover, ecological land consolidation has been proposed recently, whereby well-facilitated arable land incorporates ecological infrastructure and biodiversity restoration. In the major rice producing areas in Northeast China, conservation tillage will be applied in about 70% of total cultivated black land by returning straw to fields in 2025 (Minitry of Agriculture and Rural Affairs and Ministry of Finance 2020). To improve resource use efficiency, China extends water and fertilizer integration technology and trickle irrigation systems throughout the country's agricultural areas. The construction of 780 science and technology centres are intended to transform China's smallholder agriculture from an intense to a sustainable intensification model (Jiao et al. 2019).

Up until now, China has not fully capitalized on the contribution that agricultural diversification can make to food production and agricultural sustainability. There is already a plethora of research on the benefits of farm and landscape diversification on biodiversity, ecosystem services and yield, much of it spearheaded by Prof. Tscharntke's lifetime research efforts out of Europe. China has but could even more introduce these research efforts to improve food security and agricultural sustainability, especially the conservation and utilization of agricultural diversification. In Europe, agri-environmental schemes targeting the protection and restoration of semi-natural habitats, have been widely used at different special scales (Batáry et al. 2015). The United States also use similar approaches in the Farm

Bill to improve agricultural biodiversity and associated ecological services (Reimer 2015). However, the new 1st Central Document is now taking a firm stand on the implementation of sustainable agriculture, the implementation and multiple benefits, that farmers can directly relate to such as nutrition security and overall health improvements (Fan et al. 2021; Central Committee of the Communist Party of China and State Council of China 2023). We trust that China will fully realize and integrate agricultural diversification to ensure food security and improve agricultural sustainability in the future.

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Part V
Context: Socio-Ecological Systems

Chapter 16

The importance of diversified farming for biodiversity: a synthesis based on studies by Teja Tscharntke

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Abstract Diversified farming is an agricultural practice combining multiple crops or integrating non-crop elements in a field to promote sustainability, biodiversity, and ecosystem services. Using a meta-analysis approach based on Prof. Tscharntke's studies covering eight countries in both tropical and temperate regions, we investigated the effect of diversified farming on biodiversity. To do so, we compared diversified farming with non-crop habitats and conventional monocultures as reference habitats. We considered throughout the analysis whether these habitats were tree-containing or treeless. Compared to tree-containing non-crop habitats, tree-containing diversified farming resulted in no change in overall abundance but lower overall species richness, driven by species loss of vertebrates and trees. We found no significant effect on overall species richness and abundance when tree-containing diversified farming was compared to treeless non-crop habitats and treeless conventional monocultures. In contrast, if both diversified farming and conventional monoculture did not contain trees, diversified farming increased the overall species richness and abundance. By compiling Teja Tscharntke's research, we conclude that the effect of diversified farming on biodiversity is mediated by the identity of the reference habitat and the presence or absence of trees in both the diversified farming and reference habitat.

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16.1 Introduction

Agricultural intensification along with the simplification of the agricultural landscape is one of the major drivers of global biodiversity decline (Tilman 1999; Green et al. 2005; Outhwaite et al. 2022). The loss of biodiversity is coupled with a decline in important ecosystem functions and services threatening human well-being, agricultural production, and ecosystem health (Haines-Young and Potschin 2010; Cardinale et al. 2012; Oliver et al. 2015; Dainese et al. 2019). In contrast to intensive agricultural practices, traditional and recently introduced diversified farming offer an alternative to mitigate the loss of farmland biodiversity and support more sustainable food production (McNeely and Schroth 2006; Rosa-Schleich et al. 2019). Diversified farming covers a great variety of forms and can be implemented with annual and perennial crops, different land-use types, and across spatial and temporal scales (Kremen et al. 2012). Typically, diversified farming is characterized by an increased crop diversity which is realised by e.g. intercropping, agroforestry, polyculture, or crop rotations. Diversified farming can also include the integration of natural non-crop elements – such as hedgerows, wildflower strips, or fallow land within the agricultural landscape – or alternative management such as livestock grazing, adding organic manure, increasing genetic diversity, or adding a cover crop.

Overall, existing meta-analyses have shown that diversified farming may increase biodiversity (Lichtenberg et al. 2017; Sánchez et al. 2022), with positive effects on ecosystem services such as pollination, pest, and disease control (Tamburini et al. 2020). Moreover, diversified farming has been linked to benefits for soil fertility, water, and nutrient cycling (Kremen et al. 2012; Kremen and Miles 2012; Rosa-Schleich et al. 2019; Tamburini et al. 2020). However, the benefits of diversified farming on biodiversity greatly depend on the taxa or functional group studied (Fuller et al. 2005; Hole et al. 2005; Sánchez et al. 2022). For invertebrates, organic farming, as well as in-field diversification on the assessed biodiversity metric (e.g. intercropping, field margins, wildflower strips, hedgerows), were highlighted as most beneficial (Lichtenberg et al. 2017). In contrast, for vertebrates (i.e. birds and mammals), organic farming (Bengtsson et al. 2005; Hole et al. 2005), intercropping (Jones and Sieving 2006), and diversified agroforestry (Prabowo et al. 2016; Warren-Thomas et al. 2020) increased species richness. For plants, organic farming (Bengtsson et al. 2005; Hole et al. 2005) as well as diversified agroforestry increased species richness (Boinot et al. 2019). Consequently, understanding the overall effect of diversified farming on biodiversity requires the simultaneous assessment of multiple taxa of flora and fauna.

The benefits of diversified farming on biodiversity depend also on the assessed biodiversity metric (e.g. abundance and species richness) and the type of diversified farming (Marja et al. 2022; Sánchez et al. 2022; Jones et al. 2023). For example, the effects of diversified farming on species richness are generally positive, whereas the strength of positive effects on fauna and flora abundance varies largely across taxa (Bengtsson et al. 2005; Sánchez et al. 2022; Jones et al. 2023). Notably, tree-containing diversified farming such as agroforestry has been associated with more benefits compared to solely annual crops (Schroth 2004; Tschora and Cherubini 2020), as trees provide not only structural elements and food resources for animals (Manning et al. 2006), but also contribute to relevant ecosystem functions such as litter decomposition, biomass production, and water and nutrient cycling (Steffan-Dewenter et al. 2007; Jose 2009; Mortimer et al. 2018). Importantly, the benefit of diversified farming for biodiversity greatly depends on the reference habitat, i.e. if compared to natural habitats like a forest or intensified monoculture (Jones et al. 2023). Therefore, the relevance of diversified farming strategies must be understood across multiple contexts with global relevance.

Despite the documented ecological benefits of diversified farming, its implementation and integration in conservation planning remain low (Rosa-Schleich et al. 2019; Sánchez et al. 2022). In Europe, agri-environmental schemes promote diversified farming such as organic farming or associated plants (e.g. cover, buffer, companion crops) but other diversification measures such as intercropping or polyculture are still lacking in the portfolio (Moutier et al. 2021; European Commission 2022). Outside of Europe, agroforestry and crop rotation are more common (Beillouin et al. 2019). In particular, in the tropics, traditional diversified annual farming still exists (e.g. the milpa systems in Mesoamerica Novotny et al. 2021). Furthermore, smallholders prefer diversified farming as a measure for income diversification and income/subsistence security (Schroth and Ruf 2014). In addition, commercial perennial plantations are widespread in the tropics and serve the production of important commodities such as cacao, coffee, or rubber (Atangana et al. 2014; Beillouin et al. 2019). Here, certification schemes aim to promote diversified agroforestry (e.g. jungle rubber, shade-grown coffee, dynamic cacao agroforests: Tscharntke et al. 2015). However, globally, diversified farming is increasingly replaced by intensive large-scale monocultures, or their re-implementation is hampered by lacking financial aid and guidance (Rosa-Schleich et al. 2019; Sánchez et al. 2022).

The study of diversified farming, and land-use research in general is a recent branch in natural and interdisciplinary sciences (Verburg et al. 2013). In particular, the field of agroecology (i.e. the study of ecological processes within agricultural systems) had its uprising only in the 1980s when people increasingly started questioning the intensification of agriculture (Gliessman 2018). Prof. Dr. Teja Tscharntke made an early mark on the research field of agroecology, beginning his research on the effects of intensified agriculture on biodiversity in the early 1980s (Agroecology 2023b). At that time he mainly focused on arthropods as well as the impact of farmland measures such as set-aside fields, grasslands, and field margins. Later on, his research increasingly covered a greater diversity of land-use types, diversification measures, taxa as well as the landscape context (Agroecology 2023a). In the past twenty years, he also started researching tropical land-use systems (Clough et al. 2011; Wurz et al. 2022a). Whereas Tscharntke has co-authored or led multiple case studies on the effect of diversified agriculture on biodiversity, a quantitative summary across taxa remains to be done.

Here, we conducted a meta-analysis to assess the value of diversified farming (focus habitat) for biodiversity in comparison to non-crop habitats and conventional monoculture (reference habitats). We aim to highlight the effect of land-use change by comparing diversified farming to non-crop habitats, while the effect of land-use intensification is analysed with the comparison of diversified farming to conventional monoculture. In our analysis, we differentiate between tree-containing or treeless habitats within each of the three land-use categories (diversified farming, conventional monocultures, and non-crop habitats). Therein, we consider in-field and crop diversification measures only and do not include external and non-crop diversified farming measures such as hedgerows, wildflower strips, and field margins. Our meta-analysis focuses on the following three questions: (i)

Does diversified farming generally promote biodiversity? (ii) How does diversified farming affect the species richness and abundance of different taxonomic groups (invertebrate, vertebrate, lower strata plants)?, and (iii) how do the benefits of diversified farming vary depending on the reference habitats?

16.2 Materials and methods

16.2.1 Literature search, selection of relevant articles, and data extraction

We conducted a literature search on the Web of Science first on 15 December 2022 and updated on 21 January 2023 updated using the keyword "TSCHARNTKE TEJA" OR "TSCHARNTKE T". The search yielded 464 articles among which we selected relevant articles to this synthesis based on the following criteria: articles (i) were in English, (ii) compared diversified farming (agroforestry, intercropping, organic farming) with non-crop habitat (forest, open-land, fallow, pasture) or conventional monoculture (Table 16.1), (iii) studied at least one species of the different taxonomic groups (invertebrate, vertebrate, lower strata plant, and tree), (iv) assessed at least one of the diversity metrics (abundance and richness), (iv) were a case study, not a review or perspective or meta-analysis or thesis or monograph.

The selection yielded 46 relevant articles, from which we recorded the sample size, the mean abundance, and species richness of the different taxonomic groups and their standard deviation. When a standard error was provided, we computed the standard deviation by multiplying the standard error by the square root of the sample size. When images were provided in the articles, we retrieved all these values using *ImageJ* and *PlotDigitizer* software (Schneider et al. 2012; PlotDigitizer 2022). In total, we obtained 638 individual observations.

16.2.2 Data analysis

Before starting the analysis, we assigned non-crop habitat or conventional monoculture as the reference habitat, whereas diversified farming was the focus habitat. Then, we sorted and subsetted our data to fit our objectives. In total, we had five sub-datasets, each containing one of five possible comparisons: "tree-containing diversified farming vs. tree-containing non-crop habitat", "tree-containing diversified farming vs. treeless non-crop habitat", "tree-containing diversified farming vs. treeless conventional monoculture", "treeless diversified farming vs. treeless conventional monoculture", and "tree-containing diversified farming vs. tree-containing conventional monoculture".

To assess the effect of diversified farming on biodiversity, we performed a meta-analysis using the R program version 3.6.3 and the metafor package version 2.4.0 (Viechtbauer 2010; R Core Team 2020). First, we calculated individual effect sizes of each study within each sub-dataset using the `escalc` function. We used the Log Ratio of Means as an effect size measure. For each sub-dataset, we ran different random-effect models to estimate the overall effect size of diversified farming on the abundance and species richness by using the `rma` function. A positive value of overall effect size indicates, for instance, that treeless diversified farming has a positive effect relative to treeless conventional monoculture. The

Table 16.1: Description and examples of the focus and reference habitat considered in the present synthesis.

		Tree presence	Definition	Example
FOCUS HABITAT	Diversified farming	Tree-containing	Practices that consist of keeping/ growing trees simultaneously with crops in the same field (at least two plant species planted together of which at least one is perennial and one (annual or perennial) is managed as a crop (Beillouin et al., 2019)	Coffee agroforest, cacao agroforest, fallow-derived, vanilla agroforest, forest-derived, vanilla agroforest, jungle rubber
		Treeless	Practices that consist of growing simultaneously two or more crop species, varieties, or cultivars in the same field for part or the complete growing cycle (Beillouin et al., 2019)	Strip intercropping (wheat-oilseed rape)
		Treeless	Practices that promote agrobiodiversity through biodiversity-friendly management such as non-use of chemical inputs and crop rotation (Kremen & Miles, 2012)	Organic wheat field, organic barley field, organic legume field
REFERENCE HABITAT	Non-crop habitat	Tree-containing	Primary and secondary forests. Forests that are unmanaged or managed.	Old-growth forest, forest fragment, abandoned agroforest, secondary forest
		Tree-containing	Set-aside land which is currently not used for crop production. Covered by woody vegetation.	Woody fallow
		Treeless	Set-aside land which is currently not used for crop production. Covered by herbaceous vegetation.	Herbaceous fallow
		Treeless	Land used for grazing by ungulates	Pasture
	Conventional monoculture	Tree-containing	Practice in which a single crop or variety is cropped on the same plot and at the same time. Natural vegetation is absent.	Rubber
		Treeless	Practice in which a single crop or variety is cropped on the same plot and at the same time. Natural vegetation is absent	Wheat, rice, maize, legume, oilseed rape

statistical significance of the overall effect is determined by a p-value lower than 0.05. We tested heterogeneity (i.e. variability of effect sizes observed across studies included in the meta-analysis) using Cochran's Q test and Higgins & Thompson's I^2 Statistic (Higgins and Thompson 2002; Harrer et al. 2021). Here, a p-value lower than 0.05 in Cochran's Q test indicated a significant heterogeneity in effect sizes between studies. The I^2 value indicates the level of heterogeneity, with low heterogeneity between 0%-25%, moderate heterogeneity between 25%-75%, and substantial heterogeneity above 75% (Harrer et al. 2021). Our analysis revealed substantial heterogeneity in effect sizes between studies, as evidenced by an I^2 value greater than 75%. We expected such patterns since it is usual to have higher heterogeneity in ecology (Senior et al. 2016), thus allowing us to perform a subgroup meta-analysis. Here, in line with our objectives, we used the taxonomic group (i.e. invertebrate, vertebrate, lower strata plant, and tree) as a moderator to identify patterns that are potentially not apparent in the overall effect size analysis.

Publication bias occurs when studies reporting statistically significant results are more likely to be published, resulting in an overestimation of the effect of an intervention. To test for potential publication bias, we first generated a funnel plot based on the effect sizes of individual studies against standard errors. Then, we assessed visually whether the funnel plot is asymmetric or not. An asymmetric plot indicates a potential publication bias. Because visual analysis usually creates uncertainty, we used Egger's test to test for funnel plot asymmetry (Sterne and Egger 2001). A p-value lower than 0.05 implies that the funnel plot is significantly asymmetric, thus a presence of publication bias. We found potential publication bias for the species richness model assessing the overall effect of tree-containing diversified farming relative to treeless non-crop habitat (Egger's test, z = 2.7632, p = 0.0057), tree-containing diversified farming relative to treeless conventional monoculture (Egger's test, $z = 3.0677$, $p = 0.0022$), and treeless diversified farming relative to treeless conventional monoculture (Egger's test, $z = 5.2140$, $p < 0.0001$). We used the trim-and-fill method by imputing hypothetical missing or non-published studies to correct potential publication bias and adjust the overall effect size (Shi and Lin 2019).

16.3 Results

16.3.1 General overview of the data

We selected a total of 46 relevant articles distributed across eight countries and published between 2004 and 2022 (Fig. 16.1). Among the reference habitats, conventional monocultures were the most studied (49.4%). This included maize, rice, wheat, barley legume, rubber, oil palm, and coffee crops, with wheat being the most commonly used reference system. The second most studied reference habitat was forest (35.8%), mostly in tropical countries (22 articles). All other reference habitats were studied in $<\approx 10\%$ of the articles (Fig. 16.2).

Three types of diversified farming were found among Teja Tscharntke's studies, namely tropical agroforestry (56.2%; including cacao agroforestry = 19.3%; coffee agroforestry = 14%; vanilla agroforestry = 14%; jungle rubber = 5.3% and mixed agroforests = 3.5%); followed closely by organic farming (43.9% of studies). Only one recent study included strip intercropping as a novel diversification strategy in Europe.

16.3.2 Comparison of treeless diversified farming vs. treeless reference habitat

Overall, species richness in treeless diversified farming was 19% higher than in treeless conventional monoculture (Fig. 16.3a). Differentiated by taxonomic groups, we did not find a significant effect of treeless diversified farming compared to treeless conventional monoculture on the species richness of vertebrates or invertebrates, but lower strata plants increased by 120% (Fig. 16.3a). For the same comparison, the overall abundance increased by 27% in diversified farming (Fig. 16.3b). Grouped by taxonomic category, the abundance of vertebrates increased by 25% and invertebrates by 30% in treeless diversified farming relative to treeless conventional monocultures (Fig. 16.3b).

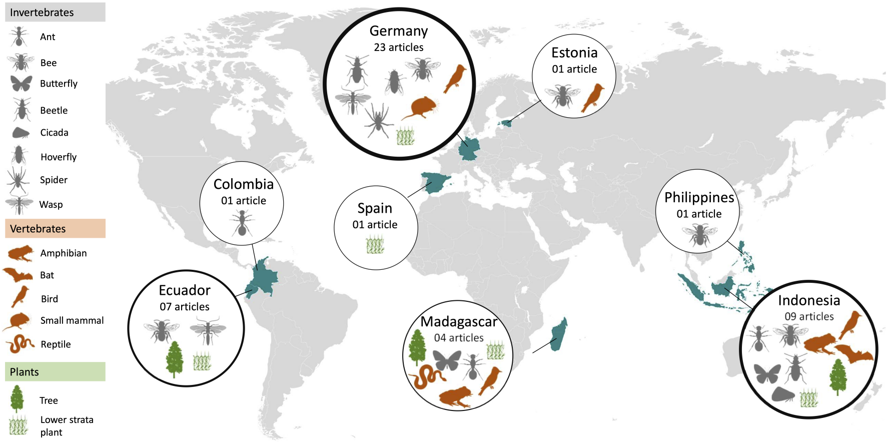

Fig. 16.1: Distribution of the relevant articles and taxonomic group studied. Studies are: Schulze et al. (2004), Roschewitz et al. (2005), Tylianakis et al. (2005, 2006), Purtauf et al. (2005), Schmidt et al. (2005), Shahabuddin et al. (2005, 2010), Kleijn et al. (2006), Lozada et al. (2007, 2008), Bos et al. (2007, 2008), Clough et al. (2007), Teodoro et al. (2009a,b), Batáry et al. (2010, 2012, 2013, 2017), Batáry and Tscharntke (2022), Hoehn et al. (2010), Holzschuh et al. (2010), Fischer et al. (2011a,b,c), Armengot et al. (2012), Gagic et al. (2014), Marja et al. (2014), Darras et al. (2016), Nurdiansyah et al. (2016), Prabowo et al. (2016), Happe et al. (2018), Hass et al. (2018), Gayer et al. (2019), Escobar-Ramirez et al. (2020), Geppert et al. (2020), Rakotomalala et al. (2021), Raveloaritiana et al. (2021), Török et al. (2021), Alarcon-Segura et al. (2022), and Wurz et al. (2022a,b).

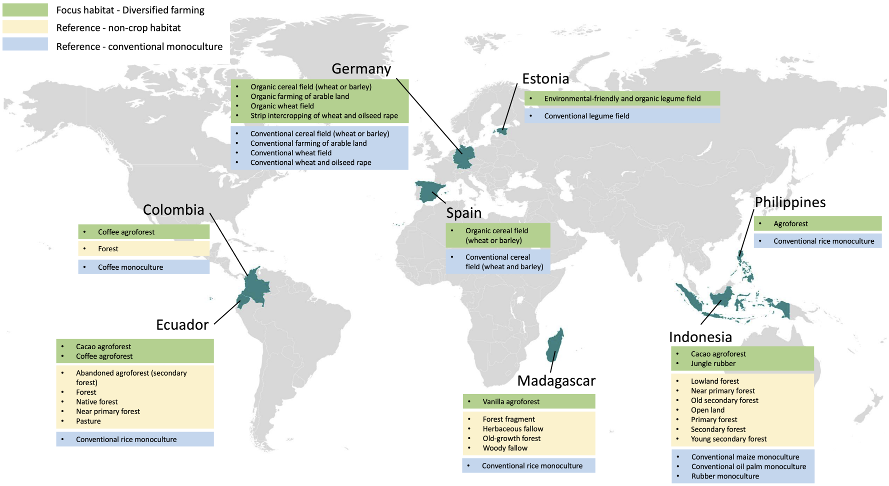

Fig. 16.2: Distribution of the focus habitat (diversified farming) and the reference habitat (non-crop and conventional monoculture).

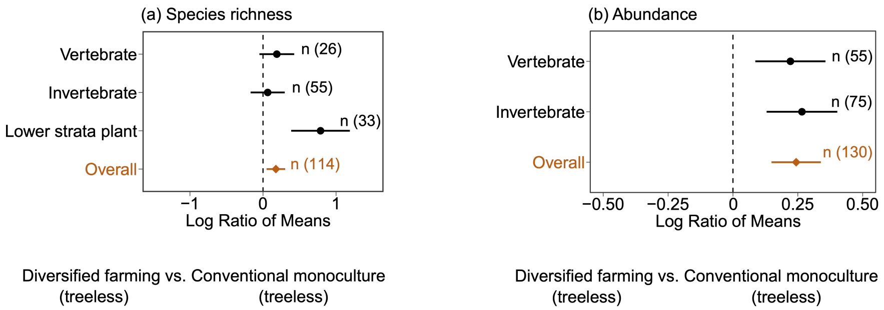

Fig. 16.3: Effect of treeless diversified farming on the species richness (a) and abundance (b) relative to treeless conventional monoculture. Points in black represent the estimated effect sizes (Log Ratio of Means) of the different taxonomic groups. Points in orange represent the overall effect size. The horizontal line around the estimated effect represents the 95% confidence interval. A Log Ratio of Means < 0 indicates, for instance, that treeless diversified farming has greater overall species richness and abundance than treeless conventional monoculture. The significance of the effect ($p < 0.05$) is determined by the non-overlapping of the confidence interval with the dashed vertical line where the value of the Log Ratio of Means is 0. The number of studies is represented by n( ).

16.3.3 Comparison of tree-containing diversified farming vs. tree-containing reference habitats

When comparing tree-containing diversified farming and tree-containing non-crop habitats, we found an overall negative effect of diversified farming on species richness, a decrease of 16% (Fig. 16.4a) but no effect on abundance (Fig. 16.4b). For the same comparison and depicted by taxonomic groups, species richness either decreased for vertebrates by 42% and trees by 69% or did not significantly change for invertebrates and lower strata plants (Fig. 16.4a). The abundance of individual taxonomic groups remained comparable between tree-containing diversified farming and tree-containing non-crop habitats (Fig. 16.4b).

When comparing tree-containing diversified farming to tree-containing conventional monoculture, we found a negative effect of diversified farming, reducing the overall species richness by 17% (Fig. 16.4c). Separated by taxonomic group, we found a decrease in species richness of invertebrates by 24% but an unchanged species richness of vertebrates in diversified farming (Fig. 16.4c).

16.3.4 Comparison of tree-containing diversified farming vs. treeless reference habitat

We did not find any significant overall change in either species richness or abundance in tree-containing diversified farming compared to treeless conventional monocultures (Fig. 16.4a-b). Sorted by taxonomic groups, the species richness of lower strata plants decreased by 44% (Fig. 16.4a) while the abundance of invertebrates increased by 54% (Fig. 16.4b). Compared to treeless non-crop habitats, tree-containing diversified farming

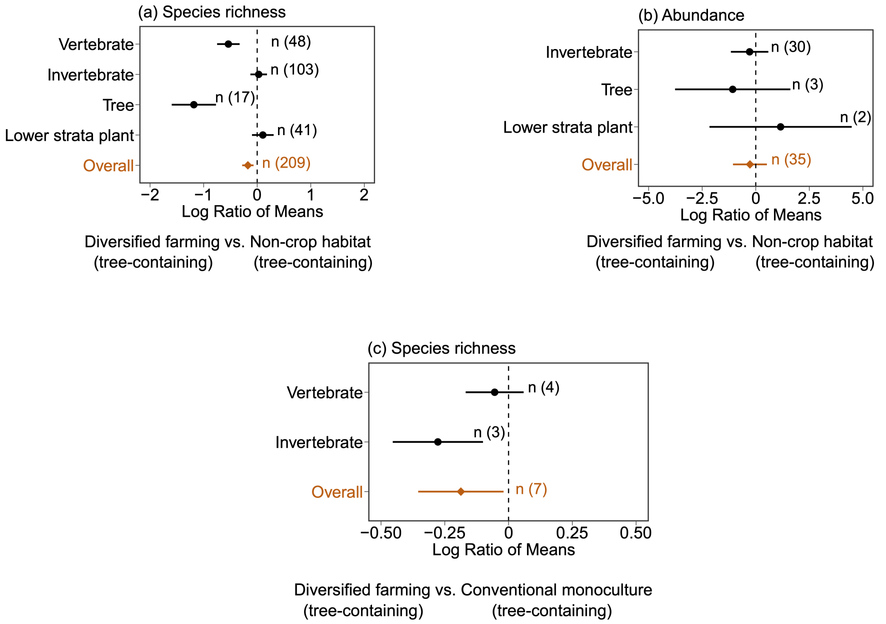

Fig. 16.4: Effect of tree-containing diversified farming on the species richness and abundance relative to tree-containing non-crop habitat (a-b), and tree-containing conventional monoculture (c). See Fig. 16.3 for details.

did not contain more species or individuals, neither overall nor for any single taxonomic group (Fig. 16.4c-d).

16.4 Discussion

Our meta-analysis provides a detailed overview of Teja Tscharntke's contribution toward the understanding of the effects of diversified farming on biodiversity, in comparison to different natural and agricultural habitats. We found that the benefits of diversified farming for biodiversity vary with the presence or absence of trees. Diversified farming enhanced biodiversity in comparison to conventional monocultures when trees were absent in both crop types, but species richness and abundance in diversified farming were still lower in comparison to tree-containing non-crop habitats. Interestingly, we did not find any effect on either overall species richness or overall abundance of tree-containing diversified farming compared to treeless non-crop habitat or treeless conventional monoculture. Furthermore, we found variable responses across taxonomic groups depending if richness or abundance was measured as well as which habitats were compared. Overall, our results highlight the complex interplay between system comparison and vegetation structure when the benefits of an intervention measure are evaluated on multiple fauna and flora taxa.

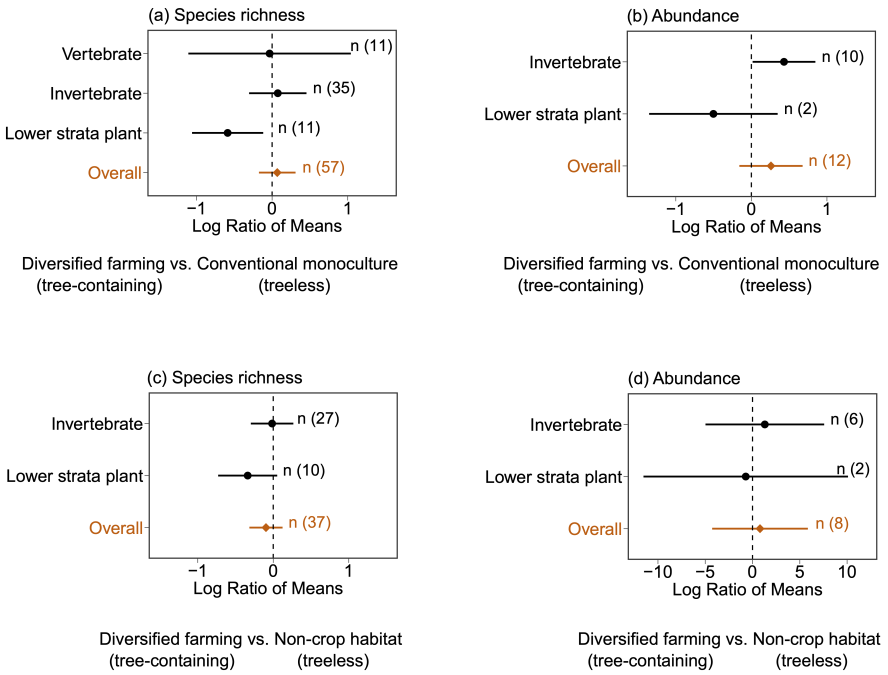

Fig. 16.5: Effect of tree-containing diversified farming on the species richness and abundance relative to treeless conventional monoculture (a-b), and treeless non-crop habitat (c-d). See Fig. 16.3 for details.

16.4.1 Benefits of diversified farming

We found that if both the diversified farming and the conventional monoculture lacked trees, diversified farming (e.g. strip intercropping, organic wheat fields) increased overall species richness and abundance. This was the only comparison with a positive effect of diversified farming on biodiversity. Treeless conventional monocultures within our analyses were relatively homogeneous annual crops, which likely provide limited resources for animals, and prevent the growth of other plant species given conventional management (e.g. Brandmeier et al. 2021). Furthermore, treeless diversified farming such as intercropping or organic farming are commonly integrated or situated within a simplified agricultural landscape (all studies with these diversification measures were from Western Europe, where intensive agriculture is commonplace). Thus, the effect of diversified farming may be amplified because of the simplified surroundings.

When comparing treeless diversified farming with treeless conventional monoculture, we found that in particular, the species richness of lower strata plants as well as the abundance of vertebrates and invertebrates increased. Lower strata plants, such as herbs and grasses, may have benefited from the increased light availability in treeless diversified farming. In conventional monoculture, the densely planted rows as well as individual species can limit the amount of light that reaches the lower strata (e.g. Gérard et al. 2017). Furthermore, decreased nutrient availability due to dense planting as well as the application of agrochemicals can reduce lower strata plants (Schmitz et al. 2014; Li et al. 2019). Strip intercropping and organic wheat fields, on the other hand, often involve multiple crop species with shorter heights that do not form a continuous cover, allowing more light to reach the lower strata. This increased light availability can create more favourable conditions for lower strata plants to grow and contribute to higher species richness (Albrecht et al. 2016). Additionally, lower strata plants may also provide important habitat and food resources for a variety of other taxa, such as insects and small vertebrates, which can explain the overall increase in abundance of vertebrates and invertebrates observed in this comparison (Holzschuh et al. 2008; Tuck et al. 2014; Brandmeier et al. 2021). In line with these explanations, we found that tree-containing diversified farming reduced the species richness of lower strata plants compared to treeless conventional monocultures. Diversified farming that contains trees have been shown to create more complex canopy structures and provide more shade, which can reduce light availability at lower strata levels.

In contrast, we did not find an effect of tree-containing diversified farming on either species richness or abundance compared to treeless non-crop habitat (e.g. herbaceous fallows, pastures). We also found no significant increase in overall species richness and abundance in tree-containing diversified farming in comparison to treeless conventional monocultures (e.g. wheat and rice fields). There could be several possible explanations for this. One possibility is that the type of trees used in diversified farming was not suitable for supporting the specific taxonomic group under consideration. For example, the identity of shade trees in tropical agroforests has been reported to impact the diversity of soil macrobiota (Rousseau et al. 2021); and the availability of flowering herbs may affect the species richness of bees and wasps (Tylianakis et al. 2006).

Another possibility is that the trees were not planted in the right locations or in sufficient density to have a significant impact on biodiversity. For example, tropical agroforests with at least 15% shade cover are already considered suitable for sustainability certifications (Rainforest Alliance 2020), but previous research shows that maximizing benefits for biodiversity and crop yield requires intermediate shade covers of ca. 40% (e.g. Bos et al. 2007; Steffan-Dewenter et al. 2007; Clough et al. 2011). Additionally, other factors associated with diversified farming (e.g. management practices, soil quality, landscape context) may have interacted with the presence of trees in complex ways that ultimately negated the positive effects on biodiversity. For example, a heterogeneous and diverse landscape may offer multiple habitats attractive to biodiversity, resulting in the dilution of abundances across the landscape instead of clustering in diversified farming (e.g. Hass et al. 2018). In contrast, highly-deforested areas may lead to overall species loss at the local scale, deeming diversified farming insufficient to maintain biodiversity if isolated from suitable natural areas (e.g. Faria et al. 2006).

16.4.2 The importance of tree-containing non-crop habitat

We found that tree-containing diversified farming held similar fauna and flora abundances in comparison to non-crop habitats, which points to the success of diversification measures for retaining biodiversity in agroecosystems. Indeed, certain species can find adequate habitat and resource availability in diversified farming, and this is expected to derive in beneficial ecosystem services for the agroecosystem (e.g. Torralba et al. 2016; Smith et al. 2019; Tamburini et al. 2020; Vansynghel et al. 2022; but see Mupepele et al. 2021). We found that lower strata plants and invertebrates were similarly species-rich and abundant in diversified farming and the tree-containing non-crop habitat.

Compared to tree-containing non-crop habitats (e.g. old-growth forests, forest fragments, woody fallow), tree-containing diversified farming (e.g. jungle rubber, vanilla agroforests) was related to overall lower species richness and unchanged abundance. In particular, the species richness of trees and vertebrates was reduced in tree-containing diversified farming compared to tree-containing non-crop habitat, while lower strata plant richness was unaffected. This negative effect of diversified farming may be largely driven by the effect of forests. Many studies, also by Teja Tscharntke, have shown that agroforests do not provide the same level of habitat complexity as natural forest ecosystems that multiple taxa require (e.g. Tylianakis et al. 2006; Prabowo et al. 2016; Darras et al. 2018; Ocampo-Ariza et al. 2022). Agroforests often have a simpler structure and fewer microhabitats, which may limit the ability of certain species to survive and thrive. Additionally, some species (e.g. insectivorous birds or large mammals) may require specific microhabitats, forest edges, or habitat sizes which are not available in agroforests (e.g. Cassano et al. 2014; Powell et al. 2015; Ferreira et al. 2020). This highlights the importance of preserving natural forest ecosystems and incorporating appropriate conservation measures in agricultural landscapes to maintain biodiversity and habitat specialists.

Against our expectations, we found that in comparison to tree-containing conventional monocultures (e.g. rubber or conventional oil palm monocultures), tree-containing diversified farming (e.g. agroforests) held fewer species richness of invertebrates. This is in line with other studies reporting more insects in conventional agricultural systems than in natural habitats or diversified farming (e.g. Torralba et al. 2016) and may be related to higher availability of resources for specific invertebrate taxa within monocultures. Phytophagous species and potential crop pests may thrive in monocultures given the high food availability, and the reduced pressure from natural enemies, which are often enhanced in diversified farming (e.g. Guenat et al. 2019; Jones et al. 2023). In contrast to invertebrates, we found that the species richness of vertebrates was comparable between tree-containing diversified farming and tree-containing monocultures. Whereas this can be explained by the ability of medium-sized and large vertebrates to move across different habitats, and visit monocultures temporarily to find food resources, current literature indicates that species richness is insufficient to compare vertebrate communities in different ecosystems. Even with comparable species richness, diversified farming and monocultures may hold largely different species compositions (e.g. Hendershot et al. 2020; Jarrett et al. 2021), and there is evidence that key functional traits disappear from monocultures in comparison to diversified farming and natural habitats (e.g. Luiza-Andrade et al. 2017; Potapov et al. 2020). Therefore, combining multiple diversity indicators is essential to have a detailed understanding of the value of diversified farming on specific taxa.

16.4.3 Outlook

Based on the studies led or co-authored by Teja Tscharntke, we could synthesize the effect of diversified farming on biodiversity while considering the reference habitat identity, the absence or presence of trees as well as the taxonomic group. As new strategies to maintain biodiversity in a world of ever-growing agriculture, it will be relevant to continue doing thorough and critical assessments of their benefits and problems.

We highlight the benefit of integrating treeless diversified farming such as intercropping or organic farming in homogeneous agricultural landscapes where trees are lacking. In recent years, there has been a growing trend towards intercropping and organic farming in Europe and other parts of the world. Intercropping, which involves planting multiple crops on one field, can increase biodiversity, soil health, and overall crop yields. Organic farming, on the other hand, involves using organic amendments and biological pest control methods and has been shown to have environmental benefits such as reduced pesticide use and improved soil quality. Both of these practices are seen as more sustainable alternatives to conventional farming methods, which can be harmful to the environment and contribute to climate change. As a result, many farmers and policymakers are promoting the adoption of intercropping and organic farming to create more sustainable and resilient agricultural systems. In the tropics, intercropping and organic farming practices are particularly important for smallholder farmers, since they require less economic investment in inputs and machinery, and may provide alternative income options enhancing socio-ecological sustainability (Maas et al. 2020; Tscharntke et al. 2023). Additionally, these practices can help mitigate the negative impacts of climate change on agriculture, by promoting agroecosystem resilience and reducing greenhouse gas emissions.

In his most recent publication on organic farming, Teja Tscharntke emphasizes that while organic farming is a step towards more sustainable agriculture, it is not enough to address all the environmental issues associated with modern agriculture. He acknowledges that organic farming can have negative impacts on biodiversity and that it is not always the best solution for promoting ecological intensification (Tscharntke 2021). Here, Teja Tscharntke argues that a more comprehensive approach is needed, which includes a combination of different farming practices, such as agroforestry and intercropping, to promote biodiversity conservation and sustainable agriculture (Grass et al. 2021).

Based on many other studies by Teja Tscharntke (e.g. Schulze et al. 2004; Steffan-Dewenter et al. 2007), it is clear that natural habitats such as forests play a crucial role in maintaining biodiversity. In particular, his research has shown that tree-containing non-crop habitats, such as old-growth forests and forest fragments, have higher species richness compared to agroforests or intensified annual crops. Overall, our results highlight the importance of conserving natural habitats to ensure the preservation of biodiversity, while also emphasizing the need for sustainable farming practices that can maintain or enhance biodiversity.

16.5 Conclusion

In conclusion, diversified farming can have both positive and negative effects on biodiversity, depending on the specific context and reference habitat. The presence or absence of trees in both the diversified farming and reference habitat is a key factor that mediates the effect on biodiversity. Overall, our meta-analysis of Teja Tscharntke's research on diversified farming highlights the complex and context-dependent relationship between diversified farming and biodiversity. Furthermore, under certain conditions, diversified farming has the potential to counteract the simplification and intensification of agriculture and align food production with biodiversity conservation. However, our study also suggests that diversified farming alone may not be enough to achieve this goal but that the protection of natural non-crop habitats, in particular forests, is essential. These findings underscore the need for further research and careful consideration of local conditions in promoting sustainable and biodiverse agriculture.

Author Contributions

A.A.N.A. R., C.O.A. conceptualized the idea of this manuscript. A.A.N.A. R., C. O.A., I. A., E. R., M. T.-H., and A.W. extracted the data. A.A.N.A. R. cleaned, analyzed and visualized the data. A.A.N.A. R., C. O.A., and A.W. led the writing of the manuscript. All authors contributed to the edition of the manuscript and gave final approval for publication.

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Appendix A
Chronological bibliography of the works of Teja Tscharntke

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