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## Land-use change and biodiversity: challenges for assembling evidence on the greatest threat to nature

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## Abstract

Land-use change is considered the greatest threat to nature, having caused worldwide declines in the abundance, diversity, and health of species and ecosystems. Despite increasing research on this global change driver, there are still challenges to forming an effective synthesis. The estimated impact of land-use change on biodiversity can depend on location, research methods, and taxonomic focus, with recent global meta-analyses reaching disparate conclusions. Here we critically appraise this research body and our ability to reach a reliable consensus. We employ named entity recognition to analyse more than 4000 abstracts, alongside full reading of 100 randomly selected papers. We highlight the broad range of study designs and methodologies used; the most common being local space-for-time comparisons that classify land use in situ. Species metrics including abundance, distribution, and diversity were measured more frequently than complex responses such as demography, vital rates, and behaviour.

We identified taxonomic biases, with vertebrates well represented whilst detritivores were largely missing. Omitting this group may hinder our understanding of how land-use change affects ecosystem feedbacks. Research was heavily biased towards temperate forested biomes in North America and Europe, with warmer regions being acutely underrepresented despite offering potential insights into the future effects of land-use change under novel climates. Various land use histories were covered, although more research in understudied regions including Africa and the Middle East is required to capture regional differences in the form of current and historical land use practices. Failure to address these challenges will impede our global understanding of land-use change impacts on biodiversity, limit the reliability of future projections, and have repercussions for the conservation of threatened species. Beyond identifying literature biases, we highlight the research priorities and data gaps that need urgent attention and offer perspectives on how to move forwards.

## 1. Introduction

The IPBES 2019 global report ranked land-use change as the greatest driver of declines in nature and biodiversity. Combined with the direct exploitation of nature through hunting, fishing, logging, and harvesting, these threats are thought to account for more than 50% of the human impacts on terrestrial and freshwater ecosystems (IPBES, 2019). During the past 300 years the terrestrial biosphere has transitioned from mostly wild to mostly anthropogenic (Ellis et al., 2010); humanity's influence now extends over three quarters of the terrestrial world (Venter et al., 2016). Agricultural expansion for cropping, plantations, and animal rearing is attributed as the leading cause of global land-use change (IPBES, 2018). The expansion and intensification of human land uses has increased our share of the planet's resources at the expense of biodiversity and the ecosystem services it provides (Díaz et al., 2019; Foley et al., 2005). It is estimated that the biodiversity of terrestrial communities has declined on average by more than one fifth (Hill et al., 2018). The global biomass of vegetation has halved (Erb et al., 2018) and that of wild mammals has dropped by more than 75%, now only accounting for 4% of mammalian biomass, the remainder being livestock and humans (Bar-On et al., 2018).

Land-use change can have direct impacts on species through the destruction of habitat and modification of the environment (Andren, 1994; Bender et al., 1998; Fahrig, 1997). However, there can also be widespread enigmatic ecological impacts that are small and cumulative, spatially removed, or difficult to detect (Raiter et al., 2014). Land-use change also interacts with other global change drivers. For example, it is known that road building facilitates the spread of invasive species (Forys et al., 2002; Schmidt, 1989) and increases accessibility for direct exploitation (Coffin, 2007; Peres, 2000). Interactions between land-use change and climate change are apparent but insufficiently researched (Sirami et al., 2017; Santos et al., 2021). The projected rise of both these threats may jeopardise the persistence of threatened species and communities. Despite land-use change presenting arguably the greatest threat to biodiversity (IPBES, 2019; Sala et al., 2000), research into this topic has lagged behind investigations into climate change impacts (Titeux et al., 2016). In the climate change and species distribution literature, the role of land use has been largely ignored (Taheri et al., 2021).

Several meta-analyses and syntheses have investigated the global impacts of land-use change on biodiversity. These studies generally report that land-use change substantially reduces local



species richness (Beckmann et al., 2019; Gerstner et al., 2014; Murphy & Romanuk, 2014; Newbold et al., 2015), alters species composition (Dornelas et al., 2014; Newbold et al., 2016), and diminishes abundance (Collen et al., 2009; Gibson et al., 2011; Newbold et al., 2015). Species functional groups also show diverse responses to land-use change (Newbold et al., 2020). A meta-analysis on the effects of agricultural and silvicultural intensification found an overall decline in species richness across many production systems and species groups (Beckmann et al., 2019). Similarly, urbanization was found to correlate with sharp declines in bird and plant density (Aronson et al., 2014).

A frequent observation of these syntheses is that the response of biodiversity depends on numerous factors including biome, taxonomic group, type of disturbance, and the biodiversity metric used (e.g., Beckmann et al., 2019; Gibson et al., 2011). Furthermore, many acknowledge limitations in the analysis and extrapolation of conclusions due to geographic and taxonomic biases inherent in the literature (e.g., De Palma et al., 2016; Murphy & Romanuk, 2014). These issues make global synthesis and projection difficult. Moving this research field forwards will require recognising, reducing, and accounting for these challenges.

Here we review the land-use change and biodiversity literature to describe the range of study designs, land use measurements, and species responses that are often used. We investigate the taxonomic, geographic, climatic, and historical distribution of the research by using named entity recognition applied to a large body of papers. Our aim is to critically evaluate the evidence base that is being used to assess the global impact of land-use change on species, and to suggest ways for moving this key research forward.

## **2. Methods**

We identified relevant studies by searching Scopus for articles that investigated the impacts of land use or land cover change on any aspect of species biology. We limited our search to terrestrial studies published prior to 2020, excluding reviews, meta-analyses, and studies from the distant past (search terms in Fig. 1d). The abstracts of all identified papers were used for automatically extracting species and location mentions, which were used in all subsequent analyses. This method may favour journals or papers that include this information in the abstract, although we assume these are still representative of wider trends. Additionally, the relative uniformity of abstracts

versus full papers allowed us to assess a large chunk of the literature while minimising uncertainties and irregularities. A subset of papers was also randomly selected for full reading and manual annotation (methods diagram Fig. S1).

#### *Extracting taxonomic and location data*

We applied automated text mining methods to the abstracts of all papers identified by the Scopus search to determine the taxonomic focus and geographic distribution of research investigating land-use change impacts on species. Our analysis utilised and built upon the methods of Millard et al. (2019) who applied named entity recognition to study the animal pollination literature. To identify mentions of species binomial names across all abstracts we used the R package ‘Taxize’, which incorporates dictionary string matching (Taxonfinder) and machine learning (Neti Neti) algorithms (Chamberlain & Szoezs, 2013; Chamberlain et al., 2020). The extracted taxonomic entities were matched with records in the 2019 Catalogue of Life database (Roskov et al., 2019), resolving to currently accepted names when necessary. Where extracted names were not directly matched with entries in the Catalogue of Life, we attempted a series of adjusted matches following Millard et al. (2019). Firstly, all punctuation was removed from the extracted name, and if a match was still not found, the abbreviation ‘spp’ was also removed. For abbreviated extracted names (e.g., *S. barbatus*), we found all matches with similarly abbreviated Catalogue of Life names, but only retained matches where the same genus was also mentioned in the abstract. For example, if an abstract mentioned *Acer rubrum* and *A. saccharum* then we kept all Catalogue of Life entries for *Acer saccharum* (including subspecies and varieties).

The process of matching extracted names with Catalogue of Life entries sometimes resulted in an extracted name being resolved to several accepted species, for example when the species was an ambiguous synonym or occasionally misapplied name. In these cases (9.9%) we kept only the directly matched accepted name from the same abstract (8.5%), or all candidate names if there were no direct matches (1.5%). Furthermore, all main analyses were conducted at genus level and above. We calculated the number of papers mentioning different taxonomic groups and used genus level mentions to assess taxonomic representation. Additionally, species counts were aggregated into taxonomic groups and compared to the number of registered species per group in the Catalogue of Life 2019 (Supplementary info Fig. S2, Roskov et al., 2019).

We extracted and geolocated all place name mentions (toponyms) from abstracts mentioning a species binomial using the Edinburgh Geoparser (Alex et al., 2015; Grover et al., 2010). Firstly, we removed from all abstracts any text following the copyright symbol to eliminate locations associated with copyright information rather than the study itself (Millard et al., 2019). Next, we created individual text files of each abstract, which were batch processed with the Edinburgh geoparser using shell scripts. We kept only unique locations for each abstract and cleaned the results by removing any locations that were misidentified genera, species, or subspecies names, and by removing clearly spurious place names e.g., “Monte-Carlo”, “Chao”, and “Taxa” (full list in Table S2). To illustrate the geographic distribution of papers we excluded mentions of continents and split all other geolocated places into two levels, country name mentions, and specific location mentions.

#### *Deriving additional data and validating*

Based on the geolocated mentions identified in the previous step we derived several attributes to assess the representativeness of the literature in a global context. Firstly, using a map of global biomes (Olson et al., 2001) we extracted the biome type at each of the specific location mentions and compared this to the global coverage of each biome. Secondly, we calculated the climate envelope covered by the studies and compared this to the global terrestrial climate using WorldClim version 2 Bioclimatic variables: annual mean temperature and annual precipitation across 1970-2000 (10 arc minute resolution, Fick & Hijmans, 2017). Lastly, we assessed the land-use history of study locations using data derived from the KK10 past human land use model to determine the representation of historical land use patterns (Ellis et al., 2013; Kaplan et al., 2011).

We manually assessed our search results and accuracy of automated text methods (full information and results in the Supplementary material). We manually identified and resolved species in a random 1% of papers, and manually geoparsed 100 random abstracts mentioning a species to assess the accuracy of the automated geoparser and the relevance of papers.

#### *In-depth review of selected papers*

To evaluate the methodological approaches used for studying land-use change impacts on species, we read and annotated a random selection of 100 papers. These were selected from papers that mention the term ‘land use’ in their title, as these constituted a particularly relevant subset. The

100 papers were downloaded and processed using Zotero reference manager (Roy Rosenzweig Center for History and New Media, 2020). We extracted detailed information on the studies by manually adding keyword tags to each entry, which were then aggregated and summarised in R. Details included the geographic extent of studies, the experimental design used (following De Palma et al., 2018), the measure of land-use change, and overall findings. All data processing, analysis, and visualisation was conducted in R version 4.0.3 (R Core Team, 2020).

### **3. Results and discussion**

#### **3.1 Approaches for studying land-use change impacts on biodiversity**

Our Scopus search yielded 12,192 papers investigating the impacts of land-use change on species. This research represents a rapidly growing field, with the rate of publication surpassing the background rate for the broader subject area (Fig. 1a/b).

##### *Common study designs*

A range of study designs are used in this field, with papers sometimes combining approaches, however space-for-time substitutions (control-impact) are by far the most common, accounting for 61 out of the 100 papers in our detailed analysis (Fig. 2a). Space-for-time studies are often the most straightforward to implement, resulting in an abundance of static data that when combined can facilitate broad scale hypothesis testing. The PREDICTS project, for example, merges spatial comparisons of land-use impacts on species presence and abundance (Hudson et al., 2014). Analyses of this dataset suggest reductions in local richness and abundance in response to land-use change, shifts in species composition, and unequal sensitivity of functional groups (Newbold et al., 2020, 2016, 2015). However, spatial comparisons make the often problematic assumption that sites are equal in all aspects besides current land use, thereby overlooking important contextual information such as site history and the fact that land-use change is not randomly distributed (Damgaard, 2019). Static comparisons miss temporal interactions with climate change and fail to capture biotic lag effects that may take decades to unfold (e.g., Wearn et al., 2012).

Time-series were the second most common design, though only accounting for 11% of papers. Studies using this design can provide valuable information on rates of change if they run for long enough to encompass time lags, are revisited at an ecologically relevant frequency, and incorporate sites fully representative of the whole landscape (Collen et al., 2009; De Palma et al.,

2018). Even so, it is difficult to ascribe changes to individual drivers as there can be many other influences including anthropogenic effects and natural population variability (Shoemaker et al., 2020). Global syntheses of time-series data have used various approaches to aggregate population trends, either by assessing the proportional changes in richness from the first to last year (Vellend et al., 2013), the slopes of individual time-series (Dornelas et al., 2014) or fitting models to abundance trends (Collen et al., 2009). Syntheses are affected by the length and sampling frequency of studies (Cardinale et al., 2018; Gonzalez et al., 2016) as well as changes in research focus over time (Collen et al., 2009). For example, a shift from studying large stable populations to studying small, threatened populations of conservation concern could artificially conflate temporal trends. When collating time-series studies it is therefore especially important to establish clear historical baselines and to include studies investigating the same process (Cardinale et al., 2018; Gonzalez et al., 2016).

Detailed before-after-control-impact (BACI) assessments can capture temporal patterns and compare changes to a dynamic baseline. For example, França et al. (2016) showed that compared with BACI, a space-for-time substitution may underestimate the impacts of human disturbance on biodiversity by half. Yet BACI designs require a far greater investment of time and resources – resulting in limited replication and therefore limited utility in syntheses (De Palma et al., 2018). In our subset of 100 papers only one was full BACI. Study designs that involved sampling prior to disturbance were generally the least common in our subset, probably because they require prior knowledge of any land-use change events, or the alteration of habitat for the sake of experiment. Our understanding of ecological processes could be enhanced by pursuing a joint framework that merges detailed causal models derived from experimental and BACI surveys with broad scale models of static spatial variation.

All study approaches entail some trade-offs, either logistical or theoretical, and make key assumptions that can influence conclusions and impede efforts to synthesise results (reviewed in De Palma et al., 2018). Furthermore, all syntheses suffer from the fact that they combine studies that were designed for a variety of different purposes. The overall finding of manually read studies was for a negative impact of land-use change on species biology, however, a low sample size for all except control-impact studies precluded us from identifying differences in the distribution of findings across study designs. The impact of land-use change on species depends on context, for

example, intensifying the use of an abandoned meadow leads to increased species diversity, but intensification of a heavily grazed meadow causes declines (Beckmann et al., 2019). This emphasizes the importance of using appropriate baselines and considering reference natural ecosystems when the interest lies in the conservation of undisturbed conditions (Trimble & van Aarde, 2012). Meta-analyses using space-for-time studies generally find negative impacts of land-use change on local species richness (e.g., Newbold et al., 2015), however, compilations of time-series have suggested changing community composition is more prevalent (e.g., Dornelas et al., 2014). Considering the disparate conclusions reached by these meta-analyses, the influence of study design is a question that deserves further attention.

### *Measuring land-use change*

Land-use change is challenging to quantify and often involves sorting complex habitats into coarse anthropocentric cover categories such as forest, agriculture, and urban – a simplification that can overlook ecologically significant within class variation. A protected, floristically diverse grassland, for example, may support more and different species than a newly created grass field used for recreation. From an organism's perspective land use classifications may be arbitrary, as they respond to myriad changes in difficult to measure environmental conditions such as light availability, resources, microclimate, and competition (Lauber et al., 2008; Stevens et al., 2011; Vallecillo et al., 2009).

There are many methods employed to measure land-use change (De Palma et al., 2018; Verburg et al., 2011). We found that most studies employed direct local observations (Fig. 2b), which are typically accurate but can be limited in spatial scale. Remote sensing has been a boon for detecting broad scale patterns of land-use change; we found this to be a commonly used method at all spatial scales, both directly and as a component of existing land use maps (Fig 2b). However, the history of an area is crucial for biodiversity, yet satellite images of a 200-year-old forest and one that was deforested 40 years ago may appear broadly similar. Despite covering a shorter period than optical imagery, new active remote sensing technologies, such as LiDAR, let us make increasingly detailed 3D habitat measurements over large expanses (Simonson et al., 2014), and thus better identify structural differences e.g., between old and young forests. These active sensors were the least common method of describing land use in our analysis, which may reflect the relative novelty and expense of this data source.

Data on land-use intensity, such as fertiliser application or livestock per hectare, attempt to reconcile observed changes in biodiversity to within land use variation, and capture more detailed facets of land-use change (Kehoe et al., 2015). The availability of intensity data is currently scarce, especially at the global level (Kuemmerle et al., 2013). Human appropriation of net primary productivity is an example metric that tries to capture intensity of land use with a single, continuous, remotely sensed variable (Haberl et al., 2004). A recent meta-analysis of the impact of increasing land-use intensity on biodiversity lamented the lack of studies reporting detailed land-use intensity measures such as input of fertilisers or pesticides (Beckmann et al., 2019). Only 22 of the 100 papers we read considered some measurable aspect of land-use intensity in their analyses; this is echoed in the fact that across all papers from the Scopus search only 9% mention the word ‘intensity’ in their abstract (Fig. 1b). Moving forwards, researchers should focus on the ecological processes that link land use and biodiversity change and seek out biologically relevant land use metrics tailored to the taxa and habitat in question. To tackle inconsistencies in the classification of land use types, we echo the call for a globally harmonized land use classification system to aid synthesis (Gerstner et al., 2014; Verburg et al., 2011).

#### *Measuring biodiversity*

The choice of species response metric also influences our interpretation of land-use change impacts, with the perceived effects completely reversing in some scenarios. To illustrate this, consider an agricultural area beside a national park, with both habitats containing equal density of a particular species. Considering occupancy or abundance, one might conclude that agriculture is suitable habitat. However, if vital demographic rates such as births, deaths, and migration are examined, one may find that the agricultural area constitutes a sink habitat, with an elevated death rate that is concealed by immigration (e.g. Lamb et al., 2017). Information on animal species behaviour may even elucidate that individuals utilise disturbed areas but are unable to shelter or reproduce within them (Love et al., 2018; Luskin et al., 2017). In these situations, the underlying dynamics may have been missed, and the long-term persistence of the population jeopardised.

Of the search terms used to identify species level effects of land-use change, ‘diversity’ was the most common, with terms related to species composition, distribution, and abundance also occurring frequently across the 12,192 papers (Fig. 1c). Terms associated with more in-depth

investigations such as demography, behaviour, and vital rates were much scarcer. Our findings are consistent with a meta-analysis of disturbed and undisturbed sites in tropical forests, which found that richness and abundance were the most often reported measures whilst demographics were the least (Gibson et al., 2011). The authors also showed that the magnitude of the negative impact of disturbance varied according to the ecological metric used. For example, richness responded more strongly to land-use change than abundance, likely due to increasing abundance of some generalist species (Gibson et al., 2011). Aggregate community metrics, such as richness, ignore species identity and can lead to erroneous conclusions when shifts in community composition are missed (Mendenhall et al., 2012). Indeed, some authors suggest that changes in beta-diversity may be the main impact of land-use change (Dornelas et al., 2014; Vellend et al., 2013).

Information on demographics and vital rates help explain how some species persist or thrive in disturbed environments (e.g., Srinivasan et al., 2015). Linking these measurements to functional traits may help us determine what characterises winners and losers. Examining species behaviour can also provide insights into subtle land-use change effects (Chapman et al., 2019; Davison et al., 2019). Still, investigating these detailed variables is difficult, resource demanding, and subject to unique local variation. Basic presence data is easier to collect and is available globally for many taxa (e.g., BIEN - Enquist et al., 2016; GBIF.org, 2020). Nonetheless, presence data overlook important variation in abundance, and the sampling procedures can be biased or inaccurate (Anderson, 2012; Araújo et al., 2019). Abundance data facilitates quantitative synthesis across comparable studies (e.g., Newbold et al., 2020), yet in-depth research can also be integrated to provide important insights. Gaynor et al. (2018) for example, conducted a meta-analysis showing that many mammals are becoming increasingly nocturnal in response to human disturbance. Going forward, the trade-off between data volume and the level of insight must be carefully balanced to maximise our understanding of the distribution, and underlying mechanisms, of land-use change impacts.

### **3.2 Biases in the literature**

#### *Taxonomic biases*

For understanding the global effects of land-use change on biodiversity it is essential to sample a diverse range of species. Broad taxonomic coverage helps us capture complex indirect impacts and trophic feedbacks (Barnes et al., 2017). Excessive focus on charismatic species can be problematic



from a conservation standpoint as their effectiveness as umbrella species is debated (Simberloff, 1998; Williams et al., 2000). Our application of taxonomic entity recognition discovered 9864 species binomial names from 4108 abstracts, 34% of the total papers. We found 77.4% of species were matched to an accepted name in the Catalogue of Life and 13.5% were matched to an abbreviated accepted name; 7.8% were matched to a synonym and 1.1% were matched to an abbreviated synonym. Species mentioned belonged to 2721 different genera, with most genera (60%) being mentioned only once (mean = 2.90, SD = 6.63, Fig. 3b). Overall, we found strong taxonomic biases in the land-use change literature (Fig. 3, Fig. S2), in line with findings from the fields of biodiversity monitoring and conservation research (Di Marco et al., 2017; Troudet et al., 2017).

Plants were mentioned in 45% of all papers with a species in their abstract. Several genera of large trees including *Pinus*, *Quercus*, and *Eucalyptus* dominated (Fig. 3b). The bias towards forested systems, may partly explain the prevalence of plants in this research area. However, we must interpret these findings with caution due to the role of forestry as a driver of land-use change, and the practice of using plant species to describe study habitats (e.g., *Pinus sylvestris* plantations). In a random subset of 100 abstracts mentioning plant species, we found that 30% did not look at the response of plants to land-use change, indicating that the bias towards plants is not as extreme as estimated. Nonetheless, plants have been found to be the most studied group in other assessments of the literature dealing with invasion ecology (Pyšek et al., 2008), climate change (Felton et al., 2009), and tropical forest fragmentation (Deikumah et al., 2014). Fungi were the least studied group and were only mentioned in 1.7% of papers. Our choice of search strings may have some influence on these patterns if researchers of particular groups traditionally use different terminology instead of “land use”, e.g., “management” in fungal biodiversity studies along forestry intensity gradients.

Vertebrates were mentioned in 43% of papers, almost equalling plants, and were therefore overrepresented considering species richness of the group (Fig. 3, Fig. S2). Birds and mammals dominated amongst the vertebrates, which aligns with observations from other meta- and literature analyses (e.g., Collen et al., 2009). Amphibians are one of the animal lineages with the highest share of threatened species (González-del-Pliego et al., 2019), yet they require far more attention in this field. Reptiles featured in the fewest papers of any vertebrate, despite having more

described species than mammals and amphibians. The scarcity of papers investigating fish may have exacerbated effects given that terrestrial and freshwater biodiversity do not align spatially (Darwall et al., 2011). Rerunning the search including terms “biomass”, “catch”, and “harvest” did not change the representation of fish in the results (original: 4.56%; new: 4.54%).<sup>39</sup>

A few mosquito genera were the focus of many arthropod studies, likely due to their role as vectors of human disease and the relationship between land-use change and their prevalence (Conn et al., 2002). The stark difference between research on vertebrates and invertebrates matches the pattern seen in global biodiversity monitoring (Butchart et al., 2010; Troudet et al., 2017) and on evaluated groups in the IUCN red list (Cardoso et al., 2011). This disparity is concerning given the conservation of vertebrates does not inherently protect invertebrates (Lawton et al., 1998; Prendergast et al., 1993). A lack of past research on invertebrates has also reduced our ability to make reliable risk assessments (Karam-Gemael et al., 2020). Considering the dearth of studies on Fungi and invertebrates, the representation of detritivores in the literature appears deficient. Missing this key functional group may have implications for synthesising how land-use change affects core ecosystem processes and feedbacks.

Taxonomic biases are a caveat to the conclusions of many land-use change meta-analyses. Some syntheses resort to investigating a handful of well-studied groups, trading generality for data availability (e.g., Aronson et al., 2014; De Palma et al., 2016). The PREDICTS project presents arguably the most taxonomically complete database but is still biased towards vertebrates and certain invertebrate groups (e.g., butterflies). While equal representation of all taxonomic groups in research on land-use change is unrealistic, encompassing more groups may improve the selection of conservation areas (Kier et al., 2009). Rare species, despite constituting a large fraction of diversity (Enquist et al., 2019) are regularly omitted from analyses due to low detectability; their omission means we are building our understanding of biodiversity change processes on common, wide-ranging species (Jetz & Rahbek, 2002). Integrating understudied taxa will benefit our understanding of the global process and further insights into how species and functional groups respond differently (Gibson et al., 2011; Newbold et al., 2020). Above all, a holistic ecosystem level approach will be possible, allowing consideration of indirect effects (Chillo et al., 2018), ecosystem functioning (Dislich et al., 2017), and trophic feedbacks (Barnes et al., 2017).

### *Geographic biases*

A well distributed literature body across space helps us infer global patterns of land-use change, identify regional mechanisms, and highlight threatened areas. Of the 4108 abstracts mentioning species, 3213 also mentioned a geographic location. Of the 147 countries mentioned, the USA appeared most often, with roughly the same number of mentions (480) as the next five countries combined (Fig. S4). The highest prevalence of studies clearly occurs in Europe and North America (Fig. 4, Fig. S3). The trend towards wealthy western countries matches that found in other literature bodies, particularly conservation research (Velasco et al., 2015). For instance, Martin et al. (2012) found that study prevalence in ecology research was strongly associated with Gross National Income – 90% of study locations were within the wealthiest 30% of countries. Derived meta-analyses are thus rarely truly global. For instance, 68% of the data used in a global analysis of plant responses to land-use change stemmed from Europe and North America and included no data from 73% of the world's countries (Gerstner et al., 2014).

In Russia, the Middle East, and Africa we found very few studies despite some hotspots in South Africa and Tanzania. The blank spots on the map – where there are few or no identified studies – reveal gaps in our knowledge of region-specific land-use change drivers and how they may be impacting ecological communities. In the conservation literature at least, research in Africa and Southeast Asia appears to be stagnant or even decreasing over time, exacerbating their underrepresentation (Di Marco et al., 2017). Access to existing research may also be hampering our understanding of some countries like Russia, where large amounts of biodiversity data exist but remain fragmented and digitally inaccessible to researchers (Ivanova & Shashkov, 2017).

The uneven geographic distribution of studies has consequences for the representation of biomes (*sensu* Olson et al., 2001, Fig. 5). Based on the coordinates of sub-country locations, we detected a surplus of studies in all temperate biomes, accounting for over half of all locations. This abundance, and disparity with global area, was most apparent for temperate forest biomes. The most underrepresented biomes regarding land area are deserts and xeric shrublands, tundra, and boreal forests. Insufficient sampling of arid regions could hamper conservation efforts as Beckmann et al. (2019) found that arid areas, alongside tropical forests, had the highest loss of biodiversity following increased land-use intensity.

Community responses to land-use change can vary geographically due to the specific nature of threats and differences in species sensitivity (De Palma et al., 2016; Murphy & Romanuk, 2014). Indeed, turnover of assemblages across land use classes is more pronounced in the tropics (Newbold et al., 2016) and the sensitivity of biota varies even between tropical regions (Gibson et al., 2011). Considering this, the data vacuum over the Afrotropics, which includes the second largest contiguous natural forest, is particularly concerning. Dependence on research from a limited geographic area, which is biased regarding the distribution of biodiversity and of land use threats, hampers our global understanding of how land-use change impacts species. Future research should arguably be focussed in areas with greater biological complexity, extinction risk, and/or current and future land use pressure. Tropical regions emerge as a key candidate in all these aspects; they harbour the most species rich assemblages on earth and are subject to increasing human pressure and rates of extinctions (Bradshaw et al., 2009). Improved sampling across biomes will be key to producing reliable syntheses of how land-use change affects biodiversity globally.

### **3.3. Further dimensions of land-use change**

#### *The role of climate*

Land use and climate change interact with implications for the distribution and persistence of species (Guo et al., 2018; Oliver & Morecroft, 2014, Santos et al., 2021). Climate change may shift the productive range of crop species poleward and uphill, influencing regional land use trajectories. Land-use change, on the other hand, can affect regional and global climate directly through changes to the surface energy budget and indirectly through the carbon cycle (Pielke et al., 2002). Climate and land-use change may exacerbate and modify the negative effects of one another on biodiversity (Oliver & Morecroft, 2014), with the quantity and arrangement of suitable habitats in a landscape influencing the strength of this interaction (Pyke, 2004). Given this interaction the scarcity of studies in our analysis that even mention the word ‘climate’ in their abstract highlights a concerning research gap (Fig. 1b; see also Titeux et al., 2017).

In our analysis we found that the climatic distribution of land use study locations did not match with the pattern of global terrestrial climate (Fig. 6). The global climate is dominated by large arid areas with high mean temperature ( $>20^{\circ}\text{C}$ ); areas of low mean temperature ( $\sim 0^{\circ}\text{C}$ ) and moderate

precipitation; and areas where warmth and high rainfall coincide. In contrast, land-use change studies were concentrated in areas that had a mild mean annual temperature (~10 to 15°C) and total annual precipitation of approximately 1000 mm, i.e. temperate conditions. The identified study locations underrepresent hot and cold arid regions and warm tropical areas.

The narrow climatic range of this research body may have several consequences as the richness of taxonomic groups peak in different climate zones (Prendergast et al., 1993) and species vary in their sensitivity to climate change (Angert et al., 2011). Mantyka-Pringle et al. (2012) found that the negative impacts of habitat loss and fragmentation on biodiversity were greatest in areas with higher maximum temperatures and lower precipitation. This finding may help explain why the impact of increasing land-use intensity on biodiversity may be greater in arid and tropical regions (Beckmann et al., 2019). Guo et al. (2018) also showed that forest loss and temperature positively interact to drive greater upslope movement of species in warmer regions. Surveying a broader range of climate conditions will allow us to capture confounding effects of land use and climate and may even help us predict the future dynamics of land-use change impacts under novel climates.

#### *Land-use history*

Extensive and persistent influences of humans date back thousands of years in some regions (Ellis et al., 2013; Miede et al., 2014). The legacy effects of this past land use are detectable in current patterns of biodiversity from local to global scales (Debinski et al., 2011; Polaina et al., 2019). Due to extinction debts and immigration credits, the time-lagged loss and gain of species following a disturbance, it is possible that not all species responses to today's disturbances are yet detectable (Jackson & Sax, 2010; Tilman et al., 1994). These transient states may influence study conclusions and can result in the underestimation of long-term threat levels (Hanski & Ovaskainen, 2002). Global maps of land-use history can help us identify prime regions for investigating the role of legacy effects and recovery times (Fig. S5).

Synthesising land-use change research requires covering the full diversity of land use histories and understanding time-lagged biotic responses. We found that studies in areas with sustained human use (>20% of area used) until the present all had a higher share of studies than their global coverage suggests (Fig. 7). The disparity in magnitude is particularly evident for areas with greater

than 2000 years sustained use, and areas with 100-250 years sustained use. Coverage of these two extremes mainly results from the geographical bias towards Europe and North America, which respectively have long and short histories of intensive use.

In some regions human impacts have declined from previous levels and what appear to be pristine ecosystems may actually be recovering. Forests regrowing after agricultural abandonment, for example, can display legacy effects lasting millennia (Bürge et al., 2017; Dupouey et al., 2002). We found that land with less than 10% recovery from peak use was underrepresented in the literature, while areas with greater than 20% recovery were overrepresented. Greater focus on the response of species in recently recovering areas may provide valuable insights for conservation and ecosystem regeneration. Considering the remoteness of unused land (NSU, Fig. S5) it featured a surprising number of studies. Martin et al. (2012) showed that ecologists typically place sites in pristine areas, even when they constitute small pockets in disturbed landscapes. However, the assumptions behind this tendency disregard the influence of humans in practically all terrestrial ecosystems (Faurby & Svenning, 2015; Martin et al., 2012). Moving forward, researchers must select appropriate baselines, encompass fluctuating population dynamics, and investigate the full range of land use histories and recovering areas. Studies across orthogonal gradients of land use, history, and climate may ultimately help us isolate the effects of land use and its interaction with other drivers.

#### **4. Conclusion**

Our comprehensive review of >4000 abstracts and 100 papers in the field of land-use change impacts on biodiversity shows that a multitude of study designs and measurement characteristics are used, each with their strengths and weaknesses. Combining methods that complement each other and studying a range of species responses will aid synthesis and allow us to detect more subtle indirect effects of land-use change and understand ecological mechanisms. Making comparisons to appropriate baselines, both spatially and temporally, will clarify the direction and magnitude of biodiversity impacts. The taxonomic bias in this field restricts our understanding of biotic feedbacks and trophic cascades, and the dearth of information on some of the most sensitive and at-risk groups will hamper conservation efforts.

The geographic bias of studies limits the applicability of findings and the reliability of future projections. Investigating the full diversity of regional land use mechanisms will be key to determining a global outlook. A bias towards forest ecosystems may be at the expense of other diverse habitats including tropical and subtropical savannas and grasslands. A key challenge moving forward will be exploring the interaction of land-use change with other global drivers as climate change is set to become an increasingly important factor into the future (IPBES, 2019). Forthcoming studies should focus on how climate interacts with land use, particularly in understudied tropical and arid climates.

The importance of land-use history and legacy effects is clear; the use of different baselines can lead to miscalculating the direction and magnitude of disturbance impacts. While the literature reflected the breadth of land use histories relatively well, recently recovering areas require more attention and may provide valuable insights for conservation. With North American and European studies dominating the research, we may be neglecting regional differences in current and historical land use pressures. Failure to cultivate a balanced body of literature, accounting for all these inherent challenges, will negatively impact our global understanding of land-use change impacts on species. These biases jeopardise the reliability of spatial and temporal projections of global change impacts on biodiversity and have repercussions for the conservation of imperilled species.

## **5. Perspectives**

To improve our understanding of how land-use change affects biodiversity we need to investigate both sides of the paradigm in greater detail through improvements in land use and biodiversity data as well as study designs (Fig. 8). Assessments of land-use change should incorporate within class variation in use intensity (Dullinger et al., 2021) and prioritise biologically relevant metrics over coarse, human-centred classes (Santos et al., 2021). Regarding biodiversity, more studies should include multiple trophic levels and focus on behaviour and demographics to reveal potential mechanisms behind land use impacts and uncover temporal trends within communities. Land use and biodiversity surveys across large extents (e.g., nationally) are important but need to be aligned spatially and temporally. Moving forward, we must also put more attention on the legacies of historical human disturbance when monitoring biodiversity and pursue further research into the interaction of land-use change with other global drivers (Titeux et al., 2017).

Geographic and taxonomic biases underpin many of the challenges facing this field. However, neither can be solved with the data that we currently have. Filling these gaps will require concerted fieldwork on neglected taxonomic groups in understudied regions, with an emphasis on collaborative research efforts. The advancement of space-borne remote sensing will also be pivotal. Global sub-metre resolution maps of vegetation and land use will be invaluable for tackling geographic biases when coupled with fieldwork in understudied systems. Proximal sensing methods such as camera traps, drones, sound recorders, and climate loggers will also help increase the effectiveness of data collection. We can't make effective conservation and policy decisions on what we don't fully understand. In this paper we have highlighted the research priorities and data gaps that need urgent attention.

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## Figure legends

**Figure 1.** Search results: (a) The background rate of papers published in the subject areas ‘Environmental’ or ‘Agricultural and Biological science’ on Scopus searched 16/07/2020 (over 93% of papers in our search have one of these subject areas). (b) Publications on the impact of land-use change on species are increasing faster than the background rate, i.e. as a percentage of (a), and mentions of ‘climate’ and ‘intensity’ are slowly increasing. (c) The frequency of papers mentioning different aspects of species biology from the search criteria. (d) Full Scopus search terms.

**Figure 2.** Features of manually assessed papers: (a) The frequency of different study designs and their general findings regarding the impact of land-use change on species attributes (e.g., richness, abundance, range). (b) The focal geographic extent and land use/cover data source of papers.

**Figure 3.** Taxonomic analysis: (a) Distribution of taxonomic mentions across papers in the literature sample. Some papers mention more than one group and are counted more than once; taxa present in less than 50 papers still occupy one square. (b) The number of papers mentioning different genera, ordered by percentage of papers mentioning each taxonomic group: plants, mammals, birds, arthropods, fish, amphibians, reptiles, other invertebrates, microorganisms, and fungi. Black lines indicate the average number of papers per genus in each group, some well represented genera are annotated.

**Figure 4.** Geographic locations of papers: (a) Countries are coloured by the number of papers mentioning them. (b) Black circles show the distribution and number of papers mentioning specific locations. A list of top countries mentioned, and a map of study density are in Supplementary information figures S3 and S4.

**Figure 5.** Representation of Earth’s biomes: Horizontal bars compare the percent of all location mentions within each biome to the global cover of that biome. Map adapted from: (Olson et al., 2001). Locations are counted once for each study that mentions them.

**Figure 6.** Representation of Earth’s climate in the land-use change literature. The left-hand side shows the number of 10 arc minute cells that fall within each precipitation and temperature combination, while the right shows the number of study locations mentioned in each zone.

**Figure 7.** Representation of land use histories as the percent of location mentions within each category versus global cover. Land use histories identified from Ellis et al. (2013) based on the KK10 historical land use model (Kaplan et al., 2011). Land use histories are split depending on whether cells have significant (>20% of area) human use in the year AD2000, in which case the number of years of sustained use above this threshold is given. For areas with less than 20% human use in AD2000 the percent recovery from peak land use is given. Some areas have never been significantly used (NSU). Full map in Supplementary info (Figure S5).

**Figure 8.** Nine recommended research priorities for developing a more comprehensive and balanced understanding of the impacts of land-use change on biodiversity.

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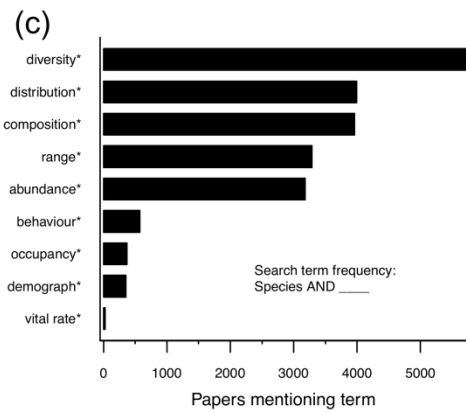
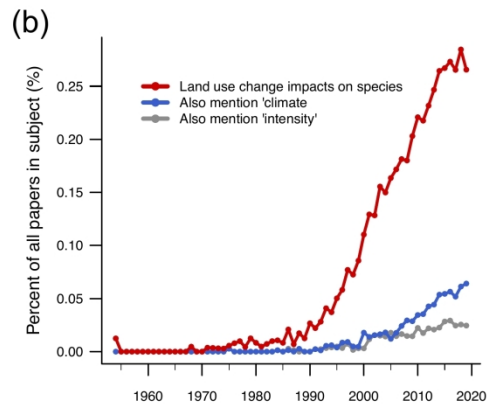
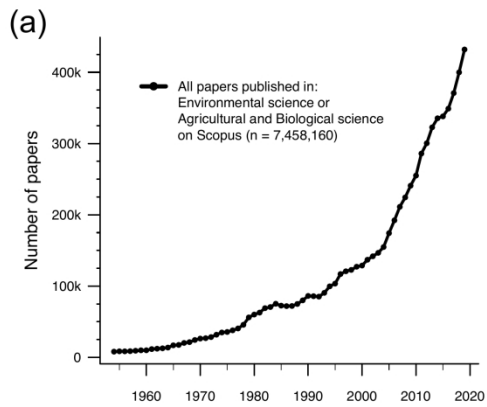
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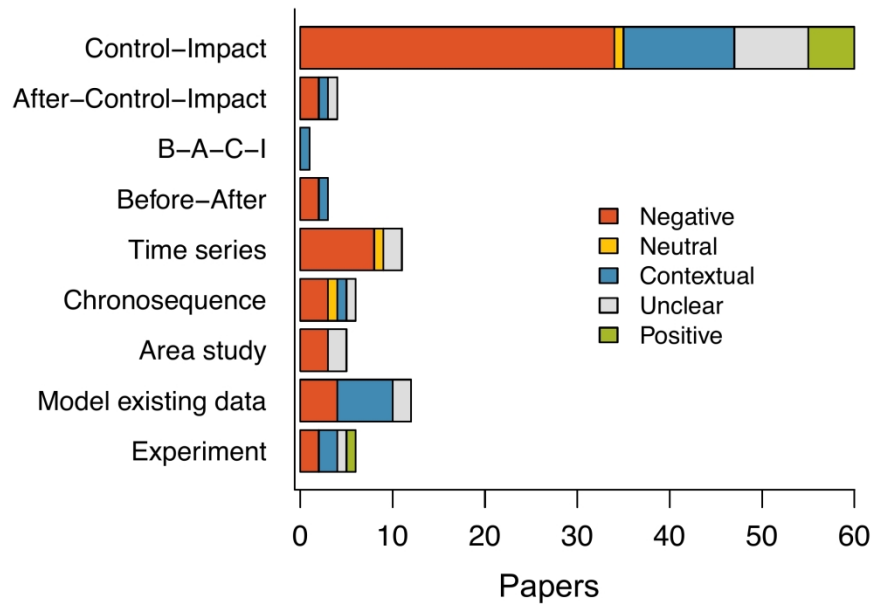


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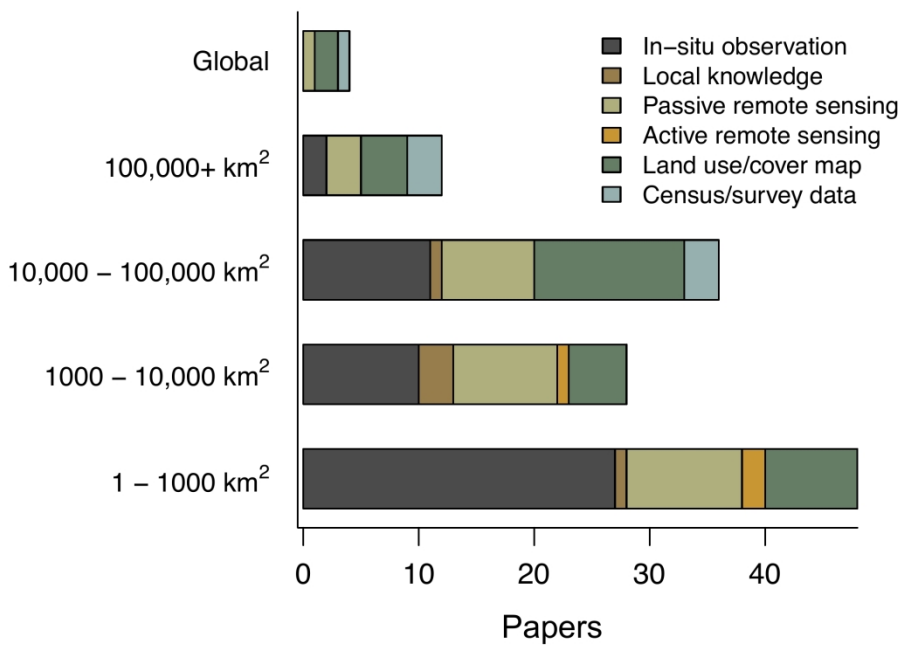
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<b>And species biology</b>	"species" AND "diversity" OR "abundance" OR "distribution" OR "occupancy" OR "demograph*" OR "range" OR "composition" OR "vital rate" OR "behaviour"
<b>Not distant past or marine</b>	NOT "Pleistocene" OR "paleo" OR "fossil" OR "glacial" OR "quaternary" OR "holocene" OR "marine" OR "ocean*" OR "sea"
<b>Not reviews</b>	NOT "review" OR "meta-analysis"
<b>Published</b>	AND LIMIT-TO (PUBSTAGE, "final") AND
<b>English journal articles pre 2020</b>	DOCTYPE (ar) AND LIMIT-TO (SCRTYPE, "j") AND LIMIT-TO (LANGUAGE, "English") AND PUBYEAR < 2020

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(a) Study design and effect of land use change on biodiversity

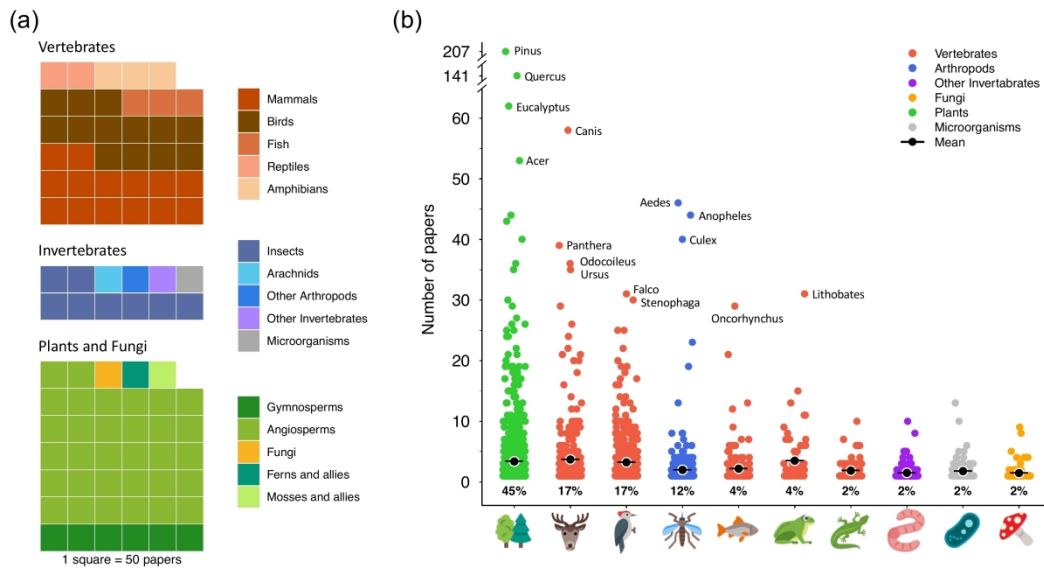


(b) Study extent and land use/cover data source

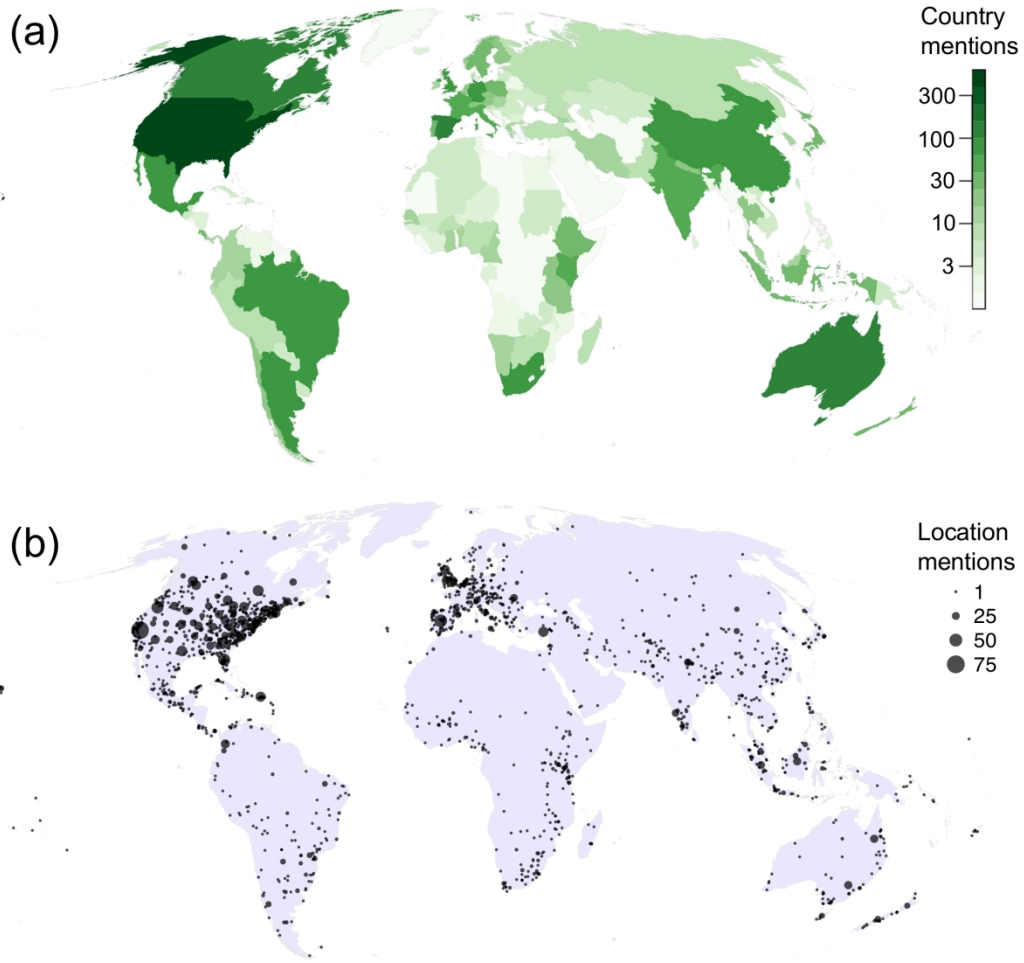


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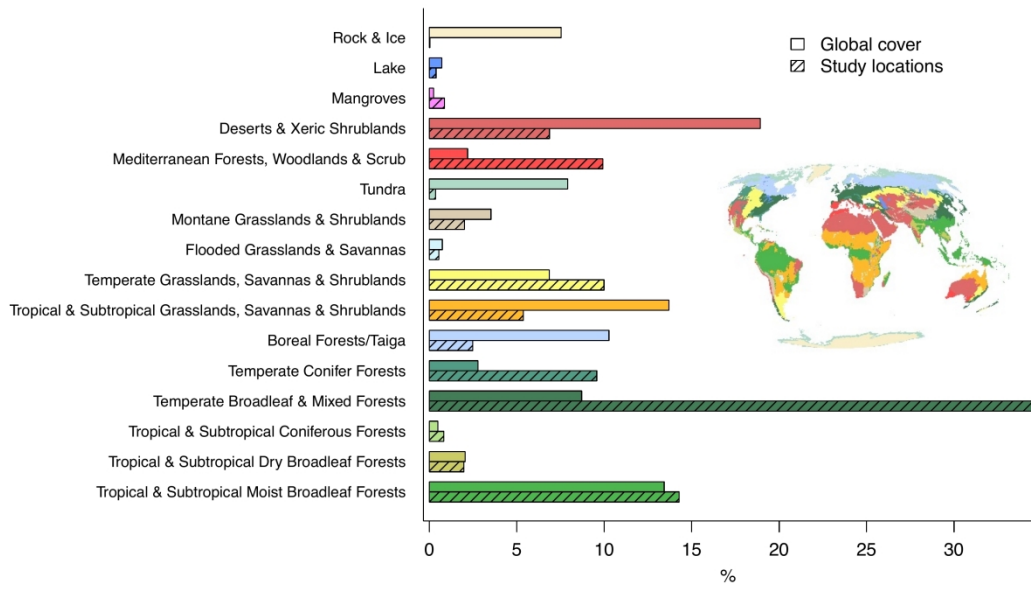




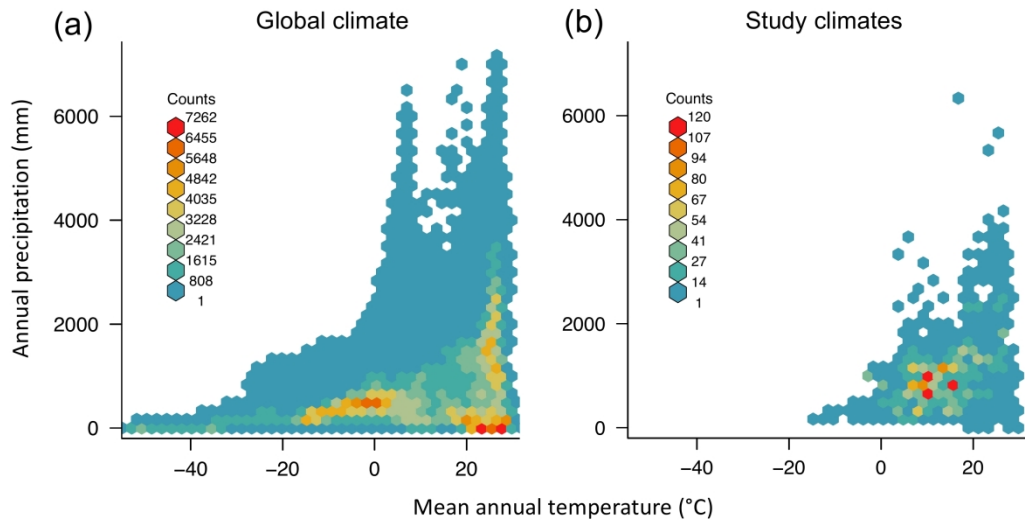
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**Regions without significant human use in AD2000:**

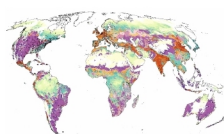
Recovery from peak use

- 0 – 1%
- 1 – 5%
- 5 – 10 %
- 10 – 20%
- 20 – 50%
- >50%
- NSU

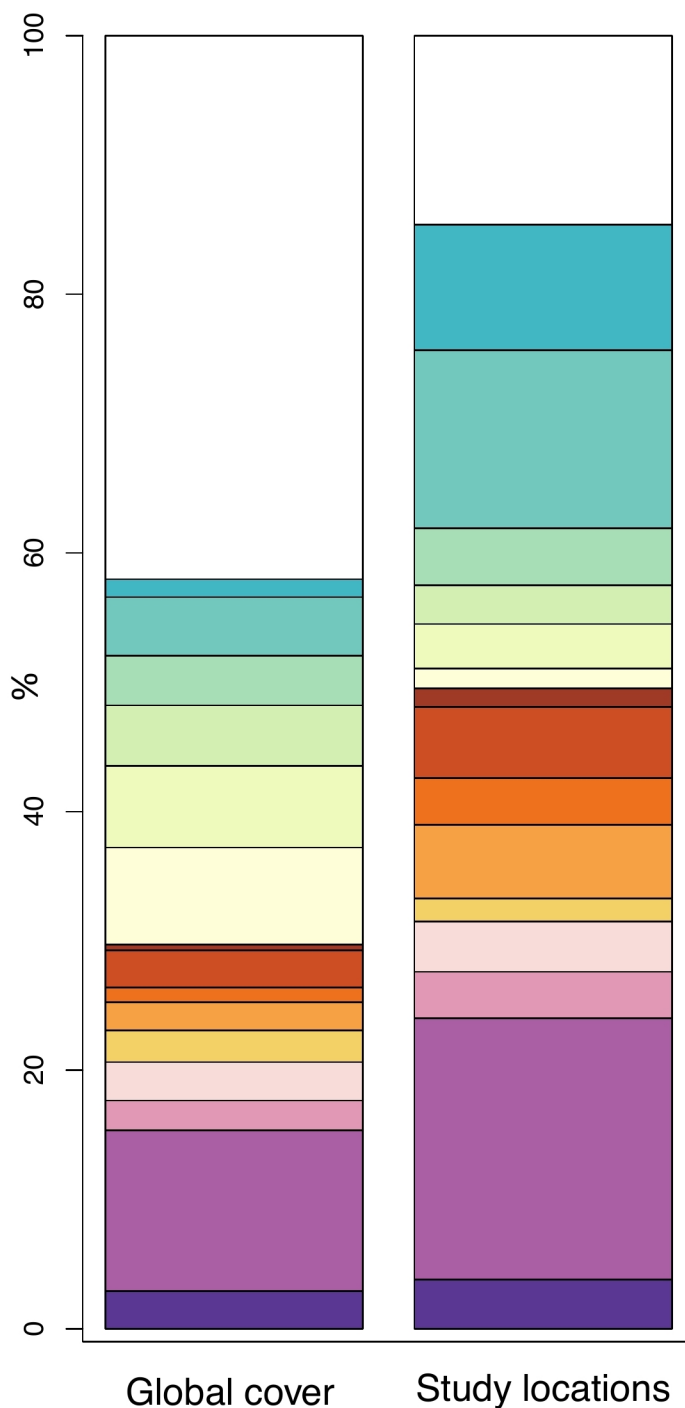
**Regions with significant human use in AD2000:**

Years of significant use

- >8000
- 5000 – 8000
- 3000 – 5000
- 2000 – 3000
- 1000 – 2000
- 500 – 1000
- 250 – 500
- 100 – 250
- <100



Supplementary Figure S5



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### Land use

**Facilitate synthesis and interpretation** by creating a harmonised framework for comparing land use change, and by focussing on intensity and ecologically relevant metrics.

**Understand the effects of past land use change** by collaborating with historians and palaeoecologists to reconstruct past changes and by incorporating observations from restoration and other management projects.

**Improve data availability and accuracy** by advancing high-resolution remote and proximal sensing methods.



### Biodiversity

**Decrease taxonomic biases** by focussing on understudied taxa via fieldwork, citizen science, and the continued development of proximate sensing technology (e.g., camera traps, drones, and sound recorders).

**Pursue a holistic understanding of land use change impacts** by investigating multiple angles of biodiversity including behaviour, demography, ecosystem functioning, and trophic feedbacks.

**Quantify biotic changes over time** by prioritising long term monitoring programs and by aggregating and resurveying historical biodiversity data.



### Study design

**Reduce geographical biases** by extending sampling across poorly represented biomes, e.g., through collaborative research with local partners.

**Understand the interaction of land use change with other drivers, especially climate change**, through studying biodiversity change along orthogonal gradients of these drivers.

**Make the most of different research approaches** by investigating the consequence of method choice on research conclusions and by integrating mechanistic models with models of spatial variation.

Research priorities and suggestions

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