



REVIEW ARTICLE

The impact of abandonment and intensification on the biodiversity of agriculturally marginal grasslands – a systematic review

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ABSTRACT

Agriculturally marginal grasslands have been traditionally managed at low intensity for centuries and are among Europe's key biodiversity hotspots. Because of their low profitability, many of them have been either abandoned or subjected to intensified management in recent decades. Both pathways threaten the high diversity of grassland species that depend on traditional management practices. To counteract the negative effects of abandonment or agricultural intensification on biodiversity, restoration and conservation practices were established. Through a systematic literature review based on 174 European studies, we investigated the impacts of abandonment and intensification on various measures of agriculturally marginal grasslands diversity. Additionally, we extracted information on the positive impacts of conservation – defined here as sustained extensive management practices – and restoration efforts aimed at previously abandoned or intensified grasslands. Abandonment had a high probability (71%) of reducing plant and lichen biodiversity, while it was significantly less likely to decrease the diversity of animals (23%). Intensification negatively affected the diversity of all organism groups to a similar extent (65% probability for plants and lichen, 47% for animals). Conservation efforts were likely to maintain or increase animal biodiversity (probability 79%), but in the studies we analysed, they were not sufficient to preserve the biodiversity of plants and lichen. The restoration of abandoned or intensified grasslands was predicted to enhance plant and lichen diversity (68% probability), while not significantly changing animal diversity. Thus, different organisms groups responded differently to changes in agricultural management, highlighting the need for targeted conservation and restoration strategies. By synthesizing biodiversity responses across taxa and management types, this review contributes to a more integrated and evidence-based understanding of how to maintain and improve the ecological value of agriculturally marginal grasslands.

Introduction

Grasslands, one of the largest terrestrial biomes, cover around 40 % of the Earth's terrestrial surface and dominate the landscape worldwide (Gibson, 2023; Squires et al., 2018). In addition to naturally occurring grasslands, long periods of human activity in areas where natural vegetation would otherwise not be herbaceous have led to the development of semi-natural grasslands (Eriksson, 2020; Hejman et al., 2013). Centuries of traditional management practices, such as extensive mowing and grazing regimes, have shaped these exceptionally species-rich habitats, which support a diverse array of plant and animal

life (Dengler et al., 2014; Ellenberg & Leuschner, 2010; Petermann & Buzhdygan, 2021). Semi-natural grasslands contribute to the conservation of many endemic and endangered species (Cerabolini et al., 2016; Stoate et al., 2009), and are considered among the most biodiverse habitats in Europe, harboring more vascular plant species on a smaller scale than tropical rainforests (Habel et al., 2013; Wilson et al., 2012). Despite their status as biodiversity hotspots with high conservation value, only 4 % of semi-natural grasslands are protected worldwide, making them one of the most threatened ecosystems in the face of current global change (P. Török et al., 2016; Petermann & Buzhdygan, 2021).

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Agriculturally marginal grasslands are a distinct type of low-productive, semi-natural grasslands, often found in areas with shallow soils, low nutrient availability, limited accessibility or steep slopes (Richards et al., 2014). The economic sustainability of managing such marginal grasslands has sharply declined in recent decades, resulting in either agricultural intensification or complete abandonment of land-use practices, with poorly understood consequences for biodiversity (Batáry et al., 2020; Shipley et al., 2024; Stoate et al., 2009). Generally, abandonment, defined as the cessation of traditional management practices, leads to the natural expansion of woody vegetation. Initially, this can be beneficial for biodiversity by increasing structural complexity, but over time it results in the loss of grassland-specific communities (Marini et al., 2009; S. Fadda et al., 2008; Schmitt & Rakosy, 2007). In contrast, intensification of agricultural practices, such as the application of organic and mineral fertilizers combined with more frequent mowing or increased livestock density, favors fast-growing herbaceous species, leading to homogenized grassland communities dominated by a few disturbance- and nutrient-tolerant species (Beckmann et al., 2019; Green, 1990; Guo et al., 2023; Simons et al., 2015). This highlights the importance of low-intensity land-use practices as a conservation strategy to preserve the high biodiversity of semi-natural grasslands (Shipley et al., 2024). On the other hand, to restore biodiversity after abandonment or intensification, restoration projects often reintroduce traditional mowing and grazing regimes to prevent succession by woody species, or reintroduce lost grassland diversity by adding seeds or planting native species, respectively (Lyons et al., 2023; Słodowicz et al., 2023). However, especially for agriculturally marginal grasslands, an overview of the impact of abandonment and intensification on biodiversity is lacking. Most existing literature consists of individual studies focused on local scales or specific species (but see Elliott et al., 2023, for a recent review regarding the impact of abandonment). Moreover, overarching evidence on the benefits of biodiversity management, such as agri-environment schemes or nature conservation practices, remains limited (Batáry et al., 2015).

We thus conducted a systematic literature review, aggregating information from scientific studies about the consequences of management practices on the biodiversity of various groups of species in European agriculturally marginal grasslands. We focused on the negative impacts of abandonment and intensification, while also addressing the extent to which conservation and restoration efforts can counteract biodiversity loss in these species-rich semi-natural ecosystems. To our knowledge, this provides a new and integrated perspective that combines both threats and recovery potential across different organism groups in agriculturally marginal grasslands. This systematic review synthesizes available scientific information to answer the following questions: 1) What are the effects of abandonment and intensification on the biodiversity of agriculturally marginal grasslands, and do these effects differ between floral and faunal organism groups. 2) Does the outcome of abandonment depend on the duration of abandonment? 3) Does the type of agriculturally marginal grassland influence how organism groups respond to intensification or abandonment? 4) Do conservation and restoration efforts benefit biodiversity across different organism groups in agriculturally marginal grasslands that faced abandonment or intensification? We hypothesized that both abandonment and intensification reduce the biodiversity of agriculturally marginal grasslands, with long-term abandonment having more detrimental effects than short-term abandonment. We hypothesized that lower trophic levels and less mobile organism groups respond more strongly and faster to the negative effects of abandonment or intensification. Furthermore, we hypothesized that conservation measures help to maintain high biodiversity in those habitats, and that restoration efforts mitigate the negative consequences of abandonment and intensification. By synthesizing information on the influence of land-use practices across taxonomic groups, this review contributes to a more integrated understanding of how biodiversity responds to two contrasting anthropogenic pressures (intensification and abandonment) on agriculturally

marginal grasslands. It also supports the growing field of evidence-based conservation and restoration planning.

Methods

Literature search and inclusion criteria

We conducted a literature search in April 2023 using the Web of Science Core Collection (Science Citation Index Expanded) and Elsevier Scopus databases, employing a combination of keywords based on the Population, Intervention, Comparison, and Outcome (PICO) framework (Higgins & Green, 2008). The PICO framework is a structured approach for systematic reviews that facilitates formulating research questions by defining the Population, Intervention, Comparison, and Outcome of interest, enabling a systematic and comprehensive synthesis of scientific evidence. The following definitions and inclusion criteria were applied:

- **Population:** We chose agriculturally marginal grasslands with limited potential for intensive agricultural production due to physical or abiotic constraints (e.g., too dry, too wet, too steep, too remote, or unsuitable to be improved by reasonable amelioration measures) as the population. The primary yield/return of these marginal grasslands is grass, hay or litter. This definition includes wooded meadows used for grazing or mowing, floodplain meadows, and grazed fens.
- **Intervention:** Relevant interventions included abandonment, intensification, or conservation of extensively used marginal grasslands, as well as restoration of previously abandoned or intensified grasslands.
- **Comparison:** Marginal grasslands that were maintained by extensive land-use practices, such as long-term traditional mowing and grazing regimes, were chosen as control/comparator.
- **Outcome:** The effects of agricultural management were assessed based on the following biodiversity metrics: species richness, species abundance, species diversity, functional diversity, or genetic diversity. Changes in biodiversity values were categorized as an increase, decrease, or no change in response to agricultural management.

The search was restricted to study sites located in Europe and included only peer-reviewed articles, conference proceedings, and book chapters. We further refined the search by limiting it to specific Web of Science categories and Scopus subject areas. To maximize the number of potentially relevant studies, keywords were linked according to the PICO framework using logical operators. A detailed structure of the PICO framework is provided in Appendix Table A1.

Exclusion criteria

The search was conducted in April 2023, yielding a total of 3003 potentially relevant studies. We applied the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA, Page et al., 2021) checklist to guide the selection process (Fig. 1).

After removing duplicates, 1944 studies remained and were screened in a three-stage process (titles, abstracts, and full-text content) using the following exclusion criteria:

- Not written in English or German.
- Located outside the European continent.
- The unit of study did not align with our definition of agriculturally marginal grasslands (e.g., urban grasslands, field margins, burial mounds, orchards, vineyards, or other agroforestry systems).
- The intervention was unrelated to local management changes (e.g., studies focusing on fragmentation, habitat connectivity, or landscape complexity).
- Reviews or modeling studies.

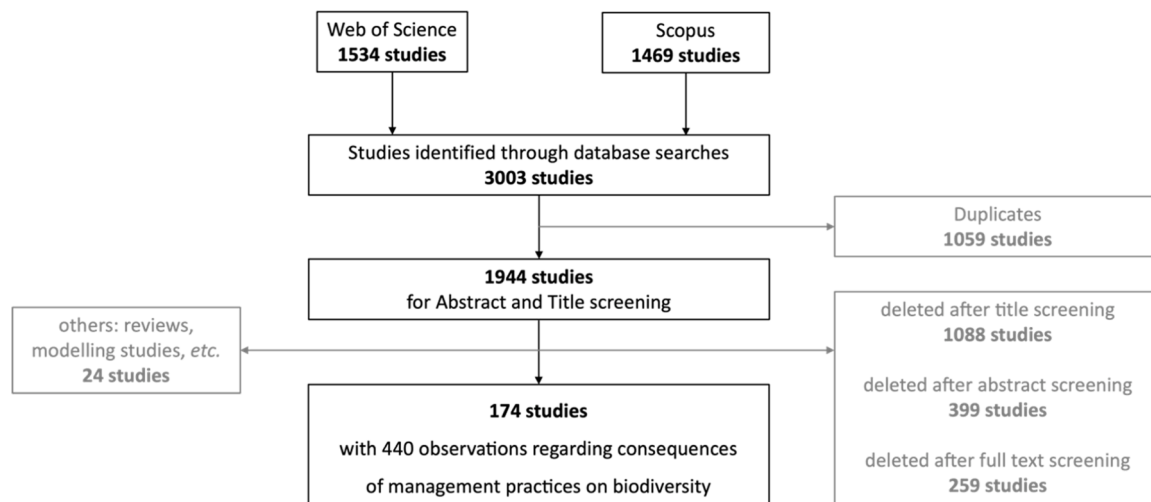


Fig. 1. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow diagram reporting the number of studies identified and excluded during the screening process.

- Experimental studies conducted in greenhouses or laboratories.

Additionally, four studies focusing on soil microbes and fungi were excluded due to their very low representation. After applying these criteria, 174 studies met the requirements outlined in our systematic review protocol.

Data extraction based on the consequences of grassland management on different classes of organisms

In this systematic review, we used the term *management* synonymous with *land-use*. We had pre-defined two major categories of land-use change occurring in agriculturally marginal grasslands: abandonment and intensification. Additionally, we gathered information on conservation, which we defined as the continuation of extensive management practices, and restoration, which involves the reintroduction of traditional management practices to previously abandoned or intensified agriculturally marginal grasslands (Fig. 2).

Data from the selected studies were recorded in a structured data extraction form focusing on management practices (categorized as abandonment, intensification, conservation, or restoration), grassland types (mountain grasslands, calcareous and dry grasslands, temperate mesic and wet grasslands), classes of organisms (plants and lichen - including vascular plants, bryophytes and lichen; invertebrates - including insects, arachnids, gastropods, and soil invertebrates; and vertebrates - such as birds and small mammals), and changes in various biodiversity values (species richness, species abundance, species diversity, functional diversity, or genetic diversity). These changes were

categorized as decrease (−1), no change (0), or increase (1) based on statistical significance and confidence intervals presented in text, figures, or tables (Appendix B). Descriptive visualisations of the raw data can be found in Appendix Fig. A1 representing the mean response of single orders of organisms to management regimes, and Appendix Fig. A2 showing the mean response of single biodiversity measures to land-use change.

To assess the effects of ongoing succession on biodiversity, we further categorized study sites into three classes based on the time since abandonment: Short-term abandonment (<5 years) was classified as early stages of succession, where grassland species remain dominant and structural changes are minimal. Mid-term abandonment was defined as an abandonment of 5–10 years. For this time range of abandonment Öckinger et al. (2006) have found a beginning of shrub encroachment and the establishment of competitive grasses, but a persistence of most semi-natural grassland species. Long-term abandonment was defined as >10 years after abandonment and is expected to correspond to structural and compositional changes, potentially accompanied by the establishment of woody vegetation and the reduction of open habitat.

Each article reported one or more management-related changes in biodiversity, enabling us to extract a total of 440 recorded observations regarding the consequences of land-use practices on different classes of organisms across the 174 studies. We applied strict selection criteria and rigorously evaluated the reported impacts of agricultural management on biodiversity values. The qualitative synthesis allowed us to include a large number of studies and integrate highly heterogeneous datasets, ensuring a broad representation of the evidence base in the field and providing a comprehensive analysis of our research question.

Data analysis

In the descriptive analysis, we categorized organisms into three groups: plants and lichens, invertebrates, and vertebrates. However, for the statistical analysis, we combined the invertebrate and vertebrate categories into a single group, called animals, due to the limited number of studies focused on vertebrates.

To assess the negative effects of abandonment or intensification on the biodiversity of agriculturally marginal grasslands, we assigned a value of 1 to each instance where a decrease in biodiversity was observed, and a value of 0 to instances where biodiversity either increased or remained unchanged. To evaluate the positive effects of conservation on biodiversity, we assigned a value of 1 to observations where biodiversity either did not change or increased (i.e., where conservation actions prevented biodiversity loss), and a value of 0 to

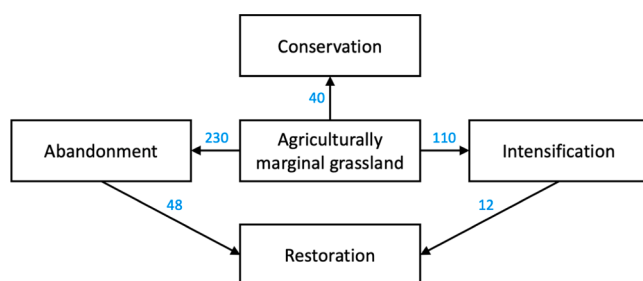


Fig. 2. Graphic representation of land-use practices in agriculturally marginal grasslands that were considered in this systematic review. Blue numbers indicate the amount of observations regarding the consequences on biodiversity for each change in management practice or intensity.

observations reporting a decrease in biodiversity. Finally, to analyze the positive effects of restoration on abandoned or intensified grasslands, we assigned a value of 1 to observations reporting an increase in biodiversity and a value of 0 to those indicating no change or a decrease in biodiversity (Table 1).

For analyzing the negative impact of abandonment and intensification of agriculturally marginal grasslands on the diversity of different groups of organisms (question 1), we calculated the probability of observing a significant decline in biodiversity following abandonment or intensification. We fitted a generalized linear mixed-effects model with a binomial distribution, using change in biodiversity as the response variable, the interaction between management (abandonment, intensification) and organism group (plants and lichen, animals) as predictors, and study ID as a random effect to account for variability between studies.

The limited number of observations for each type intensification precluded a formal statistical analyses. Nevertheless, for a descriptive analysis, we calculated the mean binary response of observing a decrease in biodiversity upon the different intensification measures.

To answer question 2, regarding whether the negative impact of abandonment depends on its duration, we calculated the probability of observing a significant decline in biodiversity following different durations of abandonment. We fitted a generalized linear mixed-effects model with a binomial distribution, using change in biodiversity as the response variable, the interaction between organism group (plants and lichen, animals) and duration of abandonment (long-term, mid-term, short-term) as predictors, and study ID as a random effect.

To determine whether different types of agriculturally marginal grasslands respond differently to abandonment or intensification (question 3), we calculated the probability of observing a significant decrease in biodiversity by fitting a generalized linear mixed-effects model with a binomial distribution using change in biodiversity as the response variable, the interaction between management (abandonment, intensification), organism group (plants and lichen, animals) and grassland type (mountain grasslands, dry and calcareous grasslands, temperate mesic and wet grasslands) as predictors, and study ID as a random effect.

For question 4 concerning the beneficial effects of conservation and restoration on preserving the diversity of different groups of organisms (plants and lichen, animals), we calculated the probability of observing an increase in biodiversity after restoration and the probability of no change or an increase in biodiversity following conservation efforts, by fitting a generalized linear mixed-effects model with a binomial distribution, using change in biodiversity as the response variable, the interaction between management (conservation, restoration) and organism group (plants and lichen, animals) as predictors, and study ID as a random effect.

To assess the significance of individual categories within the model terms, we refitted the model without an intercept. This approach estimates absolute effects for each category rather than relative differences compared to a reference level, allowing direct evaluation of the significance of each category (Agresti, 2007). We evaluated the significance of individual categories and differences to the reference level using two complementary approaches. First, we examined the p-values from the model summary output to assess whether individual predictors

significantly influenced the response variable. Second, we visualized predicted probabilities with 95 % confidence intervals (CIs) to interpret the results. As we used binomial models, we considered an effect significant if the confidence interval did not include 0.5, indicating a clear probability shift. Additionally, for comparisons between categories, we assessed significance based on whether the confidence intervals overlapped, where substantial overlap suggested no clear difference between groups.

The statistical analyses were performed using the *tidyverse* (Wickham et al., 2019) and *glmmTMB* packages (Brooks et al., 2017) in the free-ware R statistical software (version R 4.4.2, <http://r-project.org>).

Results

Geographical and temporal distribution of scientific evidence

We identified 174 scientific studies addressing management practices in agriculturally marginal areas across Europe, from which we extracted 440 observations: 230 dealt with abandonment, 110 with intensification, 40 with conservation, and 60 with restoration (Fig. 2). Among these 174 studies, the number of relevant publications has increased over the past three decades (Appendix Fig. A3), suggesting growing recognition of this issue.

The studies included in the final analysis encompassed nearly all regions of the European continent, apart from the far Eastern areas (Fig. 3). The distribution of observations was relatively similar for all types of management, with most of the studies being conducted in Central European countries.

Effect of different management practices on biodiversity of agriculturally marginal grasslands

The number of observations about the effects of agricultural management on the diversity of marginal grasslands (Fig. 4) was highest for plants (211 observations) and invertebrates (206 observations), with considerably fewer studies focusing on vertebrate biodiversity (23 observations). There was a noticeable bias towards vascular plants (210 observations) and prominent insect groups such as butterflies (55 observations), beetles (40 observations) and grasshoppers (29 observations). Only a few studies addressed the effects of land-use practices in agriculturally marginal grasslands on the diversity of bryophytes (7 observations), lichens (8 observations), gastropods (11 observations), ants (8 observations), and spiders (19 observations). Additionally, just one study investigated the impact of grassland management on small mammal diversity (Torre & Palau, 2023). The limited number of studies examining the effect of land-use practices on protists and fungal diversity precluded their inclusion in our analysis.

Due to the limited number of observations focusing on the consequences of grassland management on vertebrates, we combined the invertebrate and vertebrate categories for the statistical analysis into a single group (animals).

In line with our first question, we found a significantly high probability of observing a decline in diversity of plants and lichens due to abandonment (71 % [59 % to 81 %], Fig. 5, Appendix Table A2). Conversely, animals showed a significantly low probability of diversity decline following abandonment (23 % [15 % to 34 %]), which was also significantly lower than for plants (Fig. 5, Appendix Table A2).

Regarding our second question we found a significantly high probability of observing a decline in diversity of plants and lichen after long-term abandonment of more than 10 years (76 % [60 % to 87 %], Appendix Fig. A4, Appendix Table A3). While the predicted probabilities for mid-term (5 – 10 years) and short-term (< 5 years) abandonment were similar in magnitude, their confidence intervals included 0.5 and were therefore not statistically significant (Appendix Fig. A4, Appendix Table A3). The probability of observing a decline in animal diversity in long-term abandoned plots was 39 % [26 % to 53 %], which was

Table 1

Overview of management practices, and their effect on biodiversity with corresponding distribution of the binomial values for statistical modeling.

Management practice	Effect on biodiversity	Decrease	No change	Increase
Abandonment	negative	1	0	0
Intensification	negative	1	0	0
Conservation	positive/no effect	0	1	1
Restoration	positive	0	0	1

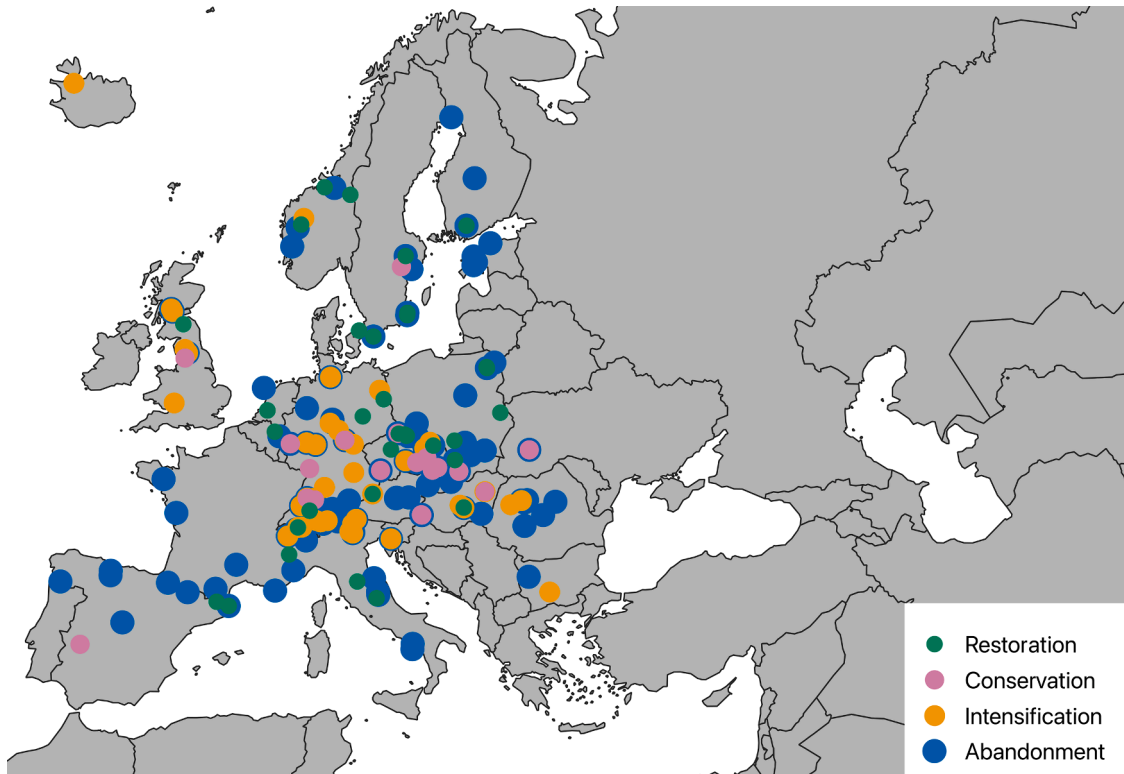


Fig. 3. Geographical distribution of observations from studies included in the final analysis. Circle size is scaled for visualization purposes to improve visibility of overlapping data points, and does not encode any quantitative information. The center of each circle corresponds to the coordinates of the research area of the included studies.

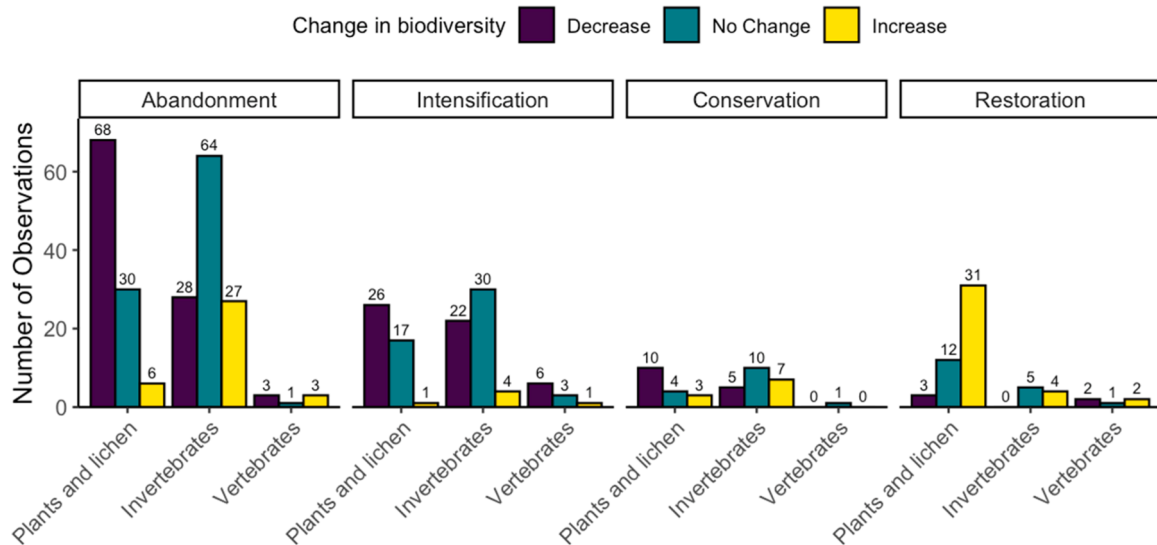


Fig. 4. Overview of observations reporting an effect of management on the diversity of different classes of organisms in agriculturally marginal grassland.

significantly higher compared to short-term (8 % [2 % to 28 %]) or mid-term abandonment (7 % [2 % to 25 %]), both of which were significantly low (Appendix Fig. A4, Appendix Table A3).

For our third question, which examined the effect of abandonment or intensification on the biodiversity of different grassland types, we found a significantly high probability of observing a decline in plant and lichen diversity after abandonment of mountain grasslands (81 % [62 % to 92 %], Appendix Fig. A5, Appendix Table A4). The probabilities of a decline in plant and lichen diversity after abandonment were 67 % [46 % to 83 %] in dry and calcareous grasslands, and 62 % [39 % to 80 %] in

temperate mesic and wet grasslands (Appendix Fig. A5, Appendix Table A4). Furthermore, there was a significantly low probability of observing a decline in animal diversity after abandonment of dry and calcareous (20 % [9 % to 39 %]), and temperate mesic and wet grasslands (20 % [10 % to 38 %], Appendix Fig. A5, Appendix Table A4). The probability of detecting a decline in animal diversity after abandonment in mountain grasslands was 31 % [15 % to 53 %] (Appendix Fig. A5, Appendix Table A4).

Further analysing our first and third question, the probability of observing a decline in biodiversity after intensification was similarly

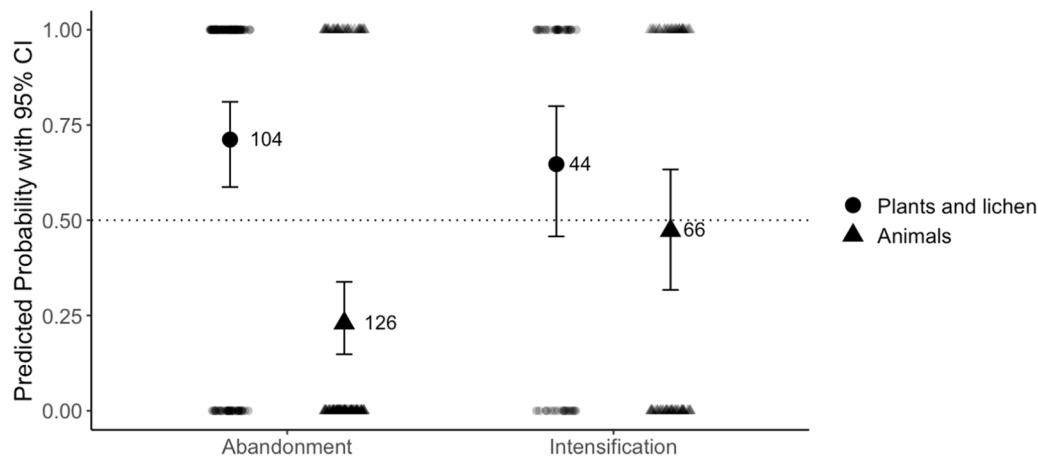


Fig. 5. Probabilities of observing a decrease in biodiversity upon abandonment or intensification of agriculturally marginal grasslands. Numbers next to datapoints represent sample sizes. Raw data are overlaid as jittered points to show the distribution of observed outcomes that informed the model.

high for both, plants and lichen as well as animals (65 % [46 % to 80 %] and 47 % [32 % to 63 %], respectively, Fig. 5, Appendix Table A2), and did not differ between different grassland types (Appendix Fig. A5, Appendix Table A4). The intensification measures analyzed in the reviewed studies primarily included intensive grazing or mowing, either separately or in combination with fertilization. Increased fertilization was predominantly applied alongside mowing, rather than as an isolated measure or in combination with grazing. Due to limited sample sizes, a formal statistical analysis was not feasible, and comparisons were instead based on the proportion of cases in which intensification led to a decrease in biodiversity (mean binary response, Appendix Fig. A6). This general assessment of patterns suggested that plants are more susceptible to the combined effects of intensive mowing and fertilization compared to animals, whereas intensive mowing alone had a similar impact on both groups of organisms (Appendix Fig. A6). Additionally, intensive irrigation appeared to negatively affect plant diversity, but not animal diversity (Appendix Fig. A6).

Addressing our fourth question, the probability of maintaining or increasing the biodiversity of animals was significantly high (79 % [55 % to 92 %]) after conservation of extensively managed agriculturally marginal grasslands, whereas it showed a significantly lower probability (41 % [20 % to 66 %]) of maintaining or improving the diversity of plants and lichen (Fig. 6, Appendix Table A5). The significance of the difference in conservation effects between plants and lichen vs. animal diversity was assessed using the model summary output (Appendix

Table A5), where the p-value for the contrast is 0.027. Furthermore, the confidence intervals do not substantially overlap, supporting a significantly stronger effect of conservation on animals than on plants and lichens.

The probability of observing an increase in diversity of plants and lichen was significantly high after restoration of previously abandoned or intensified agriculturally marginal grasslands (68 % [52 % to 80 %], Fig. 6, Appendix Table A5). In contrast, the probability of observing an increase in animal diversity upon restoration – which, according to our model, did not significantly decline following abandonment or intensification (Fig. 5) – was 44 % [20 % to 70 %] (Fig. 6, Appendix Table A5).

Discussion

This systematic literature review is comprised of 174 studies conducted in Europe over the last 30 years and focused on the effects of abandonment and intensification on biodiversity of agriculturally marginal grasslands, while also assessing the role of conservation and restoration. We combined and classified an inhomogeneous corpus of studies into statistical models, which allowed us to reveal contrasting effects of management changes. Our findings largely confirm our hypotheses: both abandonment and intensification tend to reduce biodiversity, with long-term abandonment having a more detrimental effect than short- or mid-term abandonment. Lower trophic levels and less mobile organism groups, particularly plants and lichens, were more

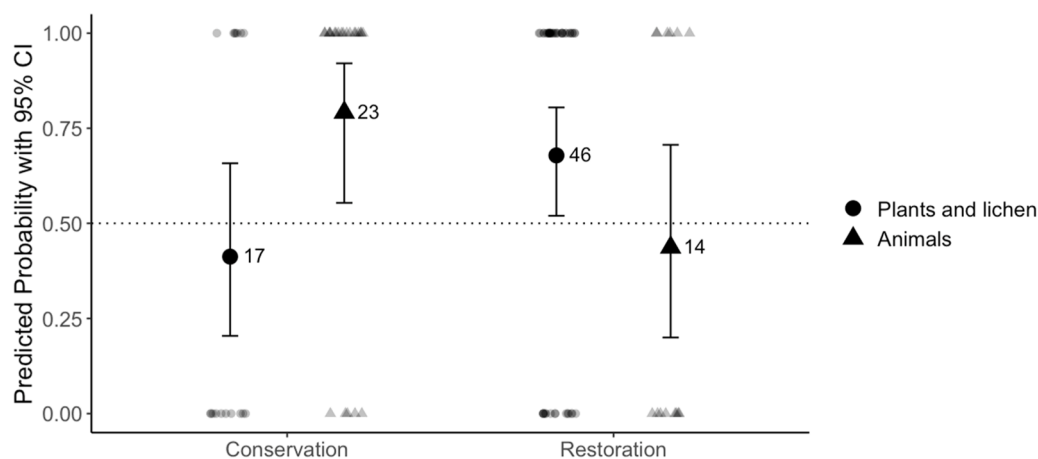


Fig. 6. Probabilities of observing an increase or no change in biodiversity upon conservation of extensively managed grasslands, and of observing an increase in biodiversity after restoration of previously abandoned or intensively used agriculturally marginal grasslands. Numbers indicate sample sizes. Raw data are overlaid as jittered points to show the distribution of observed outcomes that informed the model.

strongly and rapidly affected by abandonment than animals. Furthermore, our results support the hypothesis that conservation actions help maintain high biodiversity, most notably for animals, while restoration efforts seem particularly effective in mitigating biodiversity loss among plant communities.

Effects of abandonment

This systematic review confirms the decrease in plant diversity due to abandonment and demonstrates that mountain grasslands are particularly sensitive to the lack of disturbance compared to other agriculturally marginal grasslands. The cessation of low-intensity management practices in agriculturally marginal grasslands leads to an accumulation of biomass, which generally has negative consequences for plant communities (Dengler et al., 2014; Peco et al., 2017; Valko et al., 2018). One reason for the decline in plant diversity due to management abandonment might be that plant litter alter competition for light availability, favoring less light-demanding species, ultimately homogenising grassland species composition (J. Valkó et al., 2018). Thus, our findings stress the importance of low-intensity management (e.g., biomass removal by mowing, grazing, burning) if we were to conserve the high plant diversity of agriculturally marginal grasslands.

The comparatively weaker response of dry and calcareous, as well as temperate mesic and wet grasslands to abandonment may reflect differences in their initial plant community composition, land-use history, and environmental conditions. For example, Poptcheva et al. (2009) found no clear correlation between time since abandonment and plant species richness in wet grasslands, which they attributed to site-specific differences in successional trajectories. Grasslands dominated by stress-tolerant species and occurring on low-nutrient soils may experience slower vegetation shifts and less pronounced biodiversity loss after abandonment, while those with nutrient-demanding or disturbance-adapted species may change more rapidly. Moreover, the functional traits and competitive strategies of dominant species likely mediate how plant communities respond to the cessation of management (Poptcheva et al., 2009). This ecological heterogeneity may explain the more moderate biodiversity responses we observed in temperate mesic and wet, as well as dry and calcareous grassland types compared to mountain grasslands.

In contrast to the response of plants and lichen, we found that abandonment of agriculturally marginal grasslands had a significantly lower probability of decreasing animal diversity, confirming the findings of Elliott et al. (2023). This effect can likely be attributed to several factors. Firstly, the great diversity of taxonomic groups within invertebrates and vertebrates may result in diverse responses to land-use practices, influenced by factors such as mobility, habitat range, feeding, and nesting behaviors and thus a systematic response on the level of animals is not detectable (Ernst et al., 2017). For example, some species may be more mobile and able to migrate to suitable habitats in response to management changes. In contrast, species with limited mobility may be more vulnerable to habitat degradation (Löffler et al., 2020). Additionally, differences in feeding habits, such as herbivorous versus carnivorous diets, may cause varying degrees of dependence on plant communities or prey availability, further influencing species' responses to changes in the landscape (S. Fadda et al., 2008). Secondly, higher trophic levels (e.g., herbivores and predators) may exhibit a delayed response to changes in lower trophic levels, such as plants. Thirdly, the abandonment of grassland management initially increases structural complexity, potentially benefiting certain arthropod and bird populations (Azcarate & Peco, 2012; Koch et al., 2015; Laiolo et al., 2004; Pöyry et al., 2006). However, long-term abandonment may cause a decline in grassland-specific invertebrate species due to reduced habitat heterogeneity after bush encroachment, subsequently affecting insectivorous birds (Baur et al., 2006; O. Valkó et al., 2018). We focused our analysis primarily on the impacts of management practices on biodiversity in agriculturally marginal grasslands by examining

indicators related to species richness, abundance, species diversity, functional diversity and genetic diversity. Yet, even when those diversity indicators remain similar, alterations in species identity and therefore community composition may occur.

Effects of intensification

Although agriculturally more productive and accessible fields have historically faced greater pressure from intensification (Emmerson et al., 2016), our review still identified 110 studies investigating intensification in agriculturally marginal grasslands, which are ecosystems typically less suited to high-intensity use due to topographical and environmental constraints (Meier et al., 2022). Our analysis shows that even modest levels of intensification negatively affected the diversity of plants and lichen as well as animals to a similar extend - 65 % and 47 % probability, respectively. These probabilities of biodiversity decline following intensification did not reach statistical significance, which may reflect the comparatively lower intensity of practices applied in these areas. The similar response across taxonomic groups is consistent with numerous studies showing that even moderate intensification can lead to rapid habitat homogenization, favor the dominance of fast-growing and disturbance-tolerant species, and outcompete native grassland specialists. This not only alters community composition but also disrupts biotic interaction networks, as well as weakens the pairwise diversity correlations among taxa, with strong land-use intensification even breaking specialized species relationships, ultimately contributing to widespread biodiversity loss in marginal grasslands (Beckmann et al., 2019; Green, 1990; Guo et al., 2023; Manning et al., 2015; McKeon et al., 2022). On a larger spatial scale, the decline in biotic heterogeneity due to land-use intensification results in reduced compositional dissimilarity among different sites, which poses a major threat to overall biodiversity (Gossner et al., 2016).

Furthermore, intensification was predicted to have a significantly more detrimental effect on animal diversity than abandonment, potentially because the consequences of intensified management practices impact the diversity of grassland species considerably faster than the slow succession occurring after land abandonment (Löffler et al., 2020).

Effects of conservation measures and restoration efforts

The scientific studies that we identified in this systematic review focussed on the impact of abandonment or intensification on the diversity of marginal grasslands. Fifty of these studies also investigated the effects of conservation or restoration practices. As our search string did not include specific terms related to conservation or restoration, we do not claim to provide an exhaustive overview of their effects. Nonetheless, given their critical importance in shaping biodiversity outcomes in agriculturally marginal grasslands, we sought to incorporate relevant information where available, aiming to provide a broader context and highlight the role of conservation and restoration efforts alongside the impacts of abandonment and intensification.

The grassland conservation efforts covered in the studies included in our analysis involved traditional meadow irrigation (Schirmel & Gerlach, 2022), burning (Dmytrash-Vatseba & Shumska, 2020; Hamrik & Kosulic, 2021; Köhler et al., 2005), mechanical turf disturbance (Hamrik & Kosulic, 2021), mulching (Cabon et al., 2021; Dolezal et al., 2011; Gaisler et al., 2019; Perez-Sanchez et al., 2018), alternative low-intensity mowing regimes (Kenyeres & Szentirmai, 2017), grazing with low stocking rate (Bonari et al., 2017; P. Török et al., 2016; and others), grazing on sowing enriched pastures (Moreno-Opo et al., 2021), and leaving uncut refuges (Kalab et al., 2020; Révész et al., 2025). Our results show that these conservation efforts are predicted to maintain or even increase the diversity of invertebrates and vertebrates, although they are not predicted to be as effective in maintaining or increasing the diversity of plants and lichen. This raises concerns that low-intensive conservation actions might not always be sufficient to maintain the

high floral diversity of previously extensively grazed or mown agriculturally marginal grasslands in the face of climate change and species invasion.

Restoration efforts, on the other hand, were associated with a high predicted probability of positively affecting the diversity of plants and lichen, which also showed the highest likelihood of decline under abandonment, but were also negatively impacted by intensification according to our analysis. However, the diversity of animals was not predicted to significantly increase as a result of restoration efforts, which is expected, given that these taxa had a low predicted probability of being negatively affected by abandonment and a moderate probability of being impacted by intensification in the first place. The restoration of abandoned or intensified marginal grasslands in the studies we analyzed was predominantly achieved through the reintroduction of extensive grazing or mowing (Colom et al., 2021; Rysiak et al., 2021; and others). Abandoned grasslands were further restored by shrub clearing (Baba, 2003; Campedelli et al., 2016; Öckinger et al., 2006; Zeidler et al., 2022). These efforts seem sufficient to increase plant diversity that suffered from the consequences of abandonment or intensification. Furthermore, a recent study demonstrated that restoration through plant material transfer promoted endangered species (Sommer et al., 2025).

In order to combat global grassland degradation an integrated socio-ecological approach is required that involves increasing the recognition of grasslands in policy frameworks, developing standardized indicators for assessing degradation and restoration, employing scientific knowledge sharing and stakeholder engagement, to address the drivers of degradation, facilitate targeted restoration efforts, and ensure that ecological and socio-economic benefits are preserved and enhanced (Bardgett et al., 2021).

Limitations and directions of future research

While our systematic review offers important insights into how different management regimes affect biodiversity in agriculturally marginal grasslands, we were constrained to grouping organism responses into broader categories – “plants and lichens” vs. “animals” – due to insufficient data for many specific taxa. This prevented more fine-scale analyses across taxonomic groups and may mask important taxon-specific patterns. Future research should aim to fill these gaps by increasing the taxonomic and ecological resolution of biodiversity monitoring in grassland systems. In the long term, this will enable more detailed syntheses, ideally in the form of formal meta-analyses, which would allow for robust effect size estimation and better assessment of variability among taxa, habitat types, and management practices.

Conclusions

In conclusion, our systematic review highlights the differential impacts of management changes on biodiversity of agriculturally marginal grasslands. While abandonment poses a substantial threat to plant and lichen diversity, its negative effect on animal diversity is considerably less pronounced. Agricultural intensification similarly affects biodiversity across the investigated organism groups. Encouragingly, conservation actions – defined here as the continuation of traditional, low-intensity management – are likely to maintain or enhance animal diversity, though they were not consistently effective for plants and lichens. Restoration efforts, in turn, were most promising for plants and lichens.

Ultimately, our findings emphasize that no single management strategy benefits all taxa equally and highlight the need for taxon-specific and context-sensitive management strategies that reflect the varying ecological needs of different organism groups. Given that both abandonment and intensification undermine biodiversity, albeit in taxon-specific ways, policy frameworks should prevent either in agriculturally marginal grasslands. This is especially important in regions

where abandonment leads to rapid successional overgrowth and where intensified use exceeds the ecological carrying capacity of the habitat. Agri-environment schemes should therefore be refined to better reflect the land-use history, grassland type and target taxa of each site, e.g., differentiating between dry calcareous grasslands and wet meadows in subsidy design. Finally, integrating long-term monitoring into conservation and restoration programs will be essential to track how different organism groups respond to interventions and to support adaptive, evidence-based grassland management.

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CRediT authorship contribution statement

Susanna Hempel: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Felix Herzog:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Péter Batáry:** Writing – review & editing, Conceptualization. **Erik Öckinger:** Writing – review & editing, Conceptualization. **Eva Knop:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baee.2025.08.003.

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