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# Losers and winners: responses of grassland arthropods to land-use components

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Intensified land-use in grasslands reduces biodiversity, particularly affecting arthropod populations. However, responses of individual species vary depending on their ecological traits and habitat requirements. Some species may tolerate or even benefit from intensive land-use, while others, particularly specialists or those with narrow niches, are likely to be negatively affected. We used a quantitative niche model to evaluate species-specific responses to land-use intensity in four arthropod orders common in grasslands: Araneae, Coleoptera, Hemiptera and Orthoptera. From 2008 to 2018, a total of 214 416 individuals across 1352 species were collected on 150 grassland plots across three regions of Germany. The effects of mowing, fertilizing, and grazing on species occurrence and abundance were evaluated by their niche optima to identify winners, losers, and neutrals. Fertilizing showed the fewest winners (6%) as well as the most losers (29%) with all orders having the highest proportion being negatively affected, whereas grazing showed the most winners (10%) and fewest losers (10%). Nevertheless, most species showed neutral responses (71%). The niche optimum of grazing favored smaller species, whereas mowing and fertilizing favored larger species. Herbivores were particularly sensitive to fertilizing. Comparison with the Red List revealed that species under mowing exhibited lower niche optima with higher-risk categories, which was also reflected in declining population trends. This study highlights the high variation in species-specific responses of arthropods to the different components of land-use, showing overall three times as many loser species as winner species. This emphasizes the need for conservation strategies tailored to vulnerable species. Balancing land-use strategies with biodiversity conservation in land-use policies is essential to preserve arthropod diversity and enhance ecosystem resilience in grasslands.

Keywords: Biodiversity Exploratories, body size, feeding guilds, fertilizing, grazing, mowing, niche model, Red List

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## Introduction

In recent years, the alarming decline of populations of grassland species has become increasingly evident. Intensification of grassland management practices have shown to be associated with significant losses in plant species (Jandt et al. 2022). For arthropods, reductions in biomass, species richness, and individual numbers have been reported (Hallmann et al. 2017, Seibold et al. 2019). Despite declines, semi-natural grasslands remain among the most valuable and diverse habitats, serving as biodiversity hotspots that deliver critical ecosystem services alongside production of livestock, including water supply, carbon storage, erosion control, climate mitigation and pollination (Bengtsson et al. 2019, Shipley et al. 2024). Traditionally, grasslands were grazed by different livestock, or mown to produce hay, but the increase in land-use intensity can disrupt the delicate balance of species interactions and environmental conditions, undermining their biodiversity and functionality (Blüthgen et al. 2016, Habel et al. 2013).

In semi-natural grasslands, regular mowing or grazing is essential to prevent the succession of woody vegetation and maintain diverse plant and therefore diverse animal communities (Grime 2006). However, substantial changes in grassland management over recent decades, driven by shifts in both plant and animal husbandry, have led to the loss of valuable habitats and a dramatic decline in insect populations (Sánchez-Bayo and Wyckhuys 2019). Traditional grazing practices have played a vital role in biodiversity conservation initiatives, such as High Nature Value Farmland programs, which aim to preserve open landscapes and their associated species (Metera et al. 2010). Yet, in many areas, grazing has shifted to higher intensities, with most pastures now heavily grazed (Dallimer et al. 2009). This intensification negatively impacts grassland ecosystems by reducing habitat heterogeneity and threatening insect populations (Kruess and Tscharntke 2002). Simultaneously, changes in mowing practices have transformed grassland-use. While mowing can support a rich fauna by maintaining open habitats, it poses direct and indirect threats to arthropods, including physical harm and habitat disruption (Berger et al. 2024). Moreover, the shift from traditional hay production to silage, driven by the increasing demand for meat and dairy products, has further prioritized fodder production over ecological balance (O'Mara 2012). Improved efficiency, also driven by advancements in machinery, has led to a substantial increase in yield, primarily due to enhanced fertilization practices (Zhang et al. 2017). The increase in the number of harvests is associated with the need to increase the delivery of nutrients, foremost nitrogen, in the form of liquid manure or mineral fertilizers, favoring nutrient-demanding species (Socher et al. 2013). This shift significantly affects the soil, altering plant composition, with only a few species dominating compared to nutrient-poor areas, leading to a decline in plant diversity (Francksen et al. 2022). This shift in plant community composition impacts arthropod communities (Haddad et al. 2009, Tobisch et al. 2023), particularly herbivorous insects (Welti et al. 2017), leading to a multitrophic homogenization of grassland communities (Gossner et al. 2016). Consequently, the loss of food resources and reproduction sites for arthropods has become a serious concern, jeopardizing the survival of specific species (Scherber et al. 2010, Tobisch et al. 2023).

The management of grassland directly influences the availability and structure of ecological niches for grassland species (Tscharntke and Greiler 1995). Yet, the responses of individual species to land-use components vary, shaped by their niche requirements and ecological traits (Simons et al. 2016). Intensified land-use may promote a few species that thrive under the altered conditions (winners), while others struggle to persist (losers). Understanding these mechanistic relationships between land-use components and niche dynamics is critical for explaining species-specific responses. A quantitative niche model offers a valuable tool for analyzing these relationships, enabling predictions about species distributions under the executed land-use practices. By analyzing the current distribution of individuals and therefore their niche optima across differently managed grasslands, the model identifies variations in species' 'land-use niches' and determines which management gradients most strongly drive niche shifts (Chisté et al. 2016). Previous research, using such models for Orthoptera and Cicadinae, has shown that only a subset of the investigated species occurred in grasslands with intensified management (Chisté et al. 2016, 2018).

With this study, our aim is to evaluate how the applied land-use components shape the composition of arthropod species in grasslands. Specifically, we looked at whether species from four arthropod orders common indicator for grasslands – Araneae, Coleoptera, Hemiptera and Orthoptera – were losers, neutrals, or winners of land-use intensification. By analyzing species' responses to land-use intensities, this research provides indications of the factors influencing biodiversity loss or persistence in grassland ecosystems. We studied land-use intensity gradients related to grazing, fertilizing, and mowing (Blüthgen et al. 2012, Hartlieb et al. 2024). We quantified the species' responses to these gradients by their abundance-weighted mean (niche optima) of the plots in which each species occurred, henceforth termed 'land-use niche'. Niche optima that are significantly lower than null model simulations define 'losers', higher values define 'winners' of land-use intensity (Chisté et al. 2016, 2018, Mangels et al. 2017, Busch et al. 2019, Wehner et al. 2021). We hypothesize that grassland arthropod species vary in their responses to land-use, partly determined by species-specific traits. By analyzing the relationship between land-use niches and a number of organismic traits, we seek to identify characteristics, like body size or feeding guilds, which make certain species more susceptible to environmental disturbances. Further, by incorporating Red List categories and population trends, we want to assess the long- and short-term vulnerabilities of species under varying land-use intensities. Based on these results, recommendations on how to better protect and manage grassland ecosystems can be derived.

## Material and methods

### Study sites

The Biodiversity Exploratories, initiated in 2006, are a research platform for investigating the links between land-use and biodiversity in forest and grassland habitats across three distinct regions in Germany: the Schwäbische Alb (Baden-Württemberg in the southwest), the Hainich (Thüringen in the central region), and the Schorfheide-Chorin (Brandenburg in the northeast). These regions are characterized by different environmental factors, such as climate, geology, soil type and topography.

Our study focused on 150 grassland plots (50 per region), each measuring 50 × 50 m, spanning the entire region-specific spectrum of land-use gradients from highly intensive to scarcely managed areas. They are integrated into larger management units in which management is uniform. The plots comprised around 35% meadows, 35% pastures, 27% mown pastures (subject to both mowing and grazing in the same year), and 3% fallow land. Around two-thirds of the meadows and mown pastures, but only 15% of the pastures received fertilizing (Vogt et al. 2019). Pesticides were not used on any of the plots, except for herbicide application on five plots for one year only (Seibold et al. 2019). For a more detailed description of the sites, including comprehensive information on management and the project itself, see Fischer et al. (2010).

### Arthropod data

From 2008 to 2018, arthropods were sampled annually on the 150 grassland plots. Sampling took place twice a year, in June and August. Herb layer arthropods were sampled by sweep netting along a 150 m transect along three plot borders, with 60 double sweeps per plot (Simons et al. 2014). Sweep netting was only conducted on days without rain, with low wind speed and after the morning dew had dried. All adult specimens of the orders Araneae, Coleoptera, Orthoptera and Hemiptera (only Heteroptera and Auchenorrhyncha) were sorted and identified to species level (Neff et al. 2019, Seibold et al. 2019).

### Land-use intensity

The data on land-use components are based on the responses of the respective farmers, landowners, or tenants to a standardized questionnaire on relevant management information on the type and intensity of annual land-use and agricultural practices. These surveys were carried out on an annual basis. The survey data from Vogt et al. (2019) were used to calculate individual land-use intensity values for mowing, fertilizing and grazing, from 2008 to 2018 (Supporting information). We used the unstandardized raw data per year and plot for the indices of grazing and fertilizing intensity according to Blüthgen et al. (2012). Grazing (LSU d $ha^{-1}$) is derived by multiplying the livestock units with the duration of grazing per hectare, accounting for cattle, sheep, horses and goats, ranging from 2 to 2500 animals for 1 to 365 days per year. Fertilizing (kg N $ha^{-1}$) is quantified in kilograms of nitrogen per hectare, encompassing organic or inorganic sources such as manure, slurry, biogas, mash and nitrogen, applied from 1 to 7 times, ranging between 6 and 360 kg $ha^{-1}$ per year. For mowing intensity, we used the mowing compound intensity index $M(i)$ (cuts ± impact of mowing regime i.e. mowing machine, mowing height and use of conditioner per year) from Hartlieb et al. (2024). If there were missing values for one variable of the mowing index, the neutral benchmark (a chosen mean value of each component, representing a mid-point between favorable or unfavorable mowing practices affecting the biodiversity of meadow-dwelling species) was used instead (Hartlieb et al. 2024).

### Calculation of land-use niches

To define the ecological niche of the species, a quantitative niche model on the basis of the publication of Chisté et al. (2016) was implemented. This niche model described species-specific responses to the land-use gradients, which was coupled with a randomization procedure and was able to detect trends even for rare species. For this approach, we integrated all found adult individuals identified to species level with the minimum number of occurrences per plot of one. In total, we analyzed 214 416 individuals from 1352 species out of four arthropod orders, namely Araneae (176 species 7078 individuals), Coleoptera (762 species, 42 248 individuals), Hemiptera (384 species, 161 171 individuals) and Orthoptera (30 species 3919 individuals) found on 150 plots between 2008 and 2018. We calculated the responses of each arthropod species to the land-use gradients for fertilizing (kg N $ha^{-1}$), grazing (LSU d $ha^{-1}$), and mowing (cuts ± impact of mowing regime) (Blüthgen et al. 2012, Hartlieb et al. 2024). Gradients were averaged across the years 2008–2018, and the sampled arthropods were summed up per plot. The abundance-weighted means (AWM) were defined as the weighted mean gradient values (land-use niche optimum), weighted by the proportion of individuals of a species in each plot.

For statistical analysis of the AWM, we employed a randomization method based on a null model. This model assumes that each species had an equal likelihood of occurring at any site from the regions where the species occurred. The null model assigned mowing, grazing, or fertilizing intensity to each species from random sites, drawing from the same total number (but not identity) of sites on which the species was found. This calculation was restricted to the specific region (Schwäbisch Alb, Hainich, Schorfheide) where the respective species was found, i.e. when the species only occurred in the Schorfheide, the null model only uses plot values from the 50 Schorfheide plots. We used 10 000 iterations to produce a distribution of expected $AWM_{null}$ values (see Fig. 1 for an example distribution of *Tinotus morion*; and for a detailed description and the analysis, Supporting information). We then calculated the p-values by comparing the observed data to the null distribution generated through randomizations. Species with observed AWM lower than 95% of the $AWM_{null}$ values ($p < 0.05$) were treated as 'loser', while those with AWM higher than 95% of the $AWM_{null}$ values ($p < 0.05$) were identified as 'winner'. Species that did not

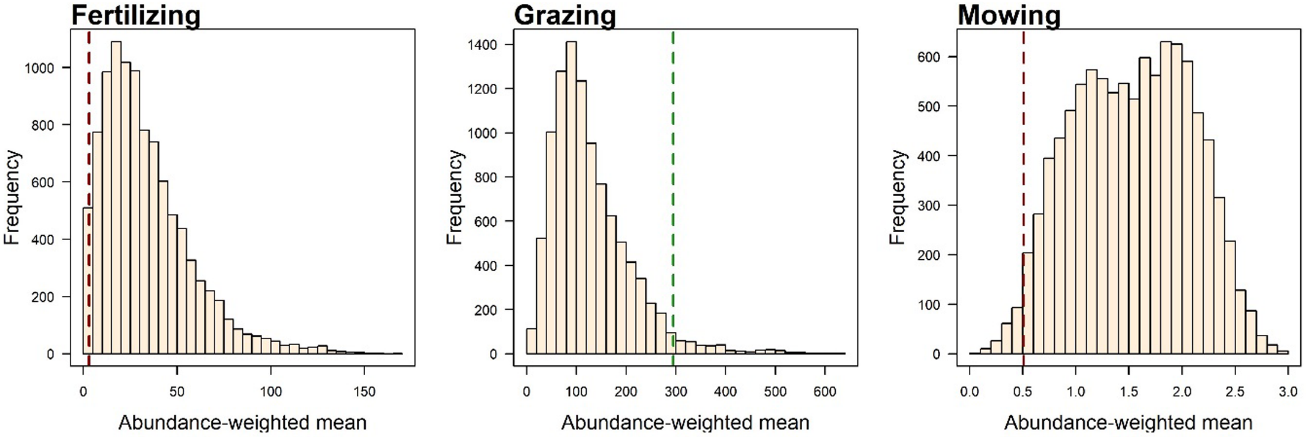

Figure 1. Observed (dashed lines: red = winner, green = loser) and expected abundance weighted means (AWM, niche optima) for the example species *Tinotus morion* (Coleoptera) of fertilizing (kg N ha$^{-1}$), grazing (LSU d/ha), and mowing (cuts ± impact of mowing regime) based on a null model randomly drawing with 10 000 iterations from the same total number of sites on which the species was found.

fit into either category were classified as 'neutral' (Supporting information).

### Threshold for rare species

To distinguish genuinely neutral responses from those driven by rarity, which results in neutrals as well, an additional simulation analysis was conducted (Supporting information). To determine how many plot occurrences are needed for a species to be classified as a significant 'loser' or 'winner', we generated random species occurrences distributions based on a log-normal model, reflecting realistic species occurrence pattern. For each land-use component, niche optima (the abundance-weighted mean of the gradient values across the plots) were calculated for a simulated species *i* occurring in 1, 2, 3, …, 150 plots. At each step in the simulation (i.e. number of plots), 1000 randomizations were run with 10 simulations, each using a newly generated log-normal distribution. This resulted in distributions of expected niche optima under the null hypothesis. The analysis identified minimum occurrence thresholds required for reliably detecting species' responses to each land-use component. These thresholds varied by component, reflecting differences in how each gradient influences species' niche optima. The Supporting information shows the simulation result for a species occurring in a defined number of plots for each component. Losers occurred in the lowest ranked plots of the gradient, winners occured in the highest ranked plots. If the abundance-weighted mean values of the simulated losers or winners fell below 95% confidence interval of the null model values, it defined the threshold for the minimum occurrences required for reliable classification of species responses for fertilizing, grazing, and mowing. To detect losers, fertilizing required at least five occurrences for reliable classification, while for mowing and grazing two occurrences were sufficient. To detect winners, no thresholds were necessary. To ensure a balanced and conservative (unbiased) comparison, we applied the fertilization threshold (< 5 plot occurrences) across all components when analyzing the distribution of losers, neutrals, and winners excluding 781 rare species with fewer than five plot occurrences (Table 1, Supporting information).

### Analysing the role of species traits

To understand species' ecological roles and predicting their responses to land-use intensification, we combined a trait-based approach with our sampled arthropod species. Therefore, we used a comprehensive trait dataset, assembled from various literature sources and validated in consultation with taxonomic experts for the respective groups (Gossner et al. 2015). We compiled the mean body size (mm) and feeding guild for all collected species of Araneae, Coleoptera, Hemiptera and Orthoptera. Feeding guild is categorised into carnivore, herbivore, omnivore, and mycetodetritivore (which is the combination of mycetophagous, detrivore and fungivore), each referring to the main food source during larval and adult stages of a species. Omnivores are defined as species using more than one feeding source (plants, animals, fungi, decaying plants or animals) to similar extent across larval and adult stages. All Araneae are carnivores and all sampled Auchenorrhyncha herbivores. For the calculations of the traits, the mean body size was log-transformed.

### Effect of conservation status

The inclusion of Red List data offers valuable insights into how land-use components impact species of varying conservation status. German Red List data were downloaded from the Rote Liste Zentrum website (www.rote-liste-zentrum.de/de/Download-Wirbellose-Tiere-1875.html, last accessed Jan. 2025; Supporting information). For our analysis, we used Red List categories (LC = Least concern, NT = Near threatened, R = Rare, G = Threatened to an unknown extent, VU = Vulnerable, EN = Endangered, CR = Critically endangered, EX = Extinct in Germany) and the short-term (last 10–25 years) and long-term (last 50–150 years) population trends (converted in decrease, stable, increase). Species with deficient data or which were not evaluated by the Red List were excluded from analysis, as were the categories Rare and Extinct in Germany, as they each had just one data point. Non-native species are not evaluated in the German Red List and hence excluded.

### Statistical analysis

For all calculations comparing the niche optimum, the grazing and fertilizing AWM were square-root transformed. To investigate differences in the orders, feeding guilds and forest fidelity (Supporting information) we performed the conservative Kruskal–Wallis rank sum test (H(2)), since partly the homogeneity of variance was violated and residuals were not normally distributed. We used the Dunn's test as a post hoc test, and to avoid type I errors we applied the Bonferroni–Holm correction. For calculations with percentage difference, the means were used. To test for relationships between the AWM of fertilizing, grazing and mowing, and the three AWM (response variable) with the mean body size (mm), as well as Red List statuses (categories, short and long-term population trends) (explanatory variables), we employed generalized linear mixed model (GLMM) using the 'glmmTMB' package (Brooks et al. 2017). A zero-inflated Gaussian model was used, with a single zero-inflation parameter applied uniformly across all observations. A random intercept was included for the taxonomic order of the species to account for potential non-independence of observations within these groups. Phylogeny of the species could not be included, since data was not available.

All our analyses were performed using R 'ver. 2023.12.1 (www.r-project.org).

## Results

### Winners and losers of land-use intensification

Individual species showed a wide range of responses (Table 1). After conducting the simulation and excluding neutral species, defined as those whose observed AWM did not differ significantly from the null distribution ($p \geq 0.05$), which were too rare to be represented in the niche model, i.e. fewer than five plot occurrences (Supporting information), 8% of the species were classified as winners and 21% as losers across all the three land-use components (n = 571). The majority, of 71%, did not show significant preferences and were thus classified as neutral. Among the orders, Hemiptera and Orthoptera showed the highest proportion of losers, 26% and 25.5%, respectively. Orthoptera also showed the highest proportion of winners (14.5%). One species of Araneae (*Araneus quadratus*) was identified as overall loser across all three land-use components (mowing, grazing and fertilizing), but conversely, no species emerged as overall winner. Among the land-use components, grazing accounted for the highest proportion of winners of 10.2%, and fertilizing for the fewest winners (5.6%). In contrast, grazing accounted for the fewest proportion of losers (9.8%), whereas fertilization accounted for most losers (28.9%) (Table 1, Supporting information).

Table 1. Species numbers of losers, neutrals and winners of the four arthropod orders (Araneae, Coleoptera, Hemiptera and Orthoptera) for the applied management intensity of fertilizing (kg N $ha^{-1}$), grazing (LSU d $ha^{-1}$), and mowing (cuts ± impact of mowing regime), analyzed by a niche-model for the years 2008–2018. Shown are 571 species, a subset of the 1352 species after the simulation excluding 781 species with a number of occurrences in < 5 plots.

| Order | Fate | Fertilizing | Grazing | Mowing |
|---|---|---|---|---|
| Araneae | Loser | 20 | 8 | 19 |
| (82 species) | Neutral | 55 | 69 | 59 |
| | Winner | 7 | 5 | 4 |
| Coleoptera | Loser | 65 | 31 | 52 |
| (279 species) | Neutral | 199 | 223 | 204 |
| | Winner | 15 | 25 | 23 |
| Hemiptera | Loser | 74 | 14 | 63 |
| (193 species) | Neutral | 112 | 153 | 116 |
| | Winner | 7 | 26 | 14 |
| Orthoptera | Loser | 6 | 3 | 4 |
| (17 species) | Neutral | 8 | 12 | 9 |
| | Winner | 3 | 2 | 4 |

### Land-use niche

The analysis revealed positive and negative relationships between the abundance-weighted means (AWM) of the 1352 species across different land-use components (Fig. 2). There was a negative correlation between the AWM for fertilizing intensity and grazing intensity ($z = -5.27$, $p < 0.001$). This shows that species in high fertilizing levels tend to occur less frequently in areas with intensive grazing and vice versa. A comparison of the AWM of grazing with the AWM of mowing revealed an even more pronounced negative relationship ($z = -23.55$, $p < 0.001$). In contrast, the relationship between the AWM of fertilizing and the AWM of mowing intensity was positive ($z = 35.37$, $p < 0.001$). Thus, approximately the same species can be found in plots with low and high intensity levels of fertilizing and mowing. However, the AWM of the land-use components differed among orders, with impacts observed for fertilizing ($H(2) = 9.66$, $p = 0.022$) and mowing ($H(2) = 24.28$, $p < 0.001$), but not for grazing ($H(2) = 1.7$, $p = 0.64$). For fertilizing, Hemiptera had significantly lower AWM in comparison to Araneae ($z = -3.03$, $p = 0.002$) and for mowing, Hemiptera had significantly lower AWM in comparison to Coleoptera ($z = -4.77$, $p < 0.001$) (Supporting information).

### Trait analysis

Mean body size (mm) of the species was negatively correlated with grazing AWM ($z = -2.47$, $p = 0.014$), meaning smaller species had their land-use niche at higher grazing intensities (Fig. 3). For mowing ($z = 3.25$, $p = 0.001$) and fertilizing ($z = 2.1$, $p = 0.035$), we found a positive correlation, meaning larger species had their land-use niche at higher land-use intensities.

Feeding guilds, grouped in carnivore, herbivore, mycetodetrivore and omnivore, were compared with the abundance-weighted means of the species and the land-use components (Fig. 4). For fertilizing, significant differences could be found ($H(2) = 14.75$, $p = 0.002$). Herbivorous species had significantly lower AWM in comparison to

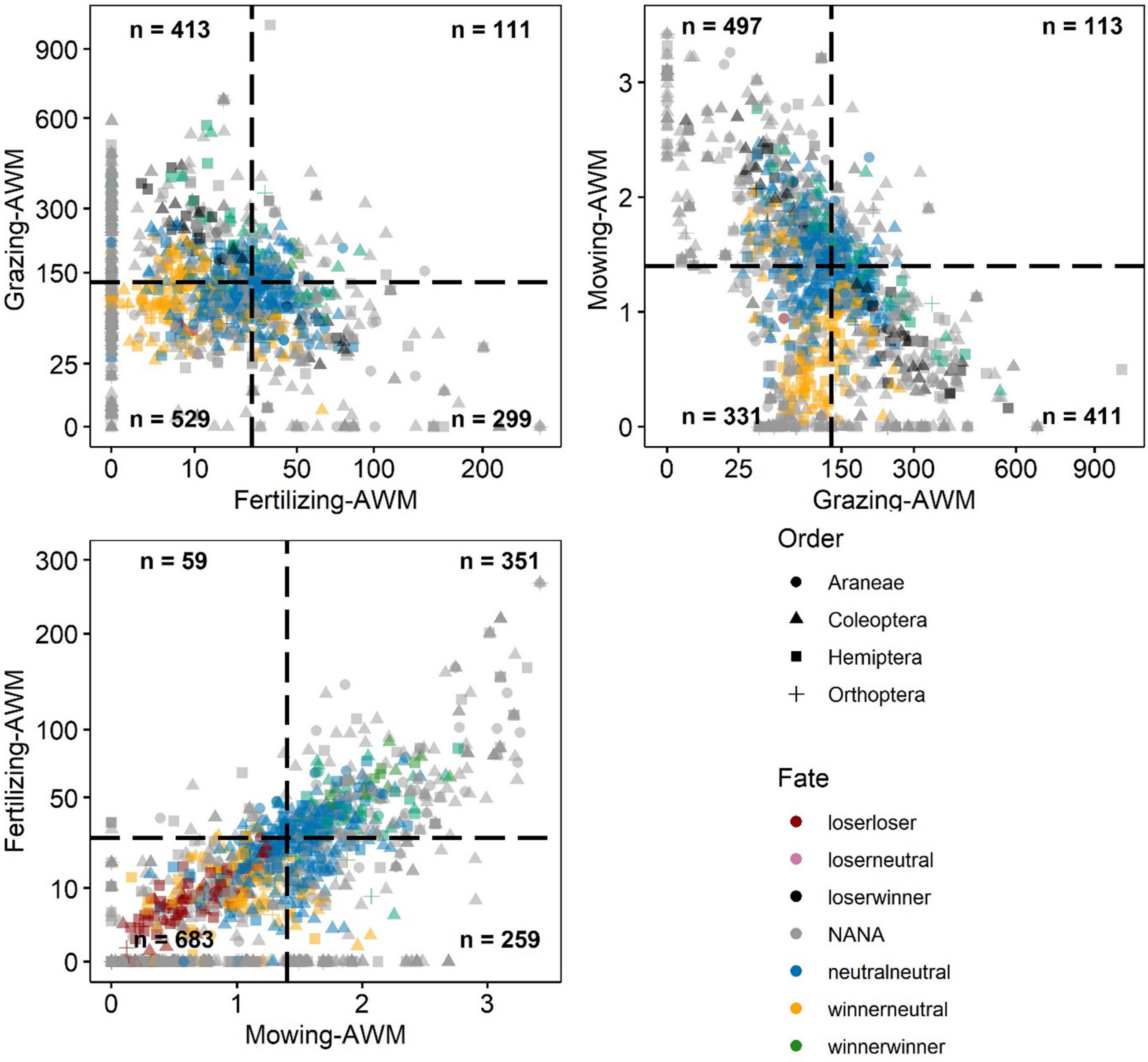

Figure 2. Correlation between the observed abundance-weighted means (AWM) for the land use components fertilizing (kg N ha$^{-1}$), grazing (LSU d ha$^{-1}$), and mowing (cuts ± impact of mowing regime) of 1352 species of the orders Araneae (circle), Coleoptera (triangle), Hemiptera (square), Orthoptera (plus). The dashed lines represent the mean land use intensity across plots (132 LSU d ha$^{-1}$ for grazing, 28.7 kg N ha$^{-1}$ for fertilizing and 1.40 cuts ± impact of mowing regime for mowing). Color depicts the matching fates of the compared AWMs: winner–winner = green, winner–neutral = orange, neutral–neutral = blue, neutral–loser = pink, loser–loser = red, winner–loser = black, NA = grey. In each quadrant, the total number of species (n) is provided. Fertilizing and grazing AWM are square-root transformed.

carnivorous species ($z = -3.34$, $p = 0.005$). For grazing ($H(2) = 0.58$, $p = 0.9$) and mowing ($H(2) = 5.42$, $p = 0.14$), no statistically clear differences between feeding guilds were observed.

### Conservation status

The effects of land-use intensity were particularly negative for arthropod species with higher-risk categories in the Red List (ranging from Least concern to Critically endangered) under mowing ($z = -4.85$, $p < 0.001$). For grazing ($z = -1.35$, $p = 0.18$) and fertilization ($z = -1.59$, $p = 0.11$) no clear effects could be found (Fig. 5).

In addition, the Red List-based short- and long-term population trends (classified as decreasing, stable or increasing) were compared with species' AWM of the land-use components (Fig. 6). Species with decreasing populations were predominantly associated with less intensively managed grasslands, characterized by lower mowing intensity for both short-term ($z = 3.98$, $p < 0.001$) and long-term population trends ($z = 4.5$, $p < 0.001$). For fertilizing, we found the

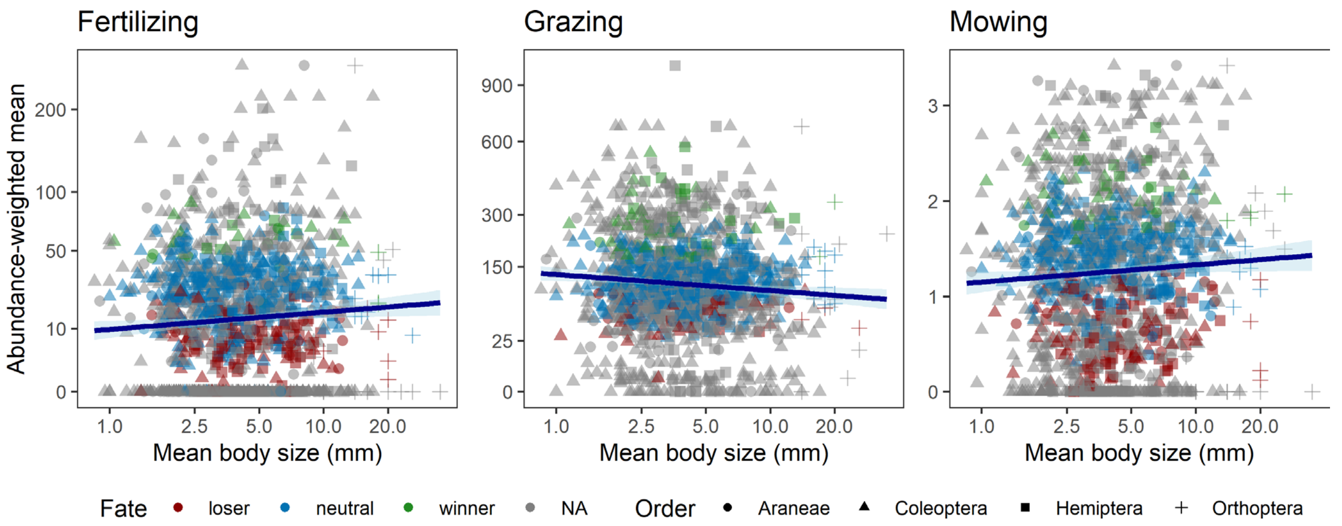

Figure 3. Mean body size (mm) with the abundance-weighted mean of fertilizing (kg N ha$^{-1}$), grazing (LSU d ha$^{-1}$), and mowing (cuts ± impact of mowing regime) for 1352 species of the orders Araneae (circle), Coleoptera (triangle), Hemiptera (square), Orthoptera (plus), showing losers (red), neutrals (blue), and winners (green); NAs are grey. Fertilizing and grazing AWM are square-root transformed, mean body size (mm) is log-transformed. Lines are model predictions with 95% confidence intervals; solid if the trend was significant.

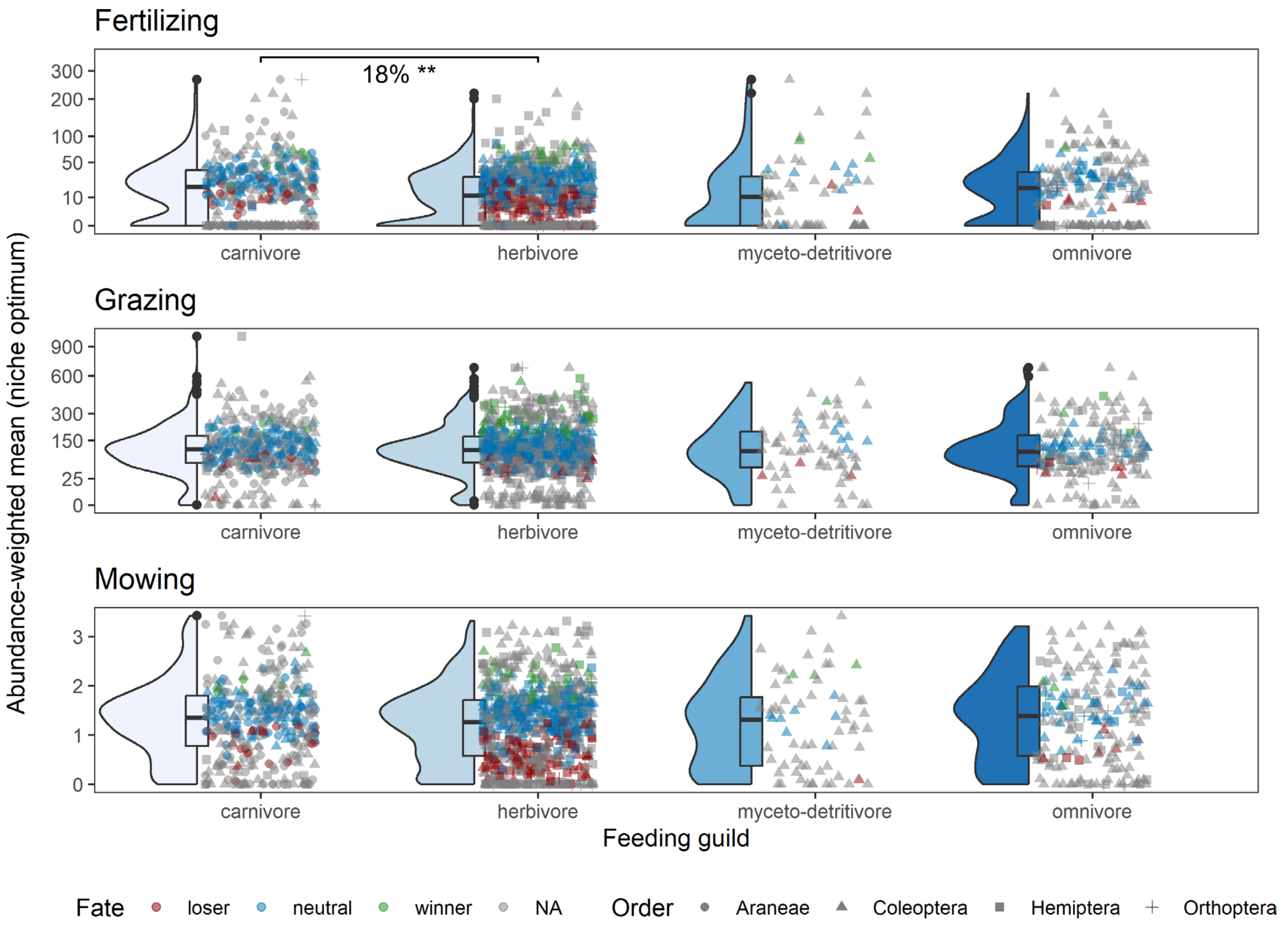

Figure 4. Feeding guilds with the abundance-weighted mean (niche optimum) of fertilizing (kg N ha–1), grazing (LSU d ha$^{-1}$), and mowing (cuts ± impact of mowing regime) for 1352 species of the orders Araneae (circle), Coleoptera (triangle), Hemiptera (square), Orthoptera (plus), showing losers (red), neutrals (blue), and winners (green); NAs are grey. Fertilizing and grazing AWM are square-root transformed.

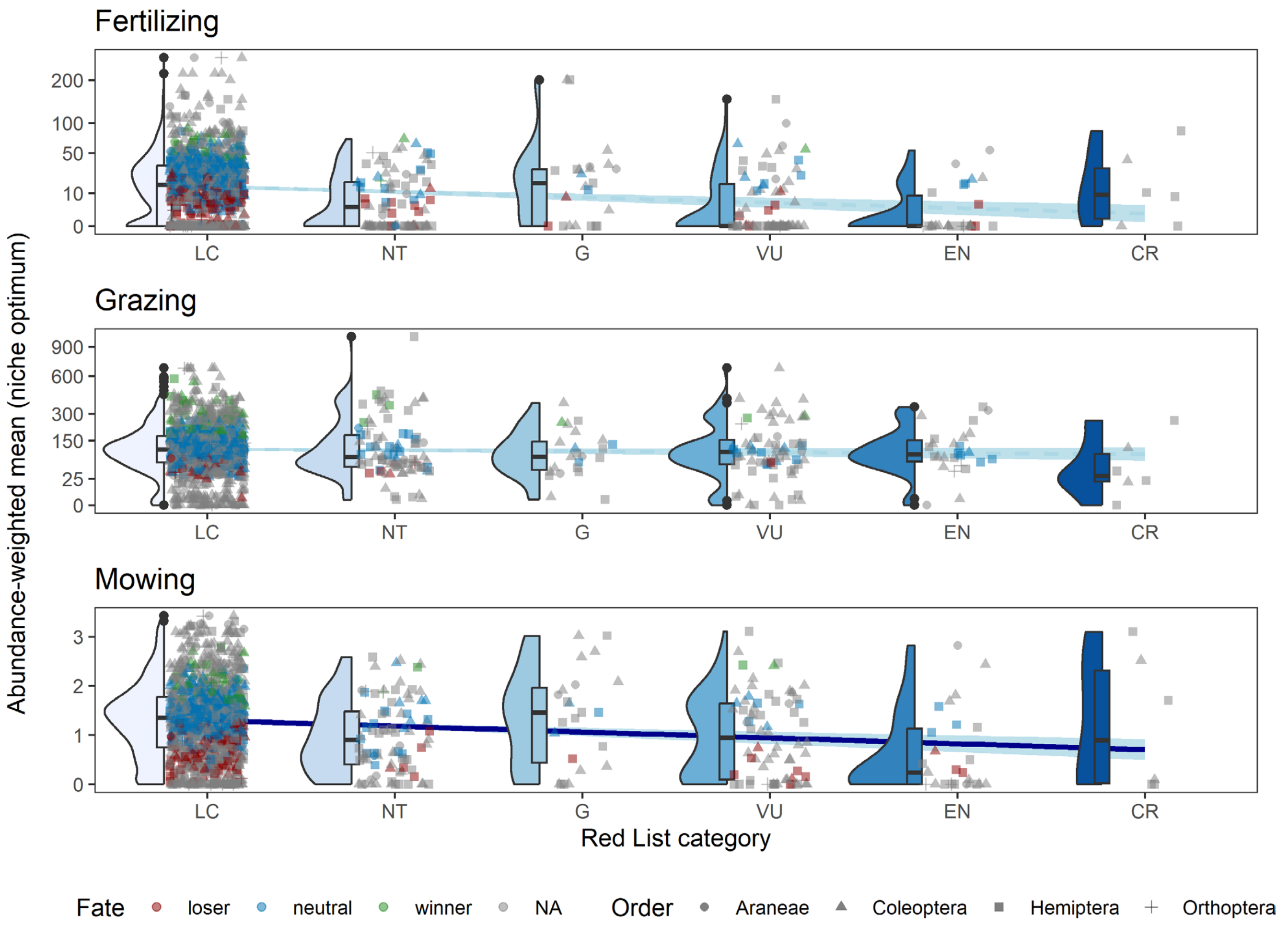

Figure 5. Conservations status (Red List categories) with the abundance-weighted mean of fertilizing (kg N ha$^{-1}$), grazing (LSU d ha$^{-1}$), and mowing (cuts ± impact of mowing regime) for 1352 species of the orders Araneae (circle), Coleoptera (triangle), Hemiptera (square), Orthoptera (plus), showing losers (red), neutrals (blue), and winners (green); NAs are grey. Red list categories: LC = Least concern, NT = Near threatened, G = Threatened to an unknown extent, VU = Vulnerable, EN = Endangered, CR = Critically endangered. Fertilizing and grazing AWM are square-root transformed. Lines are model predictions with 95% confidence intervals; solid if the trend was significant.

same significant effect just for long-term population trends ($z = 3.38$, $p < 0.001$), but not for short-term population trends ($z = 0.81$, $p = 0.42$). No clear effects were found for grazing (short-term: $z = 0.91$, $p = 0.363$; long-term: $z = 1.14$, $p = 0.25$).

## Discussion

To evaluate species-specific responses to land-use intensity, we applied a niche model (Chisté et al. 2016) to eleven years of species records covering 1352 species of Araneae, Coleoptera, Hemiptera and Orthoptera. Niche optima were calculated as abundance-weighted means and species were classified as winners, neutrals or losers based on their responses to fertilization, grazing and mowing (Blüthgen et al. 2012, Hartlieb et al. 2024). The method is inherently conservative, as species (also those occasionally colonizing unsuitable grasslands and which are sampled in low numbers) will only be identified as significant winners or losers when their observed abundance weighted means clearly exceeded the expected ones. This is particularly relevant because land-use components such as fertilization, grazing, and mowing alter plant composition and can reduce habitat diversity through nutrient input and biomass removal. These differences shape species-specific responses to land-use intensity of grassland communities, especially arthropods (Gossner et al. 2016). This can favor species that adapt to or benefit from intensified land-use, such as generalists with flexible ecological requirements (winners). In contrast, there are also species, often specialists, whose requirements are no longer met under intensified practices (losers) (Clavel et al. 2011, Mangels et al. 2017).

This study revealed that losers outnumber winners roughly 3:1 across all land-use components. This imbalance underscores the disproportionate negative effects of intensive land-use on these habitats, which are no longer suitable and contribute to insect declines (Wagner 2020).

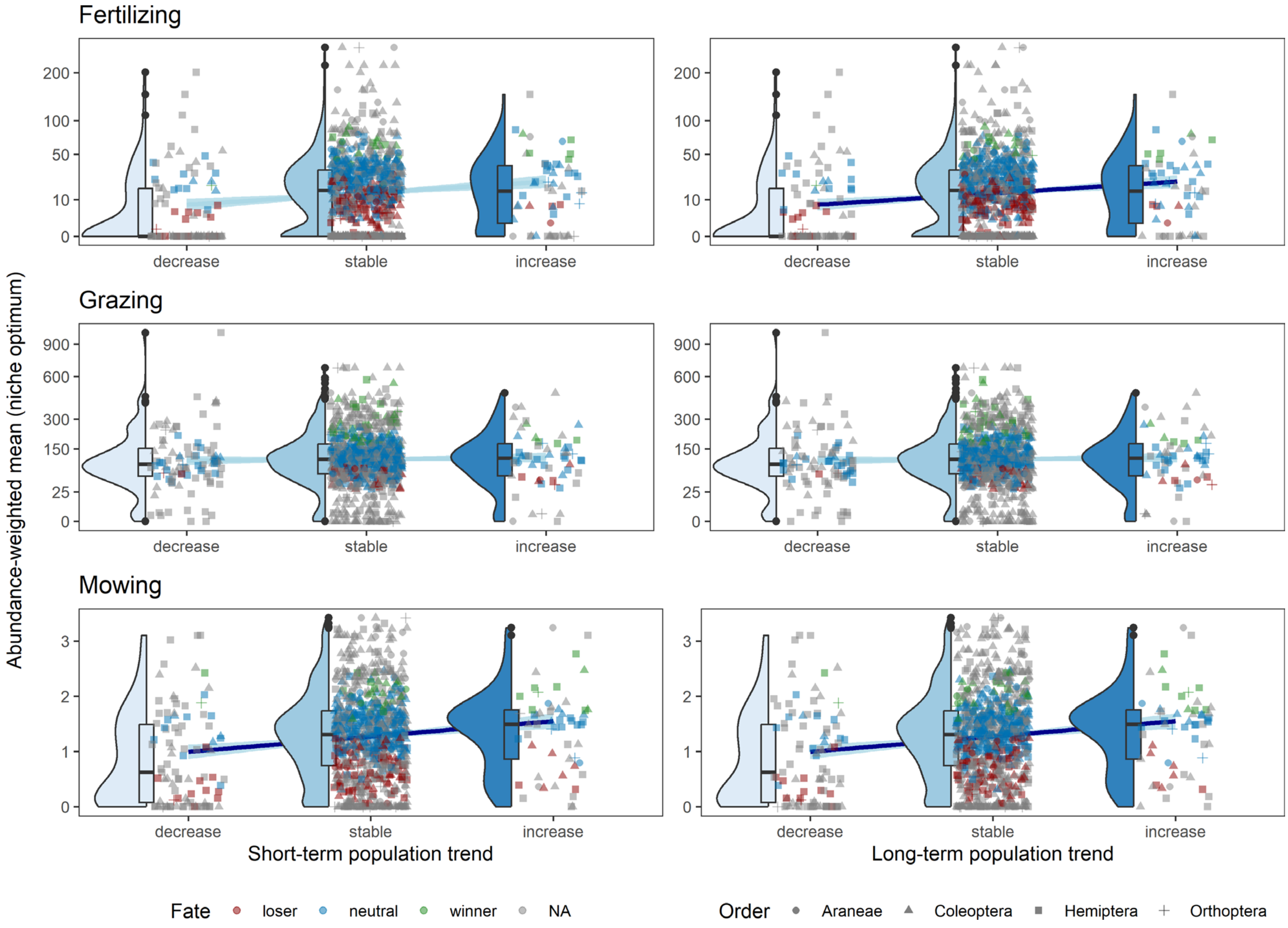

Figure 6. Short-term (last 10–25 years) and long-term (last 50–150 years) population trends (Red List) with the abundance-weighted mean of fertilizing (kg N $ha^{-1}$), grazing (LSU d $ha^{-1}$), and mowing (cuts ± impact of mowing regime) for 1352 species of the orders Araneae (circle), Coleoptera (triangle), Hemiptera (square), Orthoptera (plus), showing losers (red), neutrals (blue), and winners (green); NAs are grey. Fertilizing and grazing AWM are square-root transformed. Lines are model predictions with 95% confidence intervals; solid if the trend was significant.

Nevertheless, most species were classified as neutrals, suggesting either responding context-dependent shaped by specific management practices, having broader niches, or having adaptive traits buffering them against moderate land-use changes, as seen in moths (Mangels et al. 2017) and also in land snails (Wehner et al. 2021). We see that the response to intensification can further be mediated by species traits (Gossner et al. 2015). In our case, we found for grazing smaller, and for fertilizing and mowing larger species at higher niche optima, and herbivores in comparison to carnivores being particularly affected by fertilizing. A comparison with the Red List indicated that arthropod responses to lower niche optima under mowing were linked to higher-risk Red List categories, and with decreasing population trends. These results emphasise the need for targeted conservation efforts and stress the importance of implementing land-use strategies that promote habitat heterogeneity and support at-risk arthropod species to curb biodiversity loss.

## Winners and losers of land-use intensification

Fertilization emerged as the most harmful component for the investigated arthropod species and accounted for the highest proportion of losers and the fewest proportion of winners. This could be due to the fact that fertilizing, i.e. nutrient enrichment, increases plant cover, while reducing light in the understory, which further leads to a loss of plant species (Eskelinen et al. 2022). Lower plant diversity has significant implications for arthropods, as this translates into fewer resources for herbivores, which in turn cascades upward to affect carnivores (Schmitz et al. 2000, Simons et al. 2014), which we can also see in our results for the feeding guilds. Mowing showed similar results as fertilizing though not so drastic, as it directly modifies the physical structure of the habitat, impacting species sensitive to changes in vegetation height and density (Prather and Kaspari 2019). With mowing and the mechanical removal of flowering plant parts, flower visitors and pollinators, including those feeding on reproductive organs, are also negatively affected

(Ebeling et al. 2018). Grazing resulted in the highest proportion of winners and fewest losers, suggesting that it may create more heterogeneous environments that support a broader range of coexisting species (Palmer 1992). Grazing plays a major role in controlling plant diversity by alleviating competition for light, often surpassing the effects of fertilization (Eskelinen et al. 2022). However, insect diversity peaks under long-term ungrazed conditions, as intensive grazing leads to a greater decline in arthropod diversity, traditional grazing should be practiced (Kruess and Tscharntke 2002).

We found the highest proportion of losers among Hemiptera and Orthoptera indicating that these orders are particularly vulnerable to land-use changes, likely due to their specific ecological requirements (Chisté et al. 2016, 2018, Nickel and Hildebrandt 2003). This is also reflected in their Red List status. However, Orthoptera also exhibited by far the highest proportion of winners, which may reflect a more diverse range of responses within this group, with some species benefiting from the altered conditions (Chisté et al. 2016). Therefore, we compared the results of Chisté et al. (2016, 2018) with our results, which revealed significant positive correlations in species responses to fertilizing, grazing, and mowing for Orthoptera, and fertilizing and mowing for plant and leafhoppers. This highlights the consistency in the trends in species responses, underscoring the importance of long-term monitoring to support robust assessments of species responses to land-use intensity. However, there were also some species newly recorded and others undetected, indicating potential local extinctions from habitat unsuitability, or methodological effects, as partly different sampling methods might influence species detections (for more details see the Supporting information with the comparison of the results of the three studies).

### Land-use niche

The positive and negative correlations of the intensity of fertilizing, grazing and mowing (Vogt et al. 2019, Hartlieb et al. 2024) were reflected in the results of the AWM of the species. The negative correlation between grazing and fertilizing AWM, as well as grazing and mowing AWM indicates that these practices exert opposing pressures on species. Those benefiting from high fertilizing and mowing are disadvantaged by intensive grazing and vice versa. This may be due to the contrasting effects on vegetation structure and nutrient availability (Socher et al. 2013). Fertilizing typically enhances plant productivity and biomass, while decreasing plant species diversity (Shi et al. 2024). Grazing tends to reduce plant height and density, while promoting heterogeneity by creating patches of varied vegetation structure (Tahmasebi Kohyani et al. 2011). Mowing tends to homogenize the landscape by cutting vegetation uniformly. All components are favoring the abundance of different species and the differing ecological niches that species occupy in response to these land-use practices (Simons et al. 2017, Berger et al. 2024). The positive correlation between species of the fertilizing and mowing components suggests these practices create similar conditions that lead to an increase in certain fast-growing plant species (Raubitzek et al. 2025), which creates favorable conditions for the same arthropod species (Simons et al. 2014).

### Trait analysis

We further showed that species responses were mediated by their organismic traits by looking at body size and feeding guilds. Regarding body size, grazing appears to act as a selective pressure favoring smaller species. This pattern indicates that grazing acts as disturbance, which reduces vegetation density and increase habitat heterogeneity with specialized plants (Kapás et al. 2024). The remaining patches of taller vegetation are important microhabitats for arthropods, and smaller species, mostly for Hemiptera, which are mainly herbivores and have larger population sizes with shorter developmental times (Denno and Roderick 1991, Biedermann 2002). In comparison, fertilizing and mowing act as a selective pressure favoring larger species. After the disturbances with the machines, larger species, for example Orthopterans, might be able to relocate more easily than smaller species, as they are better in recolonising the area (Chisté et al. 2016).

Regarding feeding guilds, the clear negative response of herbivorous (mostly Coleoptera and Hemiptera) compared to carnivorous insects (mostly Araneae and Coleoptera) to fertilizing underscores the strong influence of nutrient enrichment on species that depend on diverse plants species (Neff et al. 2019). A high herbivore diversity is associated with a high plant diversity that provides diverse resources with more niches, in particular for specialized species (Simons et al. 2014). Fertilization reduces resource heterogeneity and consequently leads to a decrease in herbivores, which exhibit a great degree of dependence on vegetation (Welti et al. 2017). Carnivores, which depend more on prey abundance, may be more affected by the cascading effects of land-use on herbivore populations than by direct effects on vegetation (Schmitz et al. 2000).

### Conservation status

A comparison with Red List categories revealed that species sensitive to mowing had lower niche optima and were associated with higher-risk categories. This suggests that species sensitive to mowing are experiencing substantial threats, here Miridae and Curculionidae were particularly affected. This aligns with findings that plants and invertebrates face higher extinction risks under intensive agricultural practices (Hochkirch et al. 2023) and these species, mostly specialists, may be experiencing ongoing population declines (Simons et al. 2015). These findings are consistent with our results on short- and long-term population trends, which show that mowing had the strongest negative impact on decreasing populations across both time scales, while fertilizing was associated with the negative impact on decreasing populations only in long-term population trends. In both cases, species with increasing populations had higher niche optima, meaning that those species were in general more resilient to altered habitat conditions with higher intensities of mowing and fertilizing, due to nutrient enrichment and biomass removal. They likely represent more generalist or adaptable species, as seen in moths (Mangels et al. 2017) and also in land snails (Wehner et al. 2021). This resilience could be due to broader ecological niches or adaptive traits that allow them to thrive in more managed landscapes (Clavel et al. 2011). This means that stability does not always equate to resilience, and some species may be at the threshold of extinction while others thrive (Holling 1973). However, the absence of any effects for grazing could reflect the variability in grazing regimes, allowing more species to persist without population shifts (Kruess and Tscharntke 2002).

## Conclusion

This study provides valuable insights into the stability and vulnerability of arthropod species under anthropogenic pressures in grassland ecosystems caused by fertilizing, grazing, and mowing through its large-scale and long-term approach. Using a niche model enables a nuanced classification of ecological responses, whereby we identified three times more losers as winners, with the majority of species classified as neutral. This highlights the disproportionate negative effects of intensive land-use, though neutral species may possess adaptive traits or broader ecological niches that buffer them against the adverse impacts of moderate land-use changes. Fertilizing and mowing proved particularly detrimental to arthropods, whereas grazing often had more beneficial effects. By linking niche modeling with trait-based analyses and Red List statuses, our study integrates ecological and conservation perspectives. This underscores the urgent need for targeted conservation measures that prioritize loser-species with lower ecological tolerances, many of them which are at high risk. For instance, adopting low-input fertilization practices, implementing rotational grazing, and reducing the frequency and intensity of mowing, while leaving unmown refuges for arthropods, could help prevent further declines. By adopting management practices that maintain habitat heterogeneity, it is possible to mitigate the loss of arthropod diversity while promoting ecosystem resilience in grasslands. Integrating biodiversity conservation into agricultural policies offers a pathway to balance productivity with the preservation of ecosystem health.

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### Author contributions

**Margarita Hartlieb**: Conceptualization (equal); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Michael Staab**: Data curation (lead); Supervision (equal); Writing – review and editing (supporting). **Johanna L. Berger**: Visualization (supporting); Writing – review and editing (supporting). **Rafael Achury**: Writing – review and editing (supporting); Data curation (supporting). **Martin M. Gossner**: Data curation (supporting); Writing – review and editing (supporting). **Sebastian Seibold**: Data curation (supporting); Writing – review and editing (supporting). **Wolfgang W. Weisser**: Data curation (supporting); Funding acquisition (equal); Writing – review and editing (supporting). **Nico Blüthgen**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (supporting).

### Data availability statement

Data are available from the Biodiversity Exploratories Information System https://doi.org/10.71615/bexis.32057 (Hartlieb et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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