Land use intensification transforms grassland arthropod communities: A few winners expand but most species disappear

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ABSTRACT

Arthropod declines pose existential threats to terrestrial ecosystems but remain poorly understood. In human-dominated habitats such as managed grasslands, arthropod communities are thought to decline as a result of land-use intensification. However, studies that link land-use intensity to arthropod species richness, abundance and composition have found mixed results. These inconsistencies may stem from differences in the investigated intensification levels or arthropod communities, as different species may show different responses to land-use change. We show that effects of land-use intensification on arthropod communities can be understood better by examining the distributions of individual species along land-use intensity gradients. We sampled multiple arthropod groups along a wide gradient of grassland productivity as a proxy for land-use intensity. Species richness halved from low to high productivity levels, but overall abundance remained stable because increasing Diptera numbers counteracted strong declines in other orders. Dissimilarity metrics failed to reveal a substantial change in species composition that was shown in individual species' distributions. While low-productivity grasslands supported many species that were confined to narrow productivity ranges, high-productivity grasslands were dominated by a few widely occurring species. Overall, 56 % of all species declined or disappeared as land-use intensified at low-to-medium intensity levels ('losers'); 35 % preferred intermediate intensities, and only 9 % profited from high-intensity management. These 'winners' probably sustain overall abundance levels in high-productivity grasslands. Such large changes in species composition could have significant consequences for ecosystem functioning, necessitating further experimental studies. The uneven distribution of biodiversity losses implies that ecological restoration should focus on low-intensity grasslands.

1. Introduction

Arthropod populations in human-dominated landscapes have significantly declined in the recent past (Benton et al., 2002; Hallmann et al., 2017; Van Klink et al., 2020; Wagner, 2020). As the most abundant and diverse faunal life form (Stork et al., 2015), arthropods are central to trophic networks and ecosystem functions such as nutrient cycling and pollination (Cardinale et al., 2012; IPBES, 2019; Potts et al., 2016). Therefore, the revelation of drastic arthropod declines has been cause for alarm (Cardoso et al., 2020; Goulson, 2019). Many studies have attributed these declines to ongoing land-use intensification, causing habitat loss, declines of critical resources (e.g. through plant

diversity decline), increased disturbances and landscape simplification (Gossner et al., 2016; Harpole et al., 2016; Raven and Wagner, 2021; Seibold et al., 2019). Yet, most arthropods are challenging to survey and systematic long-term monitoring schemes exist for only a few arthropod groups (Van Swaay et al., 2025; Warren et al., 2021). Hardly any multi-decadal records of other arthropods exist, and those available may reflect already degraded reference situations or sampling locations that are not representative of environmental changes in the wider landscape (Cooke et al., 2025; Montgomery et al., 2020; Wagner et al., 2021). As a result, the effects of land-use intensification remain poorly understood for a wide range of different arthropod groups.

Studying arthropod diversity along spatial gradients in land-use

intensity provides a way to accelerate our understanding of intensification-driven changes to arthropod assemblages (Cooke et al., 2025; Wagner, 2020). Alternative to time series, biodiversity patterns along spatial gradients are more readily obtained and can provide more direct accounts of the drivers of biodiversity change (Blüthgen et al., 2022; Cardinale et al., 2018). Gradient studies may include ecologically degraded locations that are rarely part of existing long-term studies (Wagner et al., 2021), and can be considered proxies for changes over time, such as the shift from traditional extensive land management to modern intensive agriculture that occurred over the past century in Europe and other temperate regions (Bardgett et al., 2021; Emmerson et al., 2016). Global syntheses have indicated that land-use intensification is especially impacting biodiversity in grassland habitats (Newbold et al., 2015, 2016). While extensively used grasslands are known hotspots of arthropod diversity in temperate regions (Bardgett et al., 2021; Habel et al., 2019), steep declines of species richness with land-use intensity were shown among several groups of grassland arthropods, such as wild bees (Ekroos et al., 2020), Araneae, Hemiptera, Coleoptera and Orthoptera (Allan et al., 2014; Simons et al., 2015).

However, there have also been many studies that found no relation between land-use intensity and species richness (Beckmann et al., 2019). This might be due to non-linearity along the full land-use intensity gradient, as species richness losses were shown to be most profound under intensification at low intensity levels that might be missed by studies in more intensively used landscapes (Allan et al., 2014; Kleijn et al., 2009, 2011). The lack of relationships with species richness may also be influenced by the limitations of using species richness as the main response variable, notably because it does not capture changes in species composition (Chase and Knight, 2013; Hillebrand et al., 2018; Kuczynski et al., 2023). More detailed quantitative data of arthropod communities can uncover changes in species assemblages or arthropod abundances. These metrics are increasingly assessed in biodiversity studies, but also show contrasting results. Land-use intensification has been linked to biotic homogenization (i.e. increasing similarity of species assemblages between sites) across multiple taxonomic groups in European grasslands, amplifying biodiversity decline at landscape scales (Chisté et al., 2018; Gossner et al., 2016). But metrics of community dissimilarity have also revealed widespread patterns of biotic differentiation in response to land-use change (Dornelas et al., 2023; Keck et al., 2025). Furthermore, abundances of grassland arthropods have shown stronger declines than species numbers (Seibold et al., 2019; Van Strien et al., 2019), but have also been found to increase with land-use intensity (Kleijn et al., 2010; Silva-Monteiro et al., 2022). This suggests that there are also arthropods that can cope with or even profit from land-use intensification.

The contrasting results of these different studies relating changes in arthropod communities to land-use intensification might result from changes in species composition that the most commonly used community indicators failed to capture. To date, most studies aggregate the responses of many different arthropod species or entire groups into common metrics of species richness, total abundance or community dissimilarity (Cooke et al., 2025). But while species richness does not reflect changes at community and population levels (Hillebrand et al., 2018), total abundance may be largely driven by a few abundant arthropod species (Shortall et al., 2009). Furthermore, dissimilarity (beta-diversity) metrics aggregate differences that arise from the turnover of unique species (Legendre, 2014), but also from stochastic drift (e.g. dispersal outside species' reproductive habitats) and from increased fragmentation of species distributions (Araújo et al., 2022; Chase et al., 2019; Wayman et al., 2024; Zhou et al., 2022). In reality, arthropods exhibit vast ecological differences, and the effects of land-use intensification probably differ widely between arthropod groups and species. Certain species may profit from the decline of other species or from increased resource availability in intensively managed systems, e.g. when feeding on plant matter or manure (Simons et al., 2014; Simons and Weisser, 2017), and the prevalence of such species may differ

between arthropod groups (Powell et al., 2024; Simons et al., 2014). It is critical to understand which species lose and which species win under changing environmental conditions (Boyes et al., 2019; Dornelas et al., 2023; Wagner, 2020). Hence, land-use intensification-driven shifts in arthropod communities can probably be better understood by assessing the responses of individual species.

In this study, we quantified the changes in grassland arthropod communities along a land-use intensity gradient in the Netherlands. Ranging from low-productive unfertilized hay meadows to highly productive and heavily fertilized silage fields, this gradient reflected the entire range of grassland management intensities within one study region and arguably covers the variation in grassland management intensity throughout much of northwestern and central Europe. We asked whether the relationships between land-use intensity and arthropod abundance, species richness and community dissimilarity differ between the main above-ground arthropod orders. Furthermore, we asked whether responses of arthropod communities to land-use intensification can be better understood by examining the responses of individual species than by examining aggregate indices such as species richness or beta diversity. We addressed this question by analyzing the distributions of individual species along the sampled land-use intensity gradient.

2. Methods

2.1. Study sites

Data were collected in a study area situated in the valley of the river Geul in the south of the Netherlands (between 50°48'09"N, 5°49'46"E and 50°53'30"N, 5°56'24"E) (Fig. S1). This area is a regional hotspot of grassland biodiversity, supporting various grassland types on fine clay and loess soils with locally more lime-rich conditions (Willems, 2001; Wösten et al., 2013). Here, differences in land-use intensity are mainly the result of management targeting either nature conservation, biodiversity-friendly agriculture, or optimizing agricultural production. We selected 41 grasslands that represented the widest possible gradient in land use intensity (see Table S1 for specifications). Study sites included i) unfertilized nutrient-poor semi-natural grasslands that were mown once per year; ii) hay meadows in protected areas and iii) hay meadows under agri-environment schemes, both of which were cut twice a year or had limited grazing rates (<2 LSU.ha^{-1}) and no fertilizer inputs; iv) pastures used for grazing or fodder production for suckler cows or organic dairy cows, with intermediate fertilizer inputs (50-150 kg N$_{eff}$.ha^{-1}.yr^{-1}); and v) conventional dairy cow fodder production grasslands with up to six cuts per year and high fertilizer inputs (up to 330 kg N$_{eff}$.ha^{-1}.yr^{-1}). This gradient represents the entire range in grassland management intensity that is present in large parts of temperate Europe where historically, grassland habitats evolved as semi-natural systems maintained by extensive human management (mowing or grazing), which has been steadily replaced by high-input management for maximum productivity (Emmerson et al., 2016; Habel et al., 2013). The sampling sites were on average 778 ± 428 m apart and showed no spatial pattern in productivity (Fig. S1). We quantified annual productivity in terms of net metabolic energy for livestock [GJ.ha^{-1}.yr^{-1}] as an indicator of land use intensity that reflects both biomass production and forage quality, facilitating the direct comparison of different management regimes. Annual biomass production (dry yield in tons) was collected through interviews with farmers and land owners, and was multiplied by the standard energy content values of different forage types (4.1 GJ.t^{-1} for low-quality hay; 5.2 for high-quality hay; 5.9 for extensive grazing; 6.2 for conventional silage; 6.4 for conventional silage, first cut; 6.6 for conventional grazing) (CVB, 2022; Schippers et al., 2012).

2.2. Arthropod sampling

We used sweep-net sampling to collect a broad range of arthropod

groups along a 150-meter transect in each grassland. Transects were pre-defined and ran from edge to center of the grasslands. We conducted 70 1-m-wide single-sweeps per part of 50 m in June and July, but 160 in May, because we expected that this would produce a roughly similar total arthropod abundance in each month. Sweep-netting is a suitable method for representative field-scale sampling of vegetation-dwelling arthropods, including herbivores and predators, but underestimates the presence of fast-flying pollinators (Simons et al., 2014; Spafford and Lortie, 2013). Therefore, additional counts of bees (Anthophila) and hoverflies (Syrphidae) were obtained along the same transect during 15-minute pollinator walks (5 min per 50 m), surveying a width of 1 m (Scheper et al., 2015). Pollinator surveys were done on the same day but prior to sweep-netting to minimize disturbance. Both methods were conducted between 10:00 and 17:30 and under suitable weather conditions (temperature >15 °C, wind <3 Bft, sunshine >50 %) (Westphal et al., 2008). Pollinators were counted in the field and collected only when they could not be identified to species level on the wing, while sweep-net samples were collected in zip-lock bags and stored frozen. Afterwards, (sub)order-level abundance counts were obtained for adult Diptera, Auchenorrhyncha, Heteroptera, Hymenoptera, Coleoptera, Araneae and Orthoptera (other arthropod orders occurred in low numbers but were included in total abundance counts, while Sternorrhyncha, Thysanoptera, Acari and Collembola were not included in the counts). Pollinator counts were combined with the sweep-net data to complement the assessments of both pollinator groups, primarily regarding species diversity. Count data represented over 80 % of all individuals of both bees and hoverflies, but only 6 % and 1.4 % of the total abundance of Hymenoptera and Diptera recorded.

Furthermore, we obtained species identities for all specimens belonging to Heteroptera, Araneae and Orthoptera, and for subgroups of Hymenoptera (Anthophila, Formicidae), Coleoptera (Cantharidae, Chrysomelidae, Coccinellidae, Elateridae) and Diptera (Asilidae, Bibionidae, Conopidae, Opomyzidae, Platystomatidae, Rhagionidae, Sciomyzidae, Stratiomyidae, Syrphidae, Tabanidae, Tephritidae, Tipulidae, Ulidiidae). Species were identified with help of the citizen science platform Waarneming.nl and relevant identification keys (references are given in Table S2). In a few cases, identification was limited to genus or species-pair level. The selection of subgroups for species identification aimed to cover a broad range of taxonomic and ecological groups, while the inclusion of additional species groups was mainly constrained by lack of suitable identification keys or taxonomic expertise.

2.3. Data analyses

The individual samples (nine per site, referring to the three transect sections over three rounds) were summed (abundance data) or aggregated (species identity data) to obtain site-level estimates of abundance and species richness, with abundances being corrected for the increased sweep-netting effort in May and for one missing sample. We checked sampling completeness with the Jacknife-1 estimator of total richness, which was derived using R-packages 'BiodiversityR' and 'vegan' (Kindt and Coe, 2005; Oksanen et al., 2024). Sampling completeness ranged between 60 and 80 % and showed no trend with productivity. This indicates that more species-rich communities were sampled roughly as complete as simpler communities, and we therefore used the original data in our analyses. Abundance counts over all arthropods and of the seven (sub)orders, and observed richness over all identified groups and of Diptera, Heteroptera, Anthophila, Coleoptera, Araneae, Orthoptera and Formicidae, were related to productivity (metabolic energy) as a single explanatory variable. We used generalized linear models with generalized Poisson or negative binomial distributions to account for overdispersion, using R-package 'glmmTMB' (Brooks et al., 2017). Nonlinear relations were evaluated by the statistical support for quadratic and cubic model terms, which were kept if notably improving the model ($\Delta AIC_c > 2$), using R-package 'MuMIn' (Bartoń, 2023). Model residual patterns were validated using R-package 'DHARMa' (Hartig, 2022).

Non-normal residual patterns were prevented by the selected distributions and residuals were not correlated with land use factors outside the model (silage or hay production, mowing or grazing, grass-to-forb ratio), hence no additional covariates or random effects were included in the models.

We investigated community dissimilarity (beta-diversity) within classes of low productivity (4-21 GJ.ha^{-1}.yr^{-1}: 14 sites), medium productivity (21-48 GJ.ha^{-1}.yr^{-1}: 13 sites) and high productivity (48-91 GJ.ha^{-1}.yr^{-1}: 14 sites). Beta-diversity was quantified by Jaccard's dissimilarity index and was partitioned into components of replacement (true niche differentiation) and richness or abundance differences (loss or gain) (Legendre, 2014), following both abundance-based (Bray-Curtis) and incidence-based approaches, using R-package 'BAT' (Cardoso et al., 2015). We derived all possible unique comparisons of pairs of sites within one productivity class. The dissimilarity levels of adjacent classes were compared with Dunn's tests, using Bonferroni's adjustment of p-values and a threshold of $p = 0.01$ to account for the large number of comparisons, using R-package 'rstatix' (Kassambara, 2023).

To better understand how the relationships between land-use intensity and arthropod abundance, species richness and community dissimilarity were shaped by the responses of individual species, we performed additional analyses based on the center points of the distributions of individual species along the land-use intensity gradient. In line with Chisté et al. (2016), we calculated these center points as abundance-weighted means, i.e. the mean productivity (P_{mean}) over all sites (i-n) for a particular species (j) weighted by its abundance at each site (x_{ij}), using the following formula:

$$P_{mean}(j) = \frac{\sum_{i=1}^{n} x_{ij} \cdot P_i}{\sum_{i=1}^{n} x_{ij}}$$

Next, we excluded singletons (i.e. species with single observations over all samples), and classified all remaining species based on whether their center point was located at low, medium or high productivity (using the same classes as the community dissimilarity analysis). The species that were centered at low productivity levels were regarded as species 'losing' under land use intensification (their numbers decreased as land use intensified), while species centered at medium productivity levels were regarded as 'intermediate' and species centered at high productivity levels were regarded as 'winning' (their numbers increased as land use intensified). We then calculated the percentage of losing, intermediate and winning species in each taxonomic group. These percentages were compared to a simulation of 10.000 randomized distributions of species along the productivity gradient (i.e. assuming no consistent effect of productivity on species distributions). Randomized distributions were constructed by randomly rearranging the recorded counts of each species over all 41 sampling sites, thus maintaining each species' original counts. Subsequently, we recalculated each species' center point and derived the randomized percentages of losing, intermediate and winning species (i.e. the percentage of center points falling in each productivity class). The density curves of the 10.000 randomized percentages then allowed us to statistically test for differences with the measured percentages of losing, intermediate or winning species at the community level.

Finally, we assessed how the measured and randomized percentages of losing, intermediate and winning species changed with the distribution width of species. For this the percentages of losing, intermediate and winning species were calculated for subsets of species that had been recorded at an increasing minimum number of sites (range from 1 to 33, as above this number, too few species (<14) remained to reliably estimate percentages). We used saturation curves to model how the percentages of losing, intermediate and winning species changed while increasing the minimum number of occurrences, and assessed the differences between the measured and randomized data. All data analyses were performed in R 4.5 (R core team, 2025) and can be found in a Zenodo repository (De Vries et al., 2025).

3. Results

3.1. Abundance versus species richness

We collected nearly 170,000 specimens in total and identified 27,200 individuals (16 %) to species level, representing 520 species. Over all orders, total abundance did not change significantly with productivity, whereas observed species richness across all identified subgroups declined exponentially ($p = 0.01$) (Fig. 1A, C; Table S3). Total richness did not change markedly in the medium-to-high productivity range ($\pm$ 45-90 GJ.ha^{-1}.yr^{-1}), but was approximately halved from the lowest to medium productivity levels. Richness declines were found for all subgroups except Coleoptera (no trend; $p < 0.01$ for all other subgroups) and were exponential for Heteroptera and Araneae (Fig. 1D, Fig. S2B). Abundance declined significantly with productivity for Auchenorrhyncha (unimodal), Heteroptera (exponential), Araneae (cubic), Coleoptera and Orthoptera, but Hymenoptera abundance remained stable, and Diptera abundance increased significantly with productivity ($p < 0.01$) (Fig. 1B, Fig. S2A, Table S3). Being the most numerous group (46 % of all specimens), the increase in Diptera was almost as large as the decline in abundance of all other orders combined. However, only subgroups of Diptera and Hymenoptera were identified to species level and the abundance of these subgroups did not follow the whole-order trends but declined with productivity (exponential for the identified Diptera) (Table S3).

3.2. Community dissimilarity

Species assemblages of different grasslands differed markedly, particularly when differences in abundance were taken into account. Total abundance-based beta-diversity estimates over all species and for most groups were above 0.8, while incidence-based beta-diversity estimates were mostly between 0.6 and 0.8 (Table S4; class averages). However, dissimilarities between sites were generally high in both low-, medium- and high-productivity classes (4-21, 21-48 and 48-91 GJ.ha^{-1}. yr^{-1}, respectively). The majority of the beta-diversity differences between adjacent productivity classes were not significant and when differences were significant, they did not show a consistent increase or
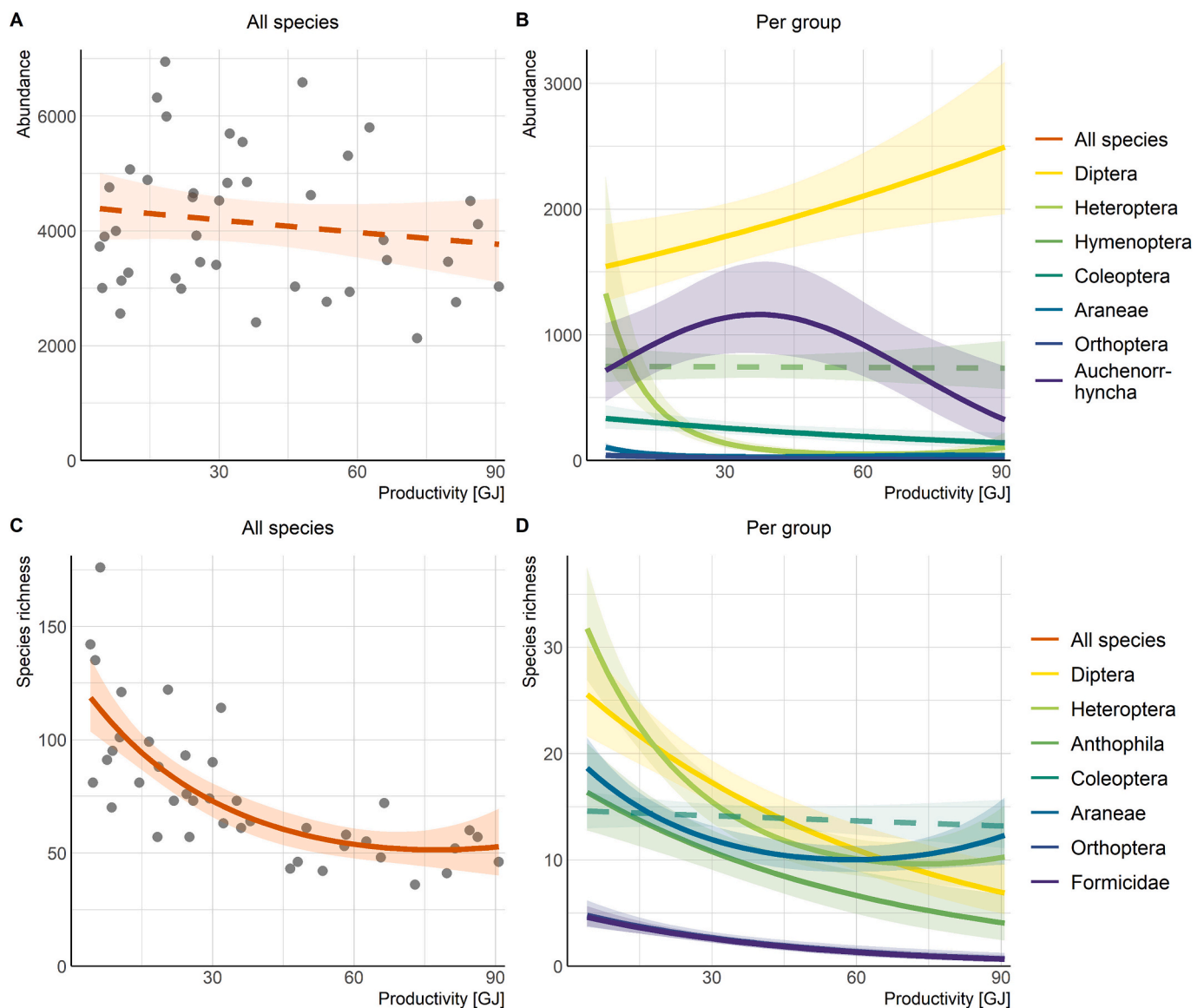
Fig. 1. Relations of arthropod abundance and observed species richness with grassland productivity [GJ.ha^{-1}.yr^{-1}]. Significant relations are shown in solid lines with 95 % confidence intervals (ribbons). Total arthropod abundance was not related to productivity (A), but different (sub)orders showed contrasting relations including an increase of Diptera abundance (B). Total observed species richness was derived over subgroups within each order that were identified to species level, and declined exponentially with productivity (C). This decline is reflected in all analyzed groups except Coleoptera (D).

decrease with grassland productivity (Table S4; class comparisons). Over all species, replacement averaged 0.5 in both abundance-based and incidence-based approaches, and was more important than richness or abundance differences (average 0.17 resp. 0.35). At group level, abundance-based dissimilarities were dominated by abundance differences in Anthophila, Heteroptera, Formicidae and Orthoptera (the last two groups being rather species-poor), while incidence-based dissimilarities were mostly driven by species replacement. Neither replacement

nor richness or abundance differences showed a consistent trend with grassland productivity.

3.3. Distributions along the land-use intensity gradient

Most species had the center of their distribution in low productivity grasslands (Fig. 2), meaning that they are declining under land use intensification from low to medium intensity levels. These 'losing'
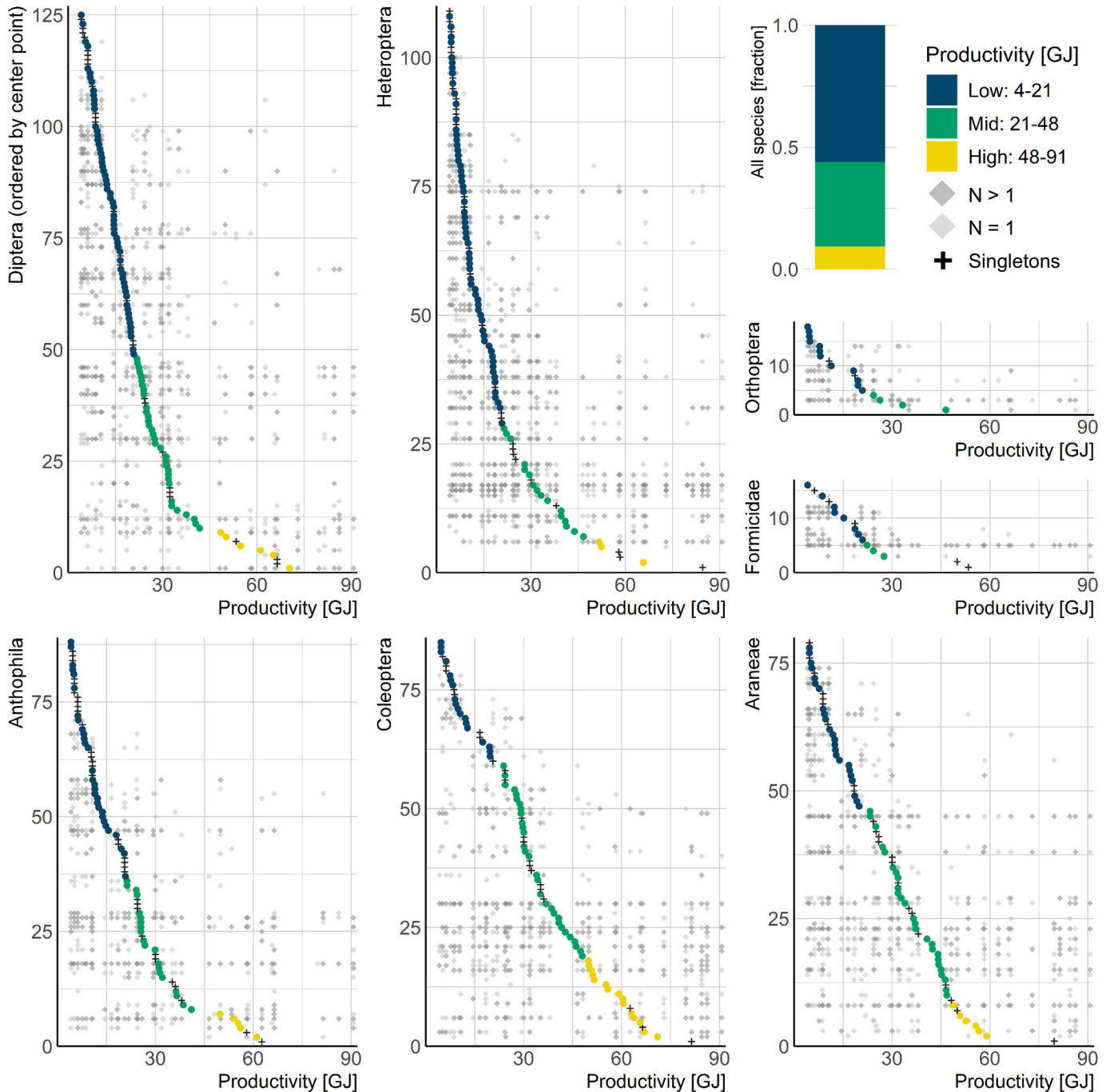

Fig. 2. Species distributions along the land use intensity gradient expressed in terms of grassland productivity [GJ.ha^{-1}.yr^{-1}]. The center point of each species' distribution was calculated as the productivity at which the abundance-weighted mean of all specimens occurred (colored dots). Species are ordered on the y-axis from high to low by increasing center points, with singletons (i.e. one record over all sites) indicated as crosses. Non-singleton species were classified by center point into low, middle and high productivity classes (representing losing, intermediate and winning species, colored in blue, green and yellow respectively; classes represent 14, 13 and 14 sites respectively): The bar plot shows the fraction of species centered in each productivity class over all species. Grey dots show all sites where a species was recorded (single records in light grey, higher numbers in dark grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species represented 56 % of the 380 species that were observed with two or more individuals, whereas 35 % were intermediate species (centered at medium productivity) and 9 % were winning species (centered at high productivity). These percentages contrast markedly with the randomized species distributions that assumed no relation with productivity, in which on average 62 % (95 %-Confidence Interval ±6) of all species were classified as intermediate species, while winning species represented 22 % (±5) and losing species represented 16 % (CI ±5) of all species (Fig. 3A-B). The observed percentage of losing species was 1.8 times higher than this mean randomized percentage for Coleoptera (29 % of species), 3.6 times higher for all species, and nearly five times higher for Hemiptera, Formicidae and Orthoptera (each >70 % of species) (p < 0.0001 for all groups). On the other hand, for all groups except Coleoptera the empirically observed percentage of winning species was

2-6 times lower than what would have been expected based on randomized distributions (p < 0.0001 for all other groups) (Fig. 3B).

Furthermore, most losing species were entirely restricted to low productivity levels or were only incidentally recorded at higher productivity levels (Fig. 2: reflected by a lack of points in the upper-right area for each subgroup). For 110 species (29 % of all species excluding singletons) more than 90 % of the specimens were observed at low-productivity sites, and for 242 species (64 %) this was the case for sites of low to medium productivity. 57 species (15 %) were recorded proportionately (i.e. at least 33 % of specimens) at high-productivity sites. High-productivity sites were dominated by species that were recorded widely across the productivity gradient (Fig. 2: reflected by a broad spread of points in the lower area for each subgroup) and supported very few range-restricted species: Only five species were
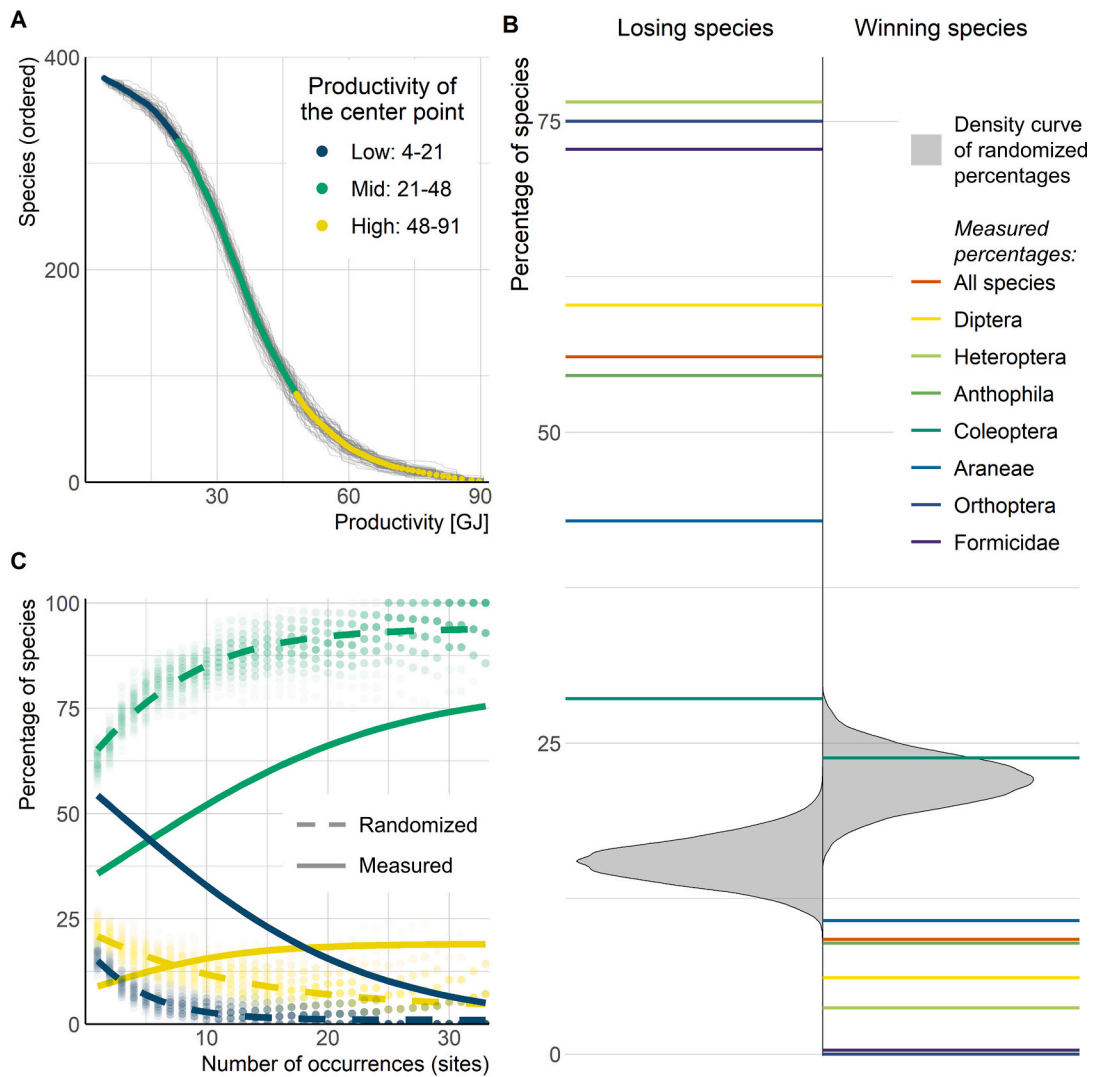
Fig. 3. The measured percentages of losing, intermediate and winning species (i.e. species centered at low, medium or high productivity levels respectively) compared to randomized simulations that assume no consistent effect of land-use intensity on species distributions. A: We randomized the distributions of species on the productivity gradient by randomly rearranging the recorded counts for each species (n = 380 excluding singletons) over all 41 sampling sites, and re-calculating their center points (i.e. the abundance-weighted mean productivity for each species). Ordered by productivity, the randomized center points show an S-shaped curve as most species are classified as intermediate species (green), while small percentages are classified as losing or winning species (blue resp. yellow). B: These randomized percentages were derived 10.000 times and plotted as density curves for losing species (left side of the graph) and winning species (right side of the graph). Compared to these randomized simulations, the measured percentages of losing and winning species differed significantly for nearly all taxonomic groups (plotted as horizontal lines). C: The percentages of losing, intermediate and winning species (blue, green resp. yellow) changed among more widely occurring species (i.e. species recorded at an increasingly high minimum number of sites). However, the changes in measured percentages (solid lines) contrast with the change of the randomized distributions (100 iterations, shown with opaque dots and dashed lines). Randomized simulations project that without the influence of land-use intensity, the percentage of intermediate species would approach 100 % among the most widely distributed species while the percentages of losing and winning species would decrease towards zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

restricted to high productivity sites and these all had fewer than five observations. These patterns are quantitatively illustrated in Fig. 3C which shows how the percentages of losing, intermediate and winning species change over subsets of increasingly widely occurring species. Randomized distributions indicate that with an increasing number of occurrences, it can be expected that the percentage of intermediate species increases towards 100 % as losing and winning species are filtered out (dashed lines: dots reflect 100 randomizations). The observed percentage of losing species indeed drops sharply when more narrow-ranged species are excluded (losing species represented two-thirds of the species found at <5 sites). However, counter to expectations based on randomized distributions, the observed percentage of winning species increases among more widely occurring species (solid yellow line crosses the dashed line) and is significantly higher than randomized percentages for species occurring at >10 sites (*p* = 0.02). 20 % of the species occurring at >20 sites (41 species, i.e. 11 % of the total) were classified as winning species.

4. Discussion

We found that with increasing land use intensity, arthropod species richness in grasslands declined but overall arthropod abundance remained stable. The stable abundance over all arthropods was mainly driven by an increase in Diptera numbers that counteracted abundance declines in most other orders. The distributions of individual species revealed large shifts in arthropod communities with increasing land-use intensity. At the landscape scale, arthropod biodiversity was strongly centered in low-productivity grasslands. High-productivity grasslands were dominated by a small set of widely distributed species which partly profit from increasing productivity. A few winning species thus probably sustained the overall arthropod abundance at high-intensity grasslands while many losing species caused biodiversity levels to be very low.

4.1. Contrasting responses of species richness and abundance

The exponential decline of arthropod species richness with increasing productivity aligns with other studies on grassland plants (Kleijn et al., 2009) and arthropods (Allan et al., 2014). In line with previous large-scale studies on grassland arthropods (Allan et al., 2014; Ekroos et al., 2020; Simons et al., 2015), we measured richness declines across multiple arthropod groups, with the exception of Coleoptera. Although they are often used as indicator groups, this lack of trend for Coleoptera does match with other studies on Coleoptera richness (Batáry et al., 2007; Mei et al., 2024). The sampled Coleoptera families include many generalist feeders and appear less sensitive to land use intensity than other arthropod groups in terms of species richness. Our results suggest that Heteroptera richness is most sensitive to land use intensity. The recorded richness declines are probably mainly driven by processes that erode niche diversity, such as declines of floral diversity or micro-habitat variation (Joern and Laws, 2013; Woodcock and Pywell, 2010). The selected sampling methods provided a broad and ecologically diverse representation of vegetation-dwelling arthropods, but did not target soil- and surface-dwelling arthropods. Hence, while our results hold within the realm of the species considered, this study can be expanded by comparisons with different area-based collection methods (e.g. suction sampling) and by the inclusion of species identity data of yet more arthropod groups. Such studies can make important contributions to our understanding of poorly studied groups that nevertheless play central roles in many ecosystems.

The abundance declines with increasing productivity that were observed in most orders were offset by the increase in abundance of a single order: true flies (Diptera). This positive relation between productivity and Diptera abundance aligns with the findings of Silva-Monteiro et al. (2022) who measured an increase of total arthropod abundance with productivity in a cross-continental study of wet grasslands, where Diptera represented 80 % of all specimens. The increase of

Diptera numbers with grassland productivity is probably driven by families that live from decaying organic matter (Powell et al., 2024). Likewise, the steep exponential decline of Heteroptera numbers most likely reflects the reliance of many species on specific forbs that are often restricted to low-productivity grasslands, while the unimodal trend of Auchenorrhyncha in this study was partly driven by high numbers occurring in humid grasslands at low-to-medium productivity levels. These different relations of separate arthropod orders with land-use intensity can largely explain the contrasting relations of overall arthropod species richness and abundance.

4.2. Shifts in species composition

Our results confirm that species richness patterns underestimate biodiversity declines with land use intensification because they ignore effects on species numbers and community composition (Chase and Knight, 2013; Gossner et al., 2016; Hillebrand et al., 2018). Species richness in low-productivity grasslands was approximately twice as large as in high-productivity grasslands, but compared to high-productivity grasslands six times more species had their distributional center-point in low-productivity grasslands (Fig. 2). This implies that on top of significant richness losses, also the number of unique species and the population size of many species declined with productivity. However, our analyses of dissimilarity (beta-diversity) and replacement in species assemblages did not reveal these patterns. This is probably because these metrics aggregate all differences between sites without considering where individual species were observed. Although many studies have interpreted dissimilarity metrics as measures of biotic homogenization or differentiation (Dornelas et al., 2023; Gossner et al., 2016; Keck et al., 2025), other mechanisms can also play a role in determining them. For example, we found an increasing dissimilarity of Anthophila assemblages from medium- to high productivity levels, most likely because species showed more fragmented distributions across high-productivity grasslands (Fig. 2 & Table S4: see also Araújo et al., 2022 and Wayman et al., 2024); a pattern that seems to reflect the dependence of a common set of species on the grass-clover mixtures that are found in some of the high-productivity grasslands in this area. Furthermore, stochastic effects such as spillover to unsuitable habitats (reflected by single records far from species' prevailing productivity ranges: see Fig. 2) can enhance dissimilarity, especially among species-poor communities (Zhou et al., 2022). The lack of consistent patterns in our results suggests that the traditionally used measures of dissimilarity do not comprehensively capture the changes in species communities resulting from contrasting land-use (Wayman et al., 2024).

The center point analyses provided more comprehensive results with which the consequences of land-use change for species communities can be evaluated. Center points of species distributions on the productivity gradient indicate whether individual species are declining or increasing in abundance, i.e. losing or winning, under land use intensification. Some previous studies did not record a clear dominance of either losing or winning species in time series, which they related to variation in the responses of species to environmental change (Dornelas et al., 2019; Outhwaite et al., 2020). We found that as land use intensifies, there are many more arthropod species that decline ('lose') than there are that increase ('win'). This finding aligns closely with several studies of single arthropod groups in managed grasslands, such as grasshoppers (Chisté et al., 2016), Auchenorrhyncha (Chisté et al., 2018), ants (Heuss et al., 2019) and moths (Mangels et al., 2017). Chisté et al. (2016) and Heuss et al. (2019) recorded largely analogous relations with land-use intensity for the Orthoptera and Formicidae species that overlap with our study, but each of these studies also recorded six additional losing species, and intermediate distributions were found for six out of the eight Formicidae species that were losing in our study. These differences probably reflect that land-use intensity levels in our area were higher than in the German regions where these studies were conducted, which may have resulted in more negative distribution patterns for the same

species, but also in regional extinction of the most sensitive species. Therefore, center point studies from different regions should be compared by the absolute values derived per species and not by relative shares of winners and losers.

Different from the approach used by Chisté et al. (2016), we compared the actual and randomized species distributions at the community level, rather than testing whether individual species increased or declined with intensification. This allowed us to incorporate the many species that were only observed a few times ($n > 2$). Across all sampled groups, we recorded much more losers and (with one exception) fewer winners than would be expected based on random distributions, even when for that group species richness showed no relation with productivity. Moreover, 'losers' (56 % of all species) represent only the species that declined in the transition from low to medium intensity levels. In our results, 'intermediate' species include species that declined as land use changed from medium to high productivity levels, as well as species that were recorded proportionately across a wide productivity range. Only 15 % of all species occurred proportionately at high-intensity grasslands, which implies that the percentage of declining species increased even to 85 % under the conversion to high land-use intensity levels.

4.3. From narrow to broad niches

Most losing species were fully or largely restricted to a narrow range of low productivity levels, whereas in each taxonomic group, a subset of intermediate and winning species occurred widely along the productivity gradient (see Figs. 2 & 3C). This pattern resembles the prevailing species abundance distribution of communities in nature with many rare species and a few common species (McGill et al., 2007). But rather than 'natural rarity', species distributions on the productivity gradient reflect their sensitivity or tolerance to land-use intensification. Species with narrow niches on the productivity gradient were often numerous in low-productivity grasslands but were progressively lost at higher productivity levels, whereas species that appear tolerant to land use intensification became increasingly dominant (see also Simons et al., 2015). This pattern results in the often-observed biotic homogenization in intensively used systems (McKinney and Lockwood, 1999; Newbold et al., 2018). Narrowly distributed species may be harder to sample, but not including them may lead to unfounded conclusions. For instance, Simons and Weisser (2017) concluded that further intensification of current German grassland landscapes is possible without biodiversity loss in arthropod communities, but their analysis was mainly based on the 25 % of species that were most widespread along gradients of productivity. Obtained at a highly comparable productivity gradient, our results indicate that these species were probably the most tolerant to land-use intensification.

The winning species in our study did not include any species that were only abundant at high-productivity grasslands. Most of these species tolerated a wide range of productivity levels. They represented only 9 % of all species but 20 % of the most widely occurring species. Most winning species seemed to profit from land-use intensification because of increased food availability. Such species include mobile generalist feeders such as the honey bee *Apis mellifera* (Hymenoptera; recorded at 33 sites, centered at 54 GJ.ha^{-1}), aphid feeders such as *Tytthaspis sedecimpunctata* (Coleoptera; recorded at 31 sites, centered at 51 GJ.ha^{-1}), and species feeding on roots and organic matter such as *Agriotes gallicus* (Coleoptera; recorded at 31 sites, centered at 64 GJ.ha^{-1}) and *Geomyza tripunctata* (Diptera; recorded at 21 sites, centered at 70 GJ.ha^{-1}). These winning species were not necessarily generalists, but tended to be well-adapted to the specific niches and high disturbance levels that characterize intensively used grasslands (Boyes et al., 2019; McKinney and Lockwood, 1999).

The presence of a small set of well-adapted species that increase in abundance with increasing productivity levels could explain the persistence of overall arthropod abundance at high land-use intensity

levels. However, arthropod communities in the more intensively used grasslands were increasingly dominated by families of Diptera and Hymenoptera that were not identified to species level. These families mainly include small and poorly known species whose larvae live as decomposers (Diptera) or parasitoids (both Diptera and Hymenoptera). As hardly any research exists on patterns in species composition of these families, it remains unknown if their numeric dominance at intensively used grasslands results from a few winning species or also from increased species diversity. While parasitoids would probably follow the patterns of their hosts, decomposer diversity may indeed persist under intensified land-use (Le Provost et al., 2021). However, the Dipteran taxa with decomposer larvae that were identified to species level (26 species belonging to 7 families) showed similar diversity losses as other arthropod groups: most species were largely confined to lower productivity levels whereas five species were winning as land-use intensified (Fig. S3). This aligns with other studies that found high turnover and strong numeric dominance of single Diptera species in intensively used systems (Powell et al., 2024; Shortall et al., 2009). It is therefore likely that also among families that remained unidentified in this study, a small set of species maintained high overall abundance levels under intensified grassland management.

4.4. Implications

Our findings suggest that when species from different taxonomic or ecological guilds are pooled together, abundance responses can differ markedly from diversity responses. We showed that land-use intensification on grasslands is related to consistent losses in diversity but not abundance. This means that local grassland intensification cannot explain the severe losses of overall arthropod abundance that were recorded over decadal timescales (Seibold et al., 2019; Van Klink et al., 2020). It is even possible that extensified management results in declining arthropod abundance in certain contexts, such as when Diptera are dominant (Silva-Monteiro et al., 2022). The absence of clear relations between land-use intensity and overall arthropod abundance at site level suggests that landscape-scale effects, such as loss of semi-natural habitat (Seibold et al., 2019), changes in cropping patterns (Litovska et al., 2025), increased frequency of climatic extremes (Boggs, 2016; Sohlström et al., 2022), or increased loading of harmful chemicals such as insecticides (Mancini et al., 2020), might be important drivers of the recorded arthropod declines over time. Moreover, declines of arthropod biomass (Hallmann et al., 2017) may be amplified by losses of large-bodied species and individuals in arthropod communities (Martínez-Núñez et al., 2024; Oliveira et al., 2016).

We also show that species richness and dissimilarity metrics underestimate the actual losses of arthropod biodiversity because species identities are not considered. The most profound consequence of land use intensification is the progressive loss of species across all arthropod groups that are sensitive to land-use intensification, most of which have a distribution that is confined to a narrow range of low productivity levels. Arthropod abundance seems more resilient to intensification because of a small subset of widespread winners that compensate for losses in the majority of species (Newbold et al., 2018). Further research is needed to better understand abundance changes across arthropods with differing ecologies, and the consequences of these changes for ecosystem functioning (Cooke et al., 2025; Wagner, 2020). Winning species can probably sustain certain ecosystem processes such as food provision for generalist insectivores, but may not support more specialized trophic interactions (Holland et al., 2006). Furthermore, winning species may also amplify dis-services such as crop damage as they often include important pest species (Zhang et al., 2007). While severe species losses are expected to erode ecosystem service provisioning, we can only assess which ecosystem services are at stake when knowing which arthropods lose or profit under environmental change (Cardinale et al., 2012; Cooke et al., 2025).

Arthropod species losses were most pronounced in grasslands at the

low-to-medium productivity range. This finding implies that biodiversity conservation will be most effective at lower land-use intensity levels, which aligns with other studies (Allan et al., 2014; Kleijn et al., 2009, 2011; Kleijn and Sutherland, 2003). Low-intensity grasslands play critical roles in preserving many arthropod species (Habel et al., 2013; Van Swaay et al., 2025; WallisDeVries et al., 2002) and we show here that losing such grasslands affects the large majority of species across multiple taxa. However, low-intensity grasslands have become rare or absent in modern agricultural landscapes where productivity levels above 50 GJ.ha^{-1}.yr^{-1} have become the norm (Bardgett et al., 2021; Emmerson et al., 2016). Grass-dominated hay meadows that are common in agri-environment schemes and nature reserves, both aimed at biodiversity restoration, typically still reach medium productivities of 20-40 GJ.ha^{-1}.yr^{-1} (Schippers et al., 2012). Although more species tolerate these productivity levels than those of high-intensity grasslands, their value for biodiversity conservation is incomparable low-productive, forb-dominated grasslands (Habel et al., 2013, 2019). Restoration of more low-intensity grassland habitats will therefore be crucial to halt and reverse the widespread biodiversity loss of grassland arthropods.

CRediT authorship contribution statement

J.P. Reinier de Vries: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **José G. van Paassen:** Writing – review & editing, Supervision, Conceptualization. **Remco Ploeg:** Writing – review & editing, Investigation, Data curation. **Aart Noordam:** Writing – review & editing, Data curation. **Koen Verhoogt:** Writing – review & editing, Data curation. **David Kleijn:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111522.

Data availability

All raw data and R code with documentation are accessible via the Zenodo digital repository. DOI: https://doi.org/10.5281/zenodo.15585342 (De Vries et al., 2025).

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