Check for updates

Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER OPEN ACCESS

Land Use Mediates Long-Term Arthropod Functional Change

Carlos Martínez-Núñez[1,2] | Martin M. Gossner[3,4] | Felix Neff[1] | Marco Moretti[3] | Martin K. Obrist[3] | Felix Herzog[1] | Kurt Bollmann[3] | Peter Duelli[3] | Eva Knop[5,6] | Henryk Luka[7] | Matthias Albrecht[1]

[1]Agricultural Landscapes and Biodiversity, Agroscope, Zürich, Switzerland | [2]Department of Ecology and Evolution, Estación Biológica de Doñana (EBD), CSIC, Sevilla, Spain | [3]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland | [4]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland | [5]Conservation Biology, University of Regensburg, Regensburg, Germany | [6]Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland | [7]Department of Crop Sciences, Research Institute of Organic Agriculture FiBL, Frick, Switzerland

Correspondence: Carlos Martínez-Núñez (carlos.nunez@ebd.csic.es)

Received: 26 November 2025 | **Revised:** 12 August 2026 | **Accepted:** 7 September 2026

Keywords: arthropod functional traits | carabids | ecosystem resilience | environmental filtering | functional redundancy | functional richness | land-use intensification | specialisation | spiders | temporal biodiversity trends

ABSTRACT

Global change reshapes arthropod communities, yet long-term effects on their functional diversity remain unclear. Using a long-term dataset comprising > 1.3 million individuals of 728 carabid and spider species, we quantified temporal trends in functional diversity across forests, grasslands and croplands. Trajectories diverged strongly among land uses: functional richness increased in forests and grasslands but declined sharply in croplands. In forests, communities became more specialised and less redundant, suggesting increasing niche differentiation, but experienced greater functional richness loss under simulated species extinctions. Cropland assemblages became functionally homogenised. Losses of key effect traits among spiders suggest potential erosion of ecosystem functions in croplands. Moreover, genera dominated by species with unique trait combinations were typically larger-bodied and less dispersive, and their loss would remove irreplaceable functional strategies from communities. Overall, our study reveals diverging long-term trajectories of arthropod functional diversity across land uses, indicating potential negative consequences for ecosystem functioning in arable landscapes.

1 | Introduction

In recent years, reports of widespread declines in arthropod populations have raised concerns among scientists and the general public (Hallmann et al. 2017; Harvey et al. 2020; Seibold et al. 2019). While some studies suggest that net trends may be less uniformly negative than initially feared (Crossley et al. 2020; Neff et al. 2022), even moderate declines and shifts in species composition (Outhwaite et al. 2022) can have important consequences for ecosystem functioning (Isbell et al. 2018; Mori et al. 2018). However, most long-term arthropod studies have focused primarily on taxonomic changes, leaving a critical gap in our understanding of the functional implications of arthropod community change.

While increased numbers of species often come along with greater trait and functional diversity (Frainer et al. 2014), the relationship between taxonomic and functional diversity is not universal. In some systems, it may be approximately linear (Birkhofer et al. 2015), whereas in others, functional richness can saturate at high levels of taxonomic richness, as new species tend to be functionally redundant (Petchey and Gaston 2002). The shape and strength of this relationship can vary depending on the functional distinctiveness of species (Greenop et al. 2021;

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2026 The Author(s). *Ecology Letters* published by John Wiley & Sons Ltd.

Hevia et al. 2016). The loss of a rare, functionally unique species may substantially impact ecosystem functioning (Dee et al. 2019), whereas the loss of a redundant species may have limited immediate effects (sensu Rosenfeld 2002). In ground-dwelling arthropods, such functional uniqueness may be represented by taxa with uncommon combinations of traits, such as large or small body sizes or restricted seasonal activity, which may not be easily replaced by more common taxa. Despite growing recognition of this variability (Hevia et al. 2016), we still lack a clear understanding of the long-term changes in the functional diversity of arthropod communities, especially across different land-use types and taxonomic groups.

The magnitude and direction of changes in functional diversity are likely to depend on land-use change and land-use intensity, with more disturbed systems expected to lose specialised and unique trait combinations more rapidly (Birkhofer et al. 2017; Martínez-Núñez et al. 2024). Croplands generally experience higher disturbance, chemical inputs, and habitat simplification than grasslands or forests, which may accelerate functional erosion (Potapov et al. 2020). Conversely, less disturbed systems, such as forests, may retain functional diversity while hosting more specialised and less redundant arthropod communities over time. However, observational studies indicate that responses to land-use intensity can be complex and may vary among arthropod groups (Birkhofer et al. 2015).

Two non-exclusive mechanisms may explain differences in the temporal shifts of arthropod functional diversity across land-use types. First, contrasting disturbance regimes and environmental filters can drive divergent trends in arthropod communities, with cascading effects on functional composition (Hevia et al. 2016). Second, ecological theory suggests that habitats differ in the availability and structure of Grinnellian (abiotic) and Eltonian (biotic) niches, which govern species coexistence and determine the degree of functional redundancy or complementarity in their communities (Chase and Leibold 2013).

In this study, we compiled a unique long-term (multi-decade) pitfall-trap dataset of carabid beetles and spiders, two diverse groups of ground-dwelling arthropods that play important roles as generalist predators in many ecosystems (Lövei and Sunderland 1996; Cardoso et al. 2025). We used these data to quantify long-term trajectories of different facets of functional diversity at a regional scale across three major land-use types (forests, grasslands, and croplands) in the Swiss lowlands. To capture these shifts, we assessed five complementary facets of functional diversity: functional richness (the range of traits present), evenness (the distribution of trait frequencies across trait space), divergence (the degree to which species are functionally distinct from each other), redundancy (the extent to which multiple species share similar trait combinations), and community-weighted mean specialisation (the degree to which species occupy unique positions in trait space). These metrics reflect different aspects of community structure and can respond differently to environmental change. In addition, we distinguished between the full set of traits and a subset of effect traits, that is, those directly linked to ecosystem functions such as body size, phenology, or trophic role. These two trait sets capture different dimensions of community change: the full trait set reflects broader ecological differentiation among species, whereas effect traits capture variation more directly linked to ecosystem functioning. Thus, trends in effect-trait diversity may diverge from those based on the full trait set and have different implications. This framework allowed us to quantify long-term trajectories of arthropod functional diversity and specialisation across a gradient of land-use intensity and to detect diverging trends among land-use types, with implications for ecological communities and ecosystem resilience. Beyond describing temporal patterns, we examined the relationship between functional and taxonomic diversity and quantified the rate of functional richness loss under simulated scenarios of species extinctions within each land-use type. This allowed us to evaluate both past changes and the potential magnitude of functional diversity loss under different scenarios of continued biodiversity decline. We hypothesize that: (1) functional diversity (richness, evenness, divergence and specialisation) will decline over time in croplands (the most intensively used land type), but redundancy will increase, while trends in forests and grasslands will remain more stable; (2) temporal trends based on effect traits will differ from those based on the full trait set, revealing contrasting potential consequences of land-use intensity on ecosystem functions provided by carabid beetles and spiders across land-use types; (3) the rate of functional richness loss under simulated species extinctions will be highest in forests and lowest in croplands; and (4) functional richness will depend disproportionately on a small set of functionally unique taxa, making these poorly redundant regions of trait space especially vulnerable to future species losses.

2 | Materials and Methods

2.1 | Study Design and Dataset

Between 1974 and 2018, 29 studies conducted at three Swiss research institutions (Agroscope, FiBL, and WSL; see Acknowledgements) used pitfall traps to survey ground-dwelling arthropods (Table S1). We compiled these datasets to analyse long-term changes in carabid beetle (Carabidae) and spider (Araneae) communities across forests, grasslands, and croplands. In total, 38,368 pitfall samples from 930 locations in the Swiss lowlands (Figure S1) yielded over 1.34 million individuals and 728 species (255 carabids, 473 spiders). Notably, this represents approximately 45% of the ~549 carabid species and nearly 50% of the ~970 spider species currently described in Switzerland, including highlands and the alpine region (CSCF–Infofauna 2024).

Sampling was conducted in 35 different years between 1974 and 2018, with all three land-use types represented across much of the 1985–2010 period, despite differences in temporal coverage and time windows among land-use types and taxa (Table S2, but see Appendix S1 for sensitivity analysis). Although pitfall-trap sampling varied in trap type, size, deployment duration and preservative fluid (Appendix S1, Figure S2), these variables either showed no noticeable temporal trend (Figure S3) or had only very small and inconsistent effects on functional diversity metrics (Figure S4).

Almost 45% of sites were sampled in multiple years (average of 2.49 years per site, ranging from 1 to 8 years) (Table S3),

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and all land-use types were broadly represented through time (Figure S5), with very high trap-day numbers (Table S2). Hence, observed temporal trends reflect regional shifts rather than site-specific trajectories. Sample coverage was very high (>98% within land-use types, >90% across years; Figures S6 and S7), and spatial distributions remained consistent (Figure S5), supporting robust temporal comparisons.

We focused on carabids and spiders because both are key predators providing ecosystem services such as pest control (Cardoso et al. 2025; Gallé et al. 2020; Lövei and Sunderland 1996). Long-term shifts in their functional diversity may thus have significant ecological and economic implications (Vidal and Murphy 2018). Both groups are efficiently sampled with pitfall traps, have well-established taxonomy in Switzerland, and respond sensitively to environmental change (Koivula 2011; Martínez-Núñez et al. 2024).

2.2 | Land-Use Types

Land-use types were ascribed to three different categories following the land-use classification in Switzerland (Delarze et al. 2015): (a) forests: interiors of forested (woody) areas; (b) grasslands: meadows and pastures; and (c) croplands: agricultural landscapes dominated by arable crops such as cereals, corn, oilseed-rape, sugar beet, or vegetable fields. These land-use classes can be sorted along a gradient of increasing anthropogenic perturbation regime, from forests to grasslands to croplands. Although local conditions and management varied within land-use types, detailed management information was not consistently available across studies, sites and years; our analyses therefore focus on general trends across major land-use categories.

2.3 | Functional Traits

Multiple traits were used to calculate functional diversity measures from a holistic approach, integrating complementary axes of species' ecological strategies (sensu Mouchet et al. 2010). We characterised the functional space using nine carabid traits and 13 spider traits. These traits represented an array of morphological, behavioural, and ecological features that reflect a great part of the trait variability found in these communities. All the traits used can be considered functional because they can impact fitness (directly or indirectly) through conditioning growth, reproduction, and survival (see Tables S4 and S5 for details about the selected traits, the type of variable, and their functionally important ecological implications). For carabids, we used body size, wing length, tolerance to drought, start of the activity period, length of the activity period, overwintering stage, altitude tolerance range, optimum altitude, and feeding guild. For spiders, we used body size, tolerance to drought, habitat use specialisation, hunting technique, temperature breadth, length of the activity period, altitude tolerance range, dispersal ability, stratum use, web building, feeding specialisation, and diurnal and nocturnal activity. Because carabids and spiders have very different characteristics, their full functional spaces are not comparable in terms of specific features, but are comparable in terms of functional variability describing different ecological living forms. All these traits showed pairwise correlations below the threshold of $|r| = 0.7$, and thus all traits were retained for further analysis. The sole exception concerned carabids, where both the length and start of the activity period (i.e., phenology) were retained despite exceeding this threshold ($r = 0.79$) because the 21% complementary information in these variables can determine great ecological differences in carabids (e.g., accessibility to resources, vulnerability to environmental perturbances, or tolerance to climatic conditions). All numeric traits were scaled and centred. Missing trait values (5% in carabids and 21% in spiders) were imputed using random forests in the *missForest* function (v1.5) in R (Stekhoven and Bühlmann 2012). Out-of-bag (OOB) error for imputed data was 5% on average across traits for carabids and 15% on average for spiders, providing a total high accuracy of 98.4% correct trait information for carabids and 94% for spiders. Traits were collected from different resources (see Appendix S1: Sources of trait information).

2.4 | Effect Traits

Response traits are those that determine how species respond to environmental changes or disturbance, while effect traits are those that determine how species influence ecosystem functioning (Lavorel and Garnier 2002). In addition to focusing on the full set of traits, we repeated the main analyses using only a subset of three key effect traits (i.e., traits expected to directly drive ecosystem functioning) to study the trends of functional diversity that likely have an impact on ecosystem functioning: body size, phenology duration, and feeding guild (carabids)/hunting technique (spiders) (see Tables S4 and S5 for a justification of why these traits are considered effect traits).

2.5 | Functional Diversity Measures

We studied changes in: (i) functional richness (FRic), which was calculated as the convex hull of the multivariate space defined by the functional distances between the species. It shows the amplitude and variety of traits represented in a species assemblage (i.e., number of unique trait value combinations) (Villéger et al. 2008); (ii) functional evenness (FEve) (homogeneity of the hypervolume), which reflects the regularity of observations' distribution within the trait hypervolume (1 meaning that all trait values are equally likely). Some authors attribute this to high competition or soft ecological filters (Fontana et al. 2016; Villéger et al. 2008); this measure has been theoretically linked to resilience of a community to perturbations (Mouillot et al. 2013); (iii) functional divergence (FDiv), which shows the dispersion of the trait space. A high divergence represents a high degree of niche differentiation and suggests low resource competition; (iv) functional redundancy (FRed), which informs about the degree of functional overlap between species (Rosenfeld 2002); and (v) assemblage-weighted mean functional specialisation, which provides information about the degree of functional closeness or specialisation found in each assemblage. Ecologically, a high FRic indicates that species in an assemblage exhibit a range of different ecological strategies, reflecting broad niche availability and potential for diverse ecosystem functions. An elevated FEve suggests that species traits are evenly distributed, potentially enhancing community stability. A high FDiv means that species

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

are concentrated at the edges of trait space, using resources differently and thus reducing direct competition. Increased FRed implies that multiple species share similar roles, providing insurance against species loss, but also showing high functional homogenisation. Finally, a high specialisation reflects assemblages dominated by species with narrow ecological roles, while low values indicate more generalist communities. Observed changes in functional diversity were not primarily driven by phylogenetic turnover (Appendix S1: Phylogenetic signal and trait-phylogeny congruence and Table S6).

We did not apply richness-corrected functional diversity metrics (e.g., null model-based standardised effect sizes) because we want to realistically interpret patterns as reflecting both taxonomic and functional turnover over time. However, for completeness, we also report temporal trends in functional richness independent of taxonomic richness by plotting the residuals of these models over time.

2.6 | Statistical Analyses

We ran all the analyses in *R 4.3.2* (R Core Team 2021). Statistical analyses used in this study can be divided into three sections:

First, we examined the long-term inter-annual trends of functional diversity metrics within each land-use type. Due to the heterogeneity of the dataset (see pitfall trap sampling section), we used an iterative resampling method (with replacement) to standardise sampling effort and get robust conservative estimates of assemblage composition, while using (potentially) all the information available in the dataset. The resampling procedure was designed to reduce the influence of individual sites or studies and to provide conservative assemblage-level estimates for each year and land-use type. Therefore, an assemblage (i.e., a meta-community) was built by pooling 90 pitfall trap samples selected randomly within each land-use type and year. We chose 90 pitfall traps because this number ensured high species coverage (> 90% in all cases) while also allowing us to retain most years in the analysis (Figure S7). This random selection was repeated 100 times to calculate variability and confidence intervals around the most expected assemblage.

For each assemblage (90 pitfall trap samples pooled), functional trait dissimilarities among species were calculated using Gower distances, as implemented in the dbFD function from the 'FD' (v1.0–12) package (Laliberté and Legendre 2010) to determine FRic, FEve and FDiv of the community. This method allows for the incorporation of species abundances to weight trait contributions, and it is particularly suited for heterogeneous trait matrices as it accounts for the mixed nature of the trait data (i.e., continuous, categorical, ordinal, and binary variables). Eight principal coordinates were retained, which represented > 90% of the total inertia in all cases (different groups and land-use types). To assess the faithfulness of the multidimensional functional space to the original trait dissimilarities, we examined the mean squared deviation (mSD) and associated R^2 between the Gower distance matrix and the Euclidean distances in the reduced-dimensional trait space. In all cases, the quality of the functional space was high, with R^2 values exceeding 0.90, indicating that the ordination preserved the original trait relationships with minimal distortion. This high-quality functional representation ensures robust estimation of functional diversity indices, while maintaining the biological integrity of mixed-type trait data. For the analysis focusing on effect traits, five principal coordinates were used, which accounted for > 98% of the variance. FRed was estimated as the inverse of species-level functional uniqueness, calculated using the *uniqueness* function from the *adiv* package (v2.2.1) (Pavoine 2020). Lastly, we calculated assemblage mean specialisation as the average distance of species to the centroid of the functional hypervolume, weighted by species abundance (Carmona et al. 2016).

We used linear mixed-effect models to assess the effect of time within each land-use type (year × land-use type) on the response variable. FRic was log-transformed to obtain a better model fit and residuals. Although FEve, FDiv and FRed were constrained between 0 and 1, and a binomial or beta-regression model would be canonical, Gaussian error distribution models were used because observed values were not close to the edges (i.e., not bounded in practice), and normal models performed better (best fit, with higher variance explained and better residual distribution). Although our resampling approach already controls for sampling effort and strongly reduces noise due to differences across studies, several covariates were quantified for each species assemblage in every iteration (subset of 90 pitfall traps randomly selected within year and land-use type) and used in these models to further account for variation across studies and sampling sites, namely: mean Euclidean distance between the sampling sites, number of sites represented in the subset, number of different weeks sampled and standard deviation of the weeks.

Second, to explore the relationship between taxonomic and functional diversity within each land-use type, we fitted a generalised additive model (GAM) for each taxonomic group and land-use type, using FRic, FEve, FDiv and FRed as the dependent variables and taxonomic richness as the sole predictor. We used the R^2 to quantify the proportion of variance explained by each model.

Third, we quantified the rate of functional richness loss within each land-use type by simulating random and non-random species extinctions on functional richness. Given the very high sampling coverage (> 98%) for carabids and spiders across forests, grasslands, and croplands (Figure S6; Chao and Colwell 2014), we used the full species set per land-use type. We modelled two extinction scenarios: (i) species lost in order of increasing abundance (rarest first), representing a realistic scenario; and (ii) random loss. Functional richness was recalculated after each species removal, with the random scenario repeated 50 times (~50,000 assemblages total). For the non-random scenario, we fitted linear models relating functional richness to the number of species removed, with the slope representing the absolute rate of functional richness loss per species removed. To ensure robustness, we repeated analyses excluding very rare species (total abundance < 2; 9% of species in forests and croplands, 6% in grasslands).

Lastly, we calculated the functional importance of each carabid and spider species according to their contribution to specialised and unique trait combinations. Hence, we first calculated the distance of each species to the centroid of the

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

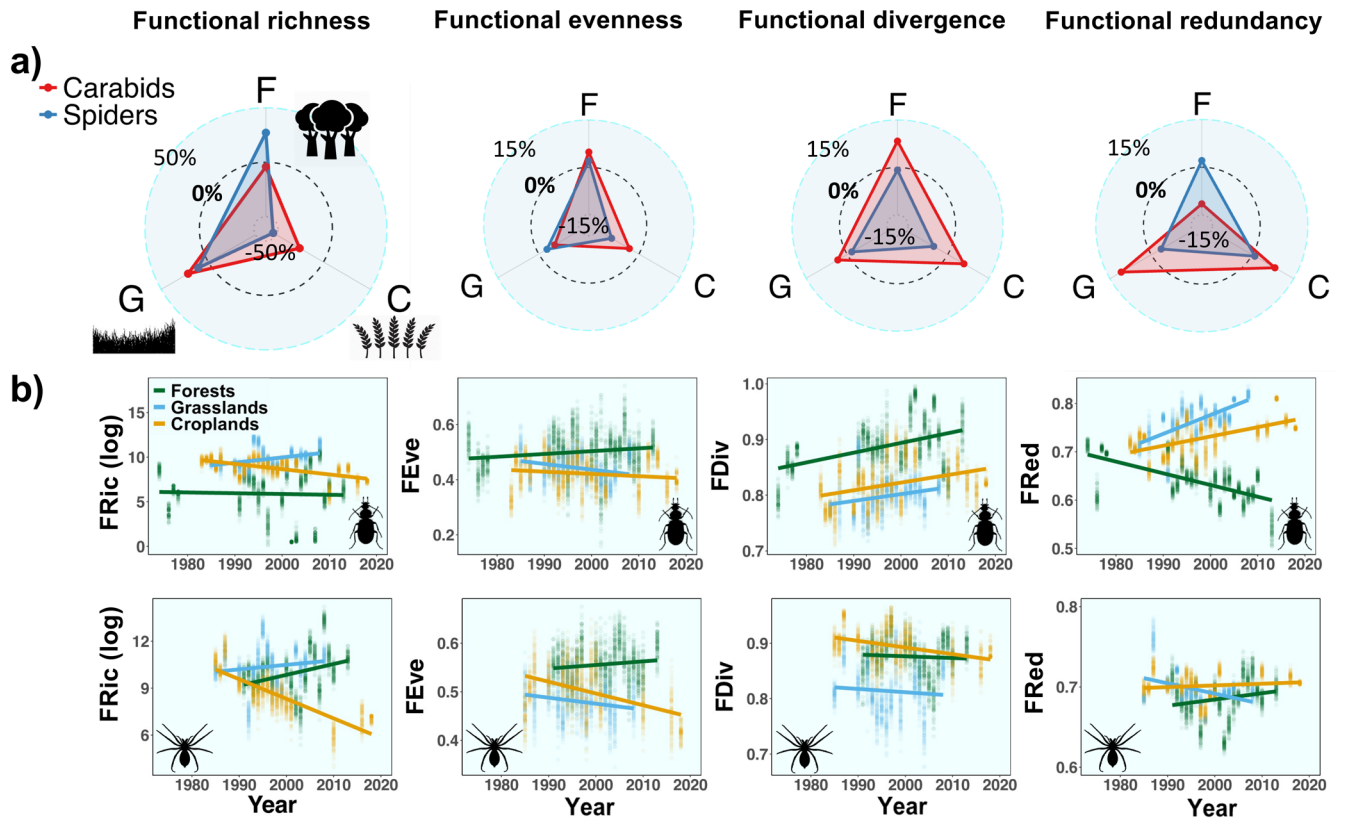


FIGURE 1 | Temporal trends in overall functional diversity of carabid and spider assemblages across three land-use types. (a) Rate of change per decade in three land-use types: F = forests, G = grasslands, C = croplands. (b) Linear fit showing the marginal effect of year (i.e., temporal trend) on carabid (top) and spider (bottom) functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional redundancy (FRed) across three land-use types. These metrics were calculated from functional distances based on the full set of traits (i.e., including response and effect traits).

functional space defined by all the species found in this study. Specialisation value was normalised between 0 (functionally most common species) and 1 (functionally most unique species). In addition, we calculated the functional distance of each species to the k-neighbour (Mouillot et al. 2013). We used from 1 to 20 neighbours, being the species ranked after each iteration according to their position (low rank meaning low uniqueness). The 20 rank values of each species were summed, and their final position was normalised from 0 (lower functional uniqueness) to 1 (higher functional uniqueness). We therefore identified the most functionally unique species (i.e., those that contribute more to functional richness). We grouped the species by genus and ran linear models to examine the relationship between uniqueness/specialisation and key traits. We used two important effect traits (body size and length of the activity period) and a key response trait (dispersal capacity), common to both carabids and spiders.

We further conducted several sensitivity analyses to test the robustness of the results to temporal coverage and model choices (see Appendix S1).

3 | Results

Overall, forests and grasslands supported a high number of carabid species (185 and 188 species, respectively), compared to croplands (156). In contrast, forests hosted the highest number of spider species (404), followed by grasslands (264) and croplands (224). These numbers were very similar to the estimated asymptotic richness in the three land-use types (Figure S6).

3.1 | Temporal Variation in Functional Measures

Temporal changes in functional diversity of carabids and spiders differed markedly among land-use types and between taxonomic groups, with the strongest changes observed for functional richness and redundancy (Figure 1). Carabid FRic increased in grasslands (7.1% per decade; 95% CI: 5.0%–9.4%), and decreased in croplands (−7.1% per decade; 95% CI: −8.3 to −6.2%), while changes in forests were comparatively weak. Spider FRic increased in forests (8.2% per decade; 95% CI: 7.4%–9.5%), grasslands (4.0%; 95% CI: 1.9%–5.2%), but declined strongly in croplands (−15.3%; 95% CI: −16.1% to −14.4%) (Figure 1b,c).

Functional redundancy showed contrasting temporal trajectories among land-use types, particularly in carabids. Carabid FRed decreased in forests (−3.2% per decade; 95% CI: −3.1% to 2.8%) but increased in croplands (2.1% per decade; 95% CI: 2.1%–2.5%) and grasslands (5.0% per decade; 95% CI: 4.4%–5.1%) (Table S6). Spider FRed followed more subtle but

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

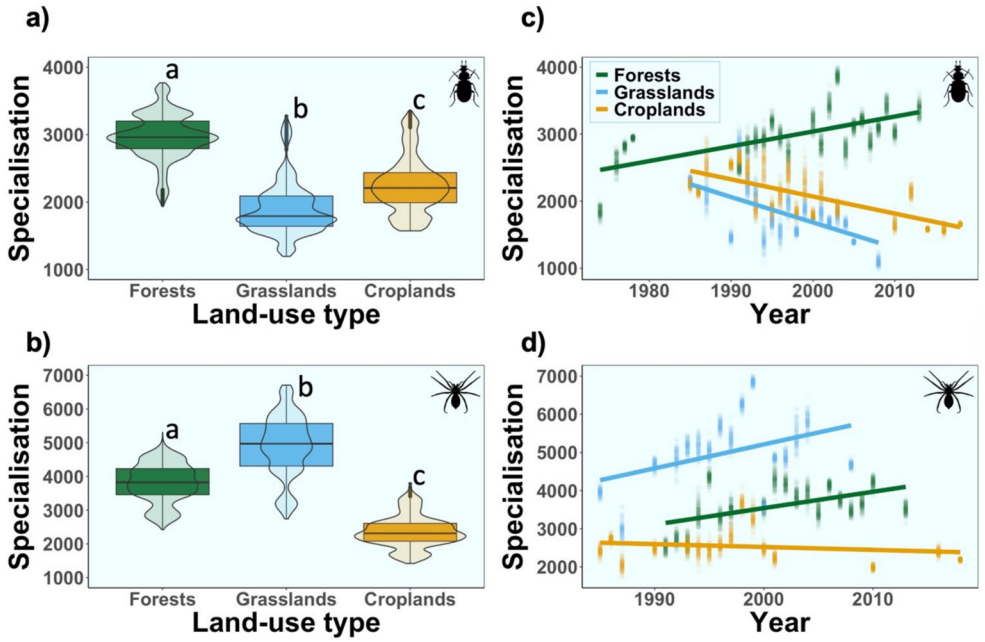


FIGURE 2 | Variation in assemblage functional specialisation across years and land-use types. Variation in (a) carabid, and (b) spider functional specialisation assemblage-weighted means across land-use types. Temporal trends of (c) carabid and (d) spider functional specialisation within each land-use type (c. Letters in panels a) and (b) show post hoc Tukey significant differences between groups. All the trends in panels (c, d) were significant (95% CI of the slope not including 0) and significantly different from each other.

similar patterns (Figure 1c, Table S7). These temporal variations resulted in substantial total changes throughout the whole study period (Table S8). Long-term trends in functional diversity metrics across land-use types remained very similar when latitude was included as a co-variate (Figure S8), and when the timeframe was restricted to the 1985–2010 period with largely overlapping sampling across land-use types (Figure S9) (see Appendix S1 for details on sensitivity analyses).

Changes in assemblage structure were also evidenced by variations in assemblage-weighted functional specialisation mean (Figure 2). Carabid communities in forests showed significantly higher functional specialisation than those in grasslands and croplands (Figure 2a). Spider communities in grasslands showed significantly higher functional specialisation than those in forests and especially in croplands (Figure 2b). Interestingly, the mean functional specialisation of carabid communities in forests increased over the past four decades (slope = 22.1 ± 0.7 SE; 95% CI: 20.8–23.5), while it strongly decreased in grasslands (slope = −38.3 ± 1.5 SE; 95% CI: −41.3 to 35.3) and croplands (slope = −25.3 ± 0.8 SE; 95% CI: −26.9 to −23.7) (Figure 2c). Similarly, spider specialisation increased in forests (slope = 40.9 ± 2.0 SE; 95% CI: 36.9–44.8) and decreased in croplands (slope = −10.9 ± 1.71 SE; 95% CI: −14.2 to −7.5), but also increased strongly in grasslands (slope = 82.7 ± 3.29 SE; 95% CI: 76.3–89.2) (Figure 2d).

When focusing on the three key effect traits, the clearest temporal changes were a sharp decline in carabid FRed in forests and marked declines in spider FRic, FEve and FDiv in croplands (Figure 3). Other changes were weaker or more metric-specific: carabid FRic and FEve remained relatively stable across land-use types, while grassland spider communities showed stable FRic and FEve but declining FDiv and Fred (Figure 3).

As expected, functional richness within each land-use type (but not across them) was mostly driven by taxonomic diversity, but not the other functional metrics (Figure S10).

3.2 | Functional Richness Response to Simulated Species Extinctions

Functional richness declined strongly under simulated species loss (Figure 4), with differences among land-use types. Forests were the most functionally rich (~30% and ~55% of total carabid and spider functional richness, respectively) and showed the steepest absolute declines in functional richness with species removal (carabids: slope or units of FRic lost per species lost = −63,605 ± 629 SE, $p < 0.001$; spiders: slope = −252,707 ± 1619 SE, $p < 0.001$). Grasslands also showed substantial declines (carabids: slope = −58,946 ± 679 SE, $p < 0.001$; spiders: slope = −118,484 ± 1190 SE, $p < 0.001$). In contrast, croplands contributed less to total functional richness (~14% and ~10% of total carabid and spider functional richness, respectively) (Figure 4) and exhibited shallower declines in functional richness with species removal (carabids: slope = −34,889 ± 416 SE, $p < 0.001$; spiders: slope = −69,752 ± 817 SE, $p < 0.001$) (Figure 4). Notably, the non-random extinction scenario (i.e., the preferential loss of the least abundant species) appeared to be associated with a faster decline in functional richness (Figure 4). When focusing on the three effect traits only, patterns of functional richness decline after species removal were very similar to those

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

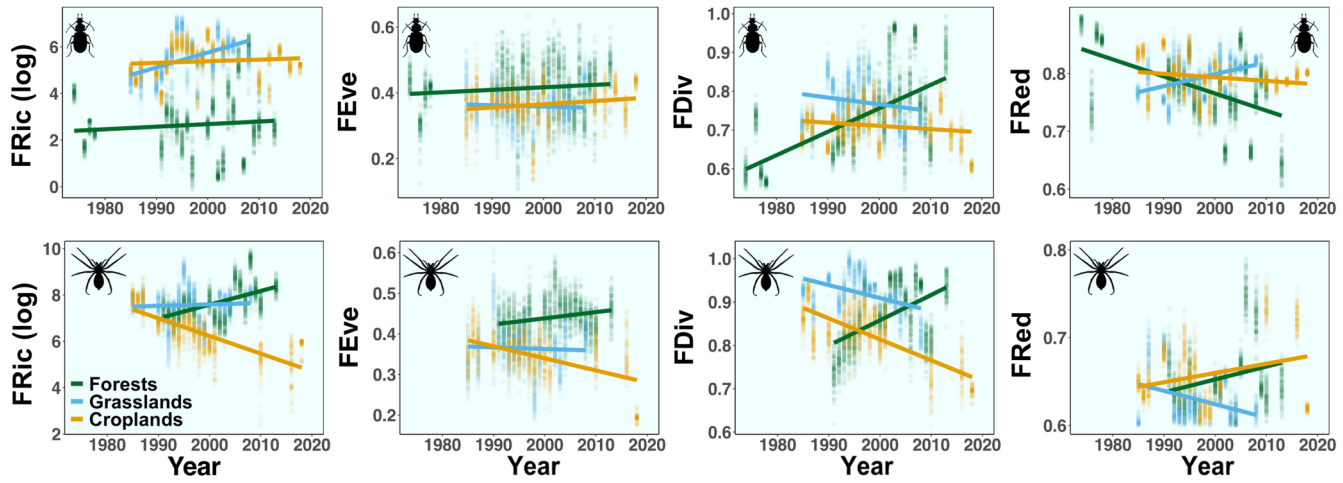


FIGURE 3 | Temporal trends in functional diversity based on three key effect traits. Each panel includes three land-use types: Forests (green), grasslands (blue) and croplands (orange). The effect traits used to define functional distances were body size, phenology duration and feeding guild (carabids)/hunting technique (spiders). FRic = functional richness, FEve = functional evenness, FDiv = functional divergence, FRed = functional redundancy. These metrics were calculated from functional distances based on three effect traits.

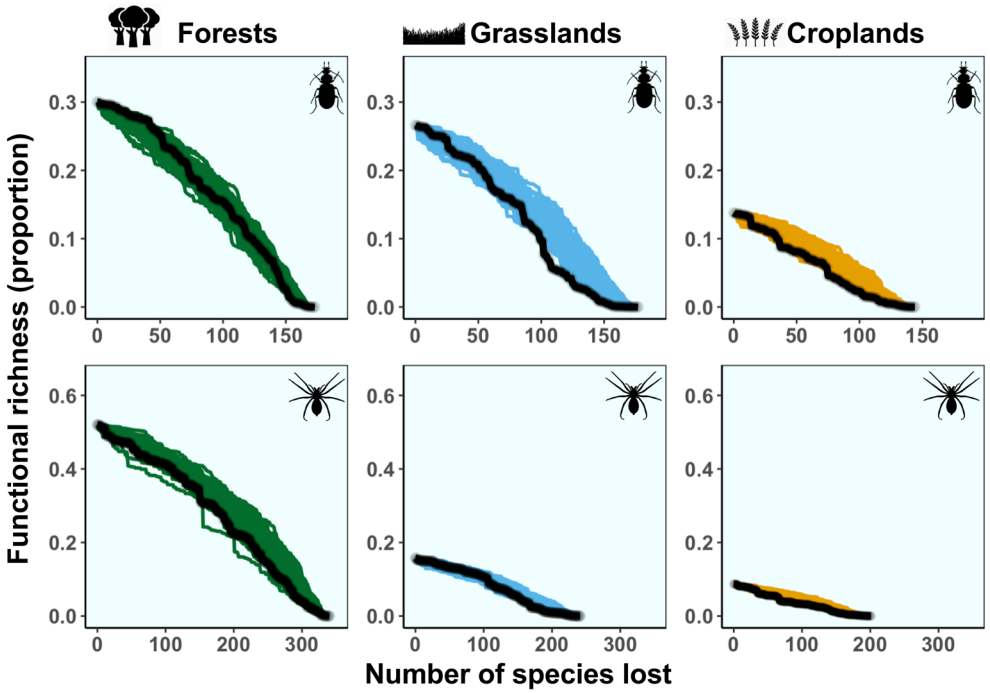


FIGURE 4 | Decrease in functional richness under different scenarios of carabid and spider species loss in forests, grasslands, and croplands. Decline rate of the functional richness space occupied by the species found in forests, grasslands, and croplands, as species are removed randomly (coloured lines, 50 iterations) or in abundance increasing order (i.e., from less abundant to more abundant) (black line). Functional richness is expressed as the proportion of the total trait space defined by all species found in the dataset. Initial values are <1 because not all species occur within a single land-use type. Notice that the scale of the *Y*-axes of carabid beetles and spiders is different.

observed when using the full set of traits, but declines in forests were even steeper (Figure S11). These patterns were very similar when very rare species (total abundance per land-use type <2) were disregarded.

There was a high variance in the contribution of different species to functional richness (Figure 5a,e) through their functional uniqueness and degree of functional specialisation (Pearson coefficient = 0.97, $p<0.001$, between specialisation and uniqueness at the assemblage level). Species that contributed more to functional uniqueness were often linked to forests and grasslands, while those functionally more common were often associated with croplands (Tables S9 and S10). In addition, genera composed of species with larger bodies (Figure 5b,f) and lower dispersal capacity (Figure 5d,h) were those with more unique trait combinations and thus the ones that contributed more to functional richness (Figure 5, Figure S12).

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

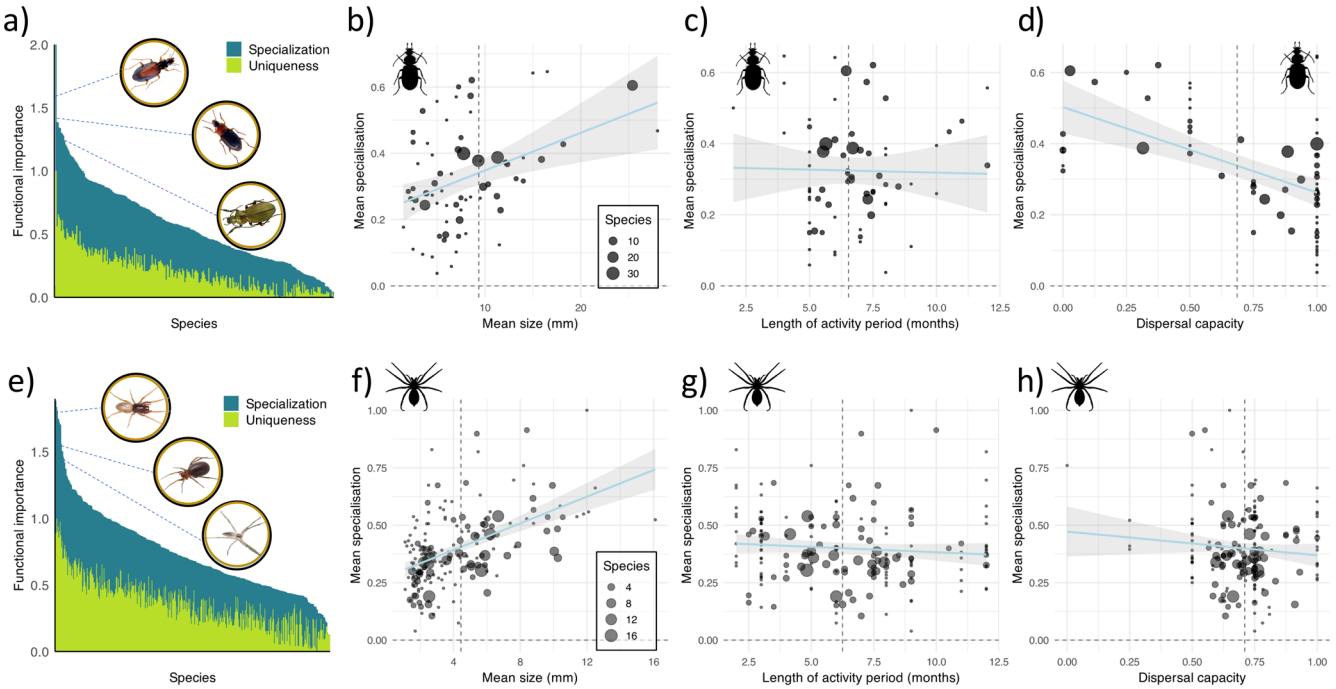


FIGURE 5 | Species and trait contribution to functional richness. Ranking of carabid (a) and spider (e) species by their functional importance, expressed as the sum of normalised (0–1) uniqueness (distance to *k* nearest neighbours; light green) and specialisation (distance to the centroid; blue). Bars represent the aggregated contribution of each species to overall functional diversity. Example species contributing most to functional richness are illustrated. Carabids: *Dolichus halensis* (photo by U. Schmidt; https://species.wikimedia.org/), *Calathus melanocephalus* and *Carabus monilis* (photos from https://www.coleoptera.org.uk, by Lech Borowiec). Spiders: *Dysdera erythrina* (photo by Arno Grabolle), *Zodarion italicum* (photo by Ulrich Kursawe) and *Pisaura mirabilis* (photo by Luis Nunes Alberto; https://commons.wikimedia.org/). Association between mean specialisation and genus-level mean traits, including body size (b, f), length of their activity period (c, g) and dispersal capacity (d, h), for carabids and spiders, respectively. Vertical dashed lines show the average value of traits across genera. Fitted lines represent linear models with 95% CIs. See Figure S12 in Supporting Information for the degree of functional specialisation, including all the genera with more than one species in our dataset.

4 | Discussion

Understanding how arthropod communities change in functional composition over time is central to anticipating future ecosystem functioning under global change (Frainer et al. 2014; Gossner et al. 2016; Greenop et al. 2021). Our long-term analysis reveals markedly divergent patterns of functional diversity across three major land-use types with increasing land-use intensity. Our results support our expectation that land-use intensity mediates both the long-term direction of changes and the stability of functional traits in arthropods.

In line with our first prediction, croplands exhibited the most substantial declines in functional richness and divergence over time, while functional richness in forests and grasslands has either remained relatively stable or increased. In croplands, both carabid and spider communities became increasingly homogenised, reflecting intensified environmental filtering and loss of niche differentiation. These declines indicate that cropland assemblages progressively lost functional trait space over the study period, rather than simply reflecting consistently low functional diversity. The functional impoverishment observed in croplands aligns with other studies showing that disturbed habitats favour functionally similar, generalist species (Gossner et al. 2016; Simons et al. 2014). Losses of carabids with specific traits, such as larger body size, lower dispersal capacity, and shorter activity periods, have also been documented in other studies (Kotze and O'Hara 2003; Martínez-Núñez et al. 2024), indicating that trait erosion is not random but reflects selective filtering of ecologically distinctive species. This reduction in arthropod functional diversity within croplands occurred despite the introduction of agri-environmental requirements such as the implementation of biodiversity-promoting areas and further measures to support a more environmentally friendly agriculture since the early 1990s (OECD 2017). However, while the proportion of biodiversity-promoting areas is relatively high (almost 20% of the Swiss agricultural area), it has considerably increased in agricultural grasslands over the past few decades. Nevertheless, it remains very low in arable croplands (below 2%) (Federal Office for Agriculture 2025). Moreover, land-use intensity in croplands has remained high, and pesticide hazard has increased worldwide, including Switzerland (Wolfram et al. 2026). In particular, the rise of systemic insecticides such as neonicotinoids from the 1990s onwards (Simon-Delso et al. 2015; Humann-Guilleminot et al. 2019), before key active substances were banned in open-field agriculture in the late 2010s in Europe (including Switzerland, Federal Office for Agriculture (FOAG/BLW) 2018), likely increased risks for arthropods. Many of these highly toxic substances are still present, not only in conventionally managed crops, but also in organic fields and biodiversity-promotion areas within Swiss croplands (Humann-Guilleminot et al. 2019).

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Functional richness in forests and grasslands has either remained relatively stable or increased over the last ~40 years in the studied Swiss landscapes. In forests, management has changed from a timber production focus towards sustainable, multifunctional forest management, with an explicit emphasis on conserving forests as close-to-nature ecosystems since the adoption of the Swiss Federal Act on Forest (1991). In practice, this approach promoted natural regeneration, mixed and site-adapted stands, structural heterogeneity, deadwood retention and low-disturbance refugia, all of which can increase microhabitat diversity for ground-dwelling arthropods (Stritih et al. 2026). In addition to local habitat conditions, broader land-use transitions may have contributed to these patterns; for instance, secondary forest expansion and increased connectivity may have facilitated forest-associated species and partly supported the positive functional trends observed in forests. In fact, in forests, carabid and spider communities also showed signs of growing resilience and niche differentiation, particularly through increased functional evenness and divergence in carabids, alongside increases in spider functional richness and reduced redundancy. These patterns suggest resilient and well-structured communities benefitting from microclimatic heterogeneity and habitat complexity, consistent with the overall improvement in structural diversity and ecological condition of Swiss forests in recent decades (de Sassi et al. 2020; Strauss and Fischer 2025; Seibold et al. 2023). Importantly, forests in this study supported ~30% of total carabid and ~55% of total spider functional richness, highlighting their role as critical reservoirs of ground-dwelling arthropod diversity at the regional scale (Brooks et al. 2012; Junggebauer et al. 2024).

Grasslands also exhibited increases in functional richness, particularly among carabids, together with gains in functional redundancy and divergence. These patterns may partly reflect Swiss agri-environmental measures promoting extensively managed grasslands through delayed mowing, reduced fertilisation, lower stocking rates and improved connectivity (Federal Office for Agriculture 2025; Meier et al. 2024; Neff et al. 2020). However, spider communities did not show such positive changes. These contrasting responses that need to be considered by conservation management (van Klink et al. 2022) likely reflect the lack of important vertical vegetation structure and habitat complexity for spiders in grasslands (Langellotto and Denno 2004). Overall, our findings suggest that permanent grasslands can support the development of diverse arthropod carabid communities over time (Allan et al. 2014; Manning et al. 2015).

Changes in assemblage structure were further reflected in contrasting trends in functional specialisation and redundancy. In forests, both carabids and spiders became progressively more functionally specialised, while functional redundancy declined. This combination suggests an increasing differentiation of functional roles, consistent with stronger niche structuring through time. In contrast, cropland assemblages showed declining functional specialisation together with increasing redundancy, indicating a shift towards more functionally similar communities. This pattern is consistent with intensified environmental filtering in croplands, where recurrent disturbance and management may constrain the set of trait combinations and promote functional homogenisation. Similar patterns of reduced functional distinctiveness under intensive land use have been reported for arthropods (Birkhofer et al. 2015, 2017).

Analyses of three key effect traits provided further insights into how assemblage shifts may influence ecosystem functions. In croplands, carabid effect traits remained relatively stable despite diversity declines, suggesting some functions persist because common species (e.g., *Poecilus cupreus*) cover much of the effect-trait space (Rouabah et al. 2024). In contrast, spiders showed strong declines, reflecting changes in functional trait composition that may have implications for functions such as prey suppression and trophic regulation. Thus, long-term species losses can alter functional dimensions in different ways depending on the taxa and traits involved. More broadly, the contrasting trajectories observed for carabids and spiders highlight the importance of multitaxon assessments when evaluating long-term changes in biodiversity and functional traits, suggesting that studies using single taxonomic groups (e.g., carabids) may provide an incomplete picture of how functional diversity shifts over time.

Finally, our results show that forests, though functionally rich, show the greatest potential for functional richness loss under future species extinctions because their low redundancy means that unique functional roles cannot easily be replaced (Mouillot et al. 2013). Grasslands showed more balanced richness and redundancy and exhibited intermediate levels of functional richness loss, while croplands showed the lowest functional richness loss under simulated species extinctions, because long-term filtering has already removed most unique traits. These results emphasise that conservation and management strategies should be tailored to the ecological context in which biodiversity change occurs. Although enhancing the ecological quality of forests and grasslands can benefit regional biodiversity, our results suggest that such measures alone may not prevent continued losses of functional diversity within croplands. Cropland biodiversity, therefore, requires targeted measures that directly reduce filtering pressures and promote habitat and resource heterogeneity within agricultural production systems. From a conservation perspective, our results suggest that forest management should prioritise the persistence of rare and functionally distinct species, for example, by maintaining habitat heterogeneity, structurally complex stands and low-disturbance refugia. Conversely, cropland restoration may be most effective where the regional species pool has not yet been severely eroded and where management reduces filtering pressures through less intensive practices and greater habitat diversification. Moreover, genera dominated by large-bodied and low-dispersal species contributed disproportionately to functional richness. As these traits are among the most threatened under anthropogenic land-use change (Martínez-Núñez et al. 2024), their consistent patterns across both carabids and spiders highlight their value as bioindicators of functional integrity and emphasise the need to prioritise conservation of species carrying these scarce trait combinations.

4.1 | Conclusions

Our findings show that long-term changes in arthropod functional diversity are strongly shaped by land-use type. Forests

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

currently maintain high functional richness, yet their low redundancy suggests greater potential for functional richness loss under future species extinctions. Grasslands show relatively stable functional trajectories, particularly for carabids, likely supported by habitat heterogeneity and targeted agri-environmental measures. In contrast, croplands exhibit pronounced functional erosion and homogenisation, potentially affecting the ecosystem functions of arthropod communities. These contrasting trajectories highlight that the capacity of ecosystems to buffer functional losses depends on habitat complexity and the degree of anthropogenic pressure. The different responses of carabids and spiders further demonstrate that assessments based on a single taxonomic group may provide an incomplete picture of biodiversity change and its potential functional consequences. Conservation strategies must therefore be tailored to land-use context: preserving forests to prevent the loss of unique functional roles, maintaining and expanding biodiversity-friendly management in grasslands, and restoring functional potential in croplands by reducing chemical inputs and increasing structural diversity. Such efforts will be crucial to sustain arthropod functional diversity and the ecosystem services it supports, including natural pest regulation, in a changing world.

Author Contributions

C.M.-N. conceived the study and led the main analyses and writing. M.M.G., F.N., M.A., and M.M. contributed substantially to the development of ideas during the early stages of the work. M.K.O., M.M.G., F.H., K.B., P.D., E.K., and H.L. contributed to data acquisition, provided expertise on the study system, and offered valuable feedback that improved successive manuscript versions. All authors discussed the results and approved the final version of the manuscript.

Acknowledgements

We are greatly thankful to all project managers, taxonomy experts, and technicians who contributed to the collection and assembly of this dataset. We also thank the three Swiss Research Institutes (Agroscope, FiBL and WSL) involved in these projects for sharing the data. We thank Henryk Luka for the identification of carabid species, Gilles Blandenier, Xaver Heer, Jaklina Steiger and Stefano Pozzi for the identification of spider species.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code associated with this article are currently available in Zenodo, in the following link: 10.5281/zenodo.17710826.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ele.70457.

References

Allan, E., O. Bossdorf, C. F. Dormann, et al. 2014. "Interannual Variation in Land-Use Intensity Enhances Grassland Multidiversity." *Proceedings of the National Academy of Sciences of the United States of America* 111, no. 1: 308–313. https://doi.org/10.1073/pnas.1312213111.

Birkhofer, K., M. M. Gossner, T. Diekötter, et al. 2017. "Land-Use Type and Intensity Differentially Filter Traits in Above-and Below-Ground Arthropod Communities." *Journal of Animal Ecology* 86, no. 3: 511–520.

Birkhofer, K., H. G. Smith, W. W. Weisser, V. Wolters, and M. M. Gossner. 2015. "Land-Use Effects on the Functional Distinctness of Arthropod Communities." *Ecography* 38, no. 9: 889–900.

Brooks, D. R., J. E. Bater, S. J. Clark, et al. 2012. "Large Carabid Beetle Declines in a United Kingdom Monitoring Network Increases Evidence for a Widespread Loss in Insect Biodiversity." *Journal of Applied Ecology* 49, no. 5: 1009–1019. https://doi.org/10.1111/j.1365-2664.2012.02194.x.

Cardoso, P., S. Pekár, K. Birkhofer, et al. 2025. "Ecosystem Services Provided by Spiders." *Biological Reviews* 100: 2217–2236. https://doi.org/10.1111/brv.70044.

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. "Traits Without Borders: Integrating Functional Diversity Across Scales." *Trends in Ecology & Evolution* 31, no. 5: 382–394. https://doi.org/10.1016/j.tree.2016.02.003.

Chao, A., and R. K. Colwell. 2014. "Rarefaction and Extrapolation With Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies Rarefaction and Extrapolation With Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." *Ecological Monographs* 84, no. 1: 45–67. https://doi.org/10.1890/13-0133.1.

Chase, J. M., and M. A. Leibold. 2013. "Ecological Niches." In *Ecological Niches*. University of Chicago Press. https://doi.org/10.7208/CHICAGO/9780226101811.001.0001.

Crossley, M. S., A. R. Meier, E. M. Baldwin, et al. 2020. "No Net Insect Abundance and Diversity Declines Across US Long Term Ecological Research Sites." *Nature Ecology & Evolution* 4, no. 10: 1368–1376. https://doi.org/10.1038/s41559-020-1269-4.

CSCF–Infofauna. 2024. "National Inventory of Swiss Fauna: Araneae and Coleoptera (Carabidae)." Neuchâtel, Switzerland. https://www.infofauna.ch.

de Sassi, C., B. Stadler, M. Bolliger, and R. Schnidrig. 2020. "Vision of Nature Conservation in Swiss Forests." In *How to Balance Forestry and Biodiversity Conservation. A View Across Europe*, edited by F. Krumm, A. Schuck, and A. Rigling, 173–181. European Forest Institute (EFI); Swiss Federal Institute for Forest, Snow and Landscape Research (WSL).

Dee, L. E., J. Cowles, F. Isbell, S. Pau, S. D. Gaines, and P. B. Reich. 2019. "When Do Ecosystem Services Depend on Rare Species?" *Trends in Ecology & Evolution* 34, no. 8: 746–758. https://doi.org/10.1016/j.tree.2019.03.010.

Delarze, R., Y. Gonseth, S. Eggenberg, and M. Vust. 2015. "Lebensräume der Schweiz Ökologie—Gefährdung—Kennarten."

"Federal Act on Forest (Forest Act, ForA) of 4 October 1991, SR 921.0." Status as of 1 August 2025. Fedlex. https://www.fedlex.admin.ch/eli/cc/1992/2521_2521_2521/en.

Federal Office for Agriculture. 2025. "Agricultural Report 2025." Bern, Switzerland.

Federal Office for Agriculture (FOAG/BLW). 2018. "Verbot von drei Neonikotinoiden im Freiland ab Ende 2018[Decision on Restricting the Use of Clothianidin, Imidacloprid, and Thiamethoxam in Open-Field Agriculture]." Bern: Federal Department of Economic Affairs, Education and Research (EAER).

Fontana, S., O. L. Petchey, and F. Pomati. 2016. "Individual-Level Trait Diversity Concepts and Indices to Comprehensively Describe Community Change in Multidimensional Trait Space." *Functional Ecology* 30, no. 5: 808–818. https://doi.org/10.1111/1365-2435.12551.

Frainer, A., B. G. McKie, and B. Malmqvist. 2014. "When Does Diversity Matter? Species Functional Diversity and Ecosystem Functioning

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Across Habitats and Seasons in a Field Experiment." *Journal of Animal Ecology* 83, no. 2: 460–469. https://doi.org/10.1111/1365-2656.12142.

Gallé, R., C. Geppert, R. Földesi, T. Tscharntke, and P. Batáry. 2020. "Arthropod Functional Traits Shaped by Landscape-Scale Field Size, Local Agri-Environment Schemes and Edge Effects." *Basic and Applied Ecology* 48: 102–111. https://doi.org/10.1016/j.baae.2020.09.006.

Gossner, M. M., T. M. Lewinsohn, T. Kahl, et al. 2016. "Land-Use Intensification Causes Multitrophic Homogenization of Grassland Communities." *Nature* 540, no. 7632: 266–269. https://doi.org/10.1038/nature20575.

Greenop, A., B. A. Woodcock, C. L. Outhwaite, et al. 2021. "Patterns of Invertebrate Functional Diversity Highlight the Vulnerability of Ecosystem Services Over a 45-Year Period." *Current Biology* 31, no. 20: 4627–4634. https://doi.org/10.1016/J.CUB.2021.07.080.

Hallmann, C. A., M. Sorg, E. Jongejans, et al. 2017. "More Than 75 Percent Decline Over 27 Years in Total Flying Insect Biomass in Protected Areas." *PLoS One* 12, no. 10: e0185809. https://doi.org/10.1371/journal.pone.0185809.

Harvey, J. A., R. Heinen, I. Armbrecht, et al. 2020. "International Scientists Formulate a Roadmap for Insect Conservation and Recovery." *Nature Ecology & Evolution 2020 4:2* 4, no. 2: 174–176. https://doi.org/10.1038/s41559-019-1079-8.

Hevia, V., C. P. Carmona, F. M. Azcárate, et al. 2016. "Effects of Land Use on Taxonomic and Functional Diversity: A Cross-Taxon Analysis in a Mediterranean Landscape." *Oecologia* 181, no. 4: 959–970. https://doi.org/10.1007/s00442-015-3512-2.

Humann-Guilleminot, S., Ł. J. Binkowski, L. Jenni, G. Hilke, G. Glauser, and F. Helfenstein. 2019. "A Nation-Wide Survey of Neonicotinoid Insecticides in Agricultural Land With Implications for Agri-Environment Schemes." *Journal of Applied Ecology* 56: 1502–1514. https://doi.org/10.1111/1365-2664.13392.

Isbell, F., J. Cowles, L. E. Dee, et al. 2018. "Quantifying Effects of Biodiversity on Ecosystem Functioning Across Times and Places." *Ecology Letters* 21, no. 6: 763–778. https://doi.org/10.1111/ELE.12928.

Junggebauer, A., C. Bluhm, G. Erdmann, S. L. Bluhm, M. M. Pollierer, and S. Scheu. 2024. "Temporal Variation of Soil Microarthropods in Different Forest Types and Regions of Central Europe." *Oikos* 2024, no. 10: e10513. https://doi.org/10.1111/oik.10513.

Koivula, M. J. 2011. "Useful Model Organisms, Indicators, or Both? Ground Beetles (Coleoptera, Carabidae) Reflecting Environmental Conditions." *ZooKeys* 100: 287–317. https://doi.org/10.3897/ZOOKEYS.100.1533.

Kotze, D. J., and R. B. O'Hara. 2003. "Species Decline—But Why? Explanations of Carabid Beetle (Coleoptera, Carabidae) Declines in Europe." *Oecologia* 135, no. 1: 138–148. https://doi.org/10.1007/s00442-002-1174-3.

Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity From Multiple Traits." *Ecology* 91, no. 1: 299–305. https://doi.org/10.1890/08-2244.1.

Langellotto, G. A., and R. F. Denno. 2004. "Responses of Invertebrate Natural Enemies to Complex-Structured Habitats: A Meta-Analytical Synthesis." *Oecologia* 139, no. 1: 1–10. https://doi.org/10.1007/s00442-004-1497-3.

Lavorel, S., and E. Garnier. 2002. "Predicting Changes in Community Composition and Ecosystem Functioning From Plant Traits: Revisiting the Holy Grail." *Functional Ecology* 16, no. 5: 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x.

Lövei, G. L., and K. D. Sunderland. 1996. "Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae)." *Annual Review of Entomology* 41, no. 1: 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311.

Manning, P., M. M. Gossner, O. Bossdorf, et al. 2015. "Grassland Management Intensification Weakens the Associations Among the Diversities of Multiple Plant and Animal Taxa." *Ecology* 96, no. 6: 1492–1501. https://doi.org/10.1890/14-1307.1.

Martínez-Núñez, C., M. M. Gossner, C. Maurer, et al. 2024. "Land-Use Change in the Past 40 Years Explains Shifts in Arthropod Community Traits." *Journal of Animal Ecology* 93, no. 5: 540–553. https://doi.org/10.1111/1365-2656.14062.

Meier, E. S., G. Lüscher, F. Herzog, and E. Knop. 2024. "Collaborative Approaches at the Landscape Scale Increase the Benefits of Agri-Environmental Measures for Farmland Biodiversity." *Agriculture, Ecosystems & Environment* 367: 108948. https://doi.org/10.1016/j.agee.2024.108948.

Mori, A. S., F. Isbell, and R. Seidl. 2018. "β-Diversity, Community Assembly, and Ecosystem Functioning." *Trends in Ecology & Evolution* 33, no. 7: 549–564. https://doi.org/10.1016/J.TREE.2018.04.012.

Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. "Functional Diversity Measures: An Overview of Their Redundancy and Their Ability to Discriminate Community Assembly Rules." *Functional Ecology* 24, no. 4: 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Mouillot, D., D. R. Bellwood, C. Baraloto, et al. 2013. "Rare Species Support Vulnerable Functions in High-Diversity Ecosystems." *PLoS Biology* 11, no. 5: e1001569. https://doi.org/10.1371/journal.pbio.1001569.

Neff, F., F. Korner-Nievergelt, E. Rey, et al. 2022. "Different Roles of Concurring Climate and Regional Land-Use Changes in Past 40 Years' Insect Trends." *Nature Communications* 13, no. 1: 7611. https://doi.org/10.1038/s41467-022-35223-3.

Neff, F., M. C. Resch, A. Marty, et al. 2020. "Long-Term Restoration Success of Insect Herbivore Communities in Seminatural Grasslands: A Functional Approach." *Ecological Applications* 30, no. 6: e02133. https://doi.org/10.1002/eap.2133.

OECD. 2017. *Reforming Agricultural Subsidies to Support Biodiversity in Switzerland: Country Study. OECD Environment Policy Papers, No. 8*. OECD Publishing. https://doi.org/10.1787/53c0e549-en.

Outhwaite, C. L., P. McCann, and T. Newbold. 2022. "Agriculture and Climate Change Are Reshaping Insect Biodiversity Worldwide." *Nature* 2022: 1–6. https://doi.org/10.1038/s41586-022-04644-x.

Pavoine, S. 2020. "Adiv: An r Package to Analyse Biodiversity in Ecology." *Methods in Ecology and Evolution* 11, no. 9: 1106–1112. https://doi.org/10.1111/2041-210X.13430.

Petchey, O. L., and K. J. Gaston. 2002. "Functional Diversity (FD), Species Richness and Community Composition." *Ecology Letters* 5, no. 3: 402–411. https://doi.org/10.1046/J.1461-0248.2002.00339.X.

Potapov, A. M., N. Dupérré, M. Jochum, et al. 2020. "Functional Losses in Ground Spider Communities due to Habitat Structure Degradation Under Tropical Land-Use Change." *Ecology* 101, no. 3: e02957. https://doi.org/10.1002/ecy.2957.

R Core Team. 2021. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rosenfeld, J. S. 2002. "Functional Redundancy in Ecology and Conservation." *Oikos* 98, no. 1: 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x.

Rouabah, A., F. Lasserre-Joulin, S. Plantureux, S. Taugourdeau, and B. Amiaud. 2024. "Functional Trait Composition of Carabid Beetle Communities Predicts Prey Suppression Through Both Mass Ratio and Niche Complementarity Mechanisms." *Insect Science* 31, no. 2: 562–574. https://doi.org/10.1111/1744-7917.13261.

Seibold, S., M. M. Gossner, N. K. Simons, et al. 2019. "Arthropod Decline in Grasslands and Forests Is Associated With Landscape-Level

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Drivers." *Nature* 574, no. 7780: 671–674. https://doi.org/10.1038/s41586-019-1684-3.

Seibold, S., W. W. Weisser, D. Ambarlı, et al. 2023. "Drivers of Community Assembly Change During Succession in Wood-Decomposing Beetle Communities." *Journal of Animal Ecology* 92, no. 5: 965–978. https://doi.org/10.1111/1365-2656.13843.

Simon-Delso, N., V. Amaral-Rogers, L. P. Belzunces, et al. 2015. "Systemic Insecticides (Neonicotinoids and Fipronil): Trends, Uses, Mode of Action and Metabolites." *Environmental Science and Pollution Research* 22: 5–34. https://doi.org/10.1007/s11356-014-3470-y.

Simons, N. K., M. M. Gossner, T. M. Lewinsohn, et al. 2014. "Resource-Mediated Indirect Effects of Grassland Management on Arthropod Diversity." *PLoS One* 9, no. 9: e107033. https://doi.org/10.1371/journal.pone.0107033.

Stekhoven, D. J., and P. Bühlmann. 2012. "MissForest—Non-Parametric Missing Value Imputation for Mixed-Type Data." *Bioinformatics* 28, no. 1: 112–118. https://doi.org/10.1093/bioinformatics/btr597.

Strauss, A., and C. Fischer. 2025. "Forest Report 2025. Development, Condition and Use of Swiss forests. Federal Office for the Environment FOEN, Bern and Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf." p. 159.

Stritih, A., J. Lecina-Diaz, J. Mohr, et al. 2026. "Can "Closer-To-Nature" Forest Management Sustain Biodiversity and Ecosystem Services in an Uncertain Future? Lessons From Central Europe." *Current Forestry Reports* 12: 1. https://doi.org/10.1007/s40725-025-00264-6.

van Klink, R., D. E. Bowler, K. B. Gongalsky, and J. M. Chase. 2022. "Long-Term Abundance Trends of Insect Taxa Are Only Weakly Correlated." *Biology Letters* 18, no. 2: 20210554. https://doi.org/10.1098/rsbl.2021.0554.

Vidal, M. C., and S. M. Murphy. 2018. "Bottom-Up vs. Top-Down Effects on Terrestrial Insect Herbivores: A Meta-Analysis." *Ecology Letters* 21, no. 1: 138–150. https://doi.org/10.1111/ele.12874.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89, no. 8: 2290–2301. https://doi.org/10.1890/07-1206.1.

Wolfram, J., D. Bussen, S. Bub, L. L. Petschick, L. Z. Herrmann, and R. Schulz. 2026. "Increasing Applied Pesticide Toxicity Trends Counteract the Global Reduction Target to Safeguard Biodiversity." *Science* 391, no. 6785: 616–621.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Methodological details and additional robustness analyses. **Table S1:** Contributing institutions and studies. **Table S2:** Annual sample numbers per land-use type (Carabidae and Araneae). **Table S3:** Number of sites with repeated measures. **Table S4:** Carabid traits and their ecological implications. **Table S5:** Spider traits and their ecological implications. **Table S6:** Phylogenetic signal in traits. **Table S7:** Temporal trends of functional diversity across land-use types. **Table S8:** Changes in functional diversity metrics by land-use type. **Table S9:** Functional importance ranking of carabid species. **Table S10:** Functional importance ranking of spider species. **Figure S1:** Map of Switzerland with sampling sites by land-use type. **Figure S2:** Distribution of sampling effort (days, timing, trap type, size). **Figure S3:** Temporal distribution of sampling effort across land-use types. **Figure S4:** Differences in trapping fluids. **Figure S5:** Spatial distribution of sites across land-use types and decades. **Figure S6:** Sampling coverage of carabids and spiders by land-use type. **Figure S7:** Coverage achieved with 90 traps per year. **Figure S8:** Sensitivity analysis: results including mean latitude as a covariate. **Figure S9:** Sensitivity analysis: results using a more common restricted timeframe. **Figure S10:** Relationship between taxonomic and functional diversity. **Figure S11:** Forecasted loss of functional richness under species loss scenarios using effect traits only. **Figure S12:** Functional uniqueness or specialisation of beetle and spider genera.

14610248, 2026, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.70457 by Felix Neff - Paul Scherrer Institut PSI , Wiley Online Library on [27/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License