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RESEARCH ARTICLE

Land-use change in the past 40 years explains shifts in arthropod community traits

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Abstract

1. Understanding how anthropogenic activities induce changes in the functional traits of arthropod communities is critical to assessing their ecological consequences. However, we largely lack comprehensive assessments of the long-term impact of global-change drivers on the trait composition of arthropod communities across a large number of species and sites. This knowledge gap critically hampers our ability to predict human-driven impacts on communities and ecosystems.

2. Here, we use a dataset of 1.73 million individuals from 877 species to study how four functionally important traits of carabid beetles and spiders (i.e. body size, duration of activity period, tolerance to drought, and dispersal capacity) have changed at the community level across ~40 years in different types of land use and as a consequence of land use changes (that is, urbanisation and loss of woody vegetation) at the landscape scale in Switzerland.

3. The results show that the mean body size in carabid communities declined in all types of land use, with particularly stronger declines in croplands compared to forests. Furthermore, the length of the activity period and the tolerance to drought of spider communities decreased in most land use types. The average body size of carabid communities in landscapes with increased urbanisation in the last ~40 years tended to decrease. However, the length of the activity period, the tolerance to drought, and the dispersal capacity did not change significantly. Furthermore, urbanisation promoted increases in the average dispersal capacities of spider communities. Additionally, urbanisation favoured spider communities with larger body sizes and longer activity periods. The loss of woody areas at the landscape level was associated with trait shifts to carabid communities with

larger body sizes, shorter activity periods, higher drought tolerances and strongly decreased dispersal capacities. Decreases in activity periods and dispersal capacities were also found in spider communities.

4. Our study demonstrates that human-induced changes in land use alter key functional traits of carabid and spider communities in the long term. The detected trait shifts in arthropod communities likely have important consequences for their functional roles in ecosystems.

KEYWORDS
body size, carabid beetles, dispersal capacity, phenology, spiders, tolerance to drought, urbanisation

1 | INTRODUCTION

Concern over human-induced alteration of arthropod communities has grown in the last years (Seibold et al., 2019; Wagner et al., 2021). Recently, some studies have reported pronounced long-term impacts of global change on arthropod communities (Crossley et al., 2020; Outhwaite et al., 2022). However, how anthropogenic activities such as land use change can alter the trait composition of arthropod communities over long time periods remains largely unexplored. Environmental filtering of communities imposed by land-use change is hypothesised to adversely affect some species disproportionally while favouring others, depending on their response traits (i.e. traits that determine the response of species to environmental factors) (Birkhofer et al., 2017; Lamarre et al., 2022; Neff et al., 2022; Outhwaite et al., 2022). Such changes involving loser and winner species (Lamarre et al., 2022) can lead to directional and potentially predictable shifts in the trait composition of arthropod communities (Brousseau et al., 2018; Gebert et al., 2022; Wong et al., 2019) which can affect their functional properties (Correa-Carmona et al., 2022; Gallé et al., 2020; Gámez-Virués et al., 2015; Gebert et al., 2022; Martinson & Raupp, 2013) and thus ecosystem functioning (Wang et al., 2022; Wong et al., 2019). For example, smaller arthropod species are likely less adversely affected than larger ones in perturbed and low-resource habitats due to their lower energetic requirements, faster development and higher probability of escaping from perturbations (Moretti et al., 2017; Peters, 1983). In addition, arthropods that exhibit brief activity periods could thrive more successfully in disturbed habitats, associated with the need to exploit increasingly restricted resources and escape from perturbations (Johansson et al., 2020; Leather et al., 1993). Species with higher drought tolerance could be favoured compared to species with lower tolerance in more open and exposed habitats because they could cope better with warmer and drier environmental conditions (Potapov et al., 2020; Weldon et al., 2016), and species with a high dispersal capacity could be better able to (re)colonise more fragmented and frequently disturbed habitats (Entling et al., 2011; Kneitel, 2018; Lövei & Sunderland, 2003). Some of these predictions have been tested in small-scale experiments or temporal snapshot studies across anthropogenic gradients for single species or communities of arthropods in single case studies. However, there is a significant need for comprehensive studies that consider long-term temporal changes in the trait composition of whole arthropod communities across a large number of sites to better understand and predict anthropogenic shifts in arthropod traits at the community level.

Land use change is considered a key global change driver affecting arthropod communities (Birkhofer et al., 2017). In particular, urbanisation and the loss of woody areas are two major processes that can erode abundance and diversity of arthropods (Forman & Baudry, 1984; Meyfroidt & Lambin, 2011; Tscharntke et al., 2005, 2012) and potentially cause functional filtering (Correa-Carmona et al., 2022; Martinson & Raupp, 2013; Merckx et al., 2018; Schirmel et al., 2016; Simons et al., 2016). In addition, arthropod communities inhabiting different major land-use types of the temperate zone such as forests, managed grasslands or crops are likely to differ in their vulnerability to environmental changes. Therefore, these different communities may exhibit contrasting long-term temporal responses to anthropogenic perturbations (Newbold et al., 2015; Seibold et al., 2019). However, most previous studies have focused on temporal snap shots of arthropod communities sampled across sites differing in land use at a local scale typically considering relatively few species. Hence, we largely lack comprehensive assessments of long-term changes in arthropod community composition and potential trait changes, hampering our ability to understand and predict long-term consequences for arthropod communities and their functional roles in ecosystems (Schirmel et al., 2016; Simons et al., 2016). In particular, we lack knowledge on whether changes in community traits are consistent across different types of land use and how they can differ between local and larger scales. In addition, we still do not know which traits are characteristic of species that are more vulnerable than others to land-use changes and how important species turnover is compared to less evident changes in species relative abundances (Whittaker, 1965). Although this knowledge is crucial for a better understanding of the processes underlying temporal shifts in community traits, our comprehension of the environmental impact on multiple functional key traits remains limited.

Here, we examine long-term (~40 years) changes in four key response traits of carabid and spider communities (i.e. body size,

length of the activity period, the tolerance to drought and dispersal capacity) for three main land-use types (i.e. forests, managed grasslands and crops) and two different scenarios of landscape change (i.e. increasing vs. not increasing urbanisation—impervious area including buildings and roads—and loss vs. no loss of woody area—open forested areas, treelines, groups of trees, thickets, shrublands and hedgerows) across a large number of species and sites. We analysed an extensive data set of 1.73 million individuals from 877 carabid and spider species collected with 51,250 pitfall traps in Switzerland. We tested five predictions for long-term trait changes in arthropod communities associated with local land use type and landscape change: arthropod communities (i) will change over time towards a smaller mean body size, especially in the most perturbed and intensively used land use types (i.e. crops and grasslands); (ii) the mean length of the activity period will decrease, as a consequence of requirements to exploit increasingly restricted resources and escape from perturbations; (iii) the mean tolerance to drought will increase, likely related to urbanisation and loss of woody vegetation (Dias et al., 2013; Potapov et al., 2020; Weldon et al., 2016); and (iv) mean dispersal capacity will increase in perturbed and fragmented areas. Furthermore, we expect (v) stronger changes when focusing on species turnover only (community mean) compared to accounting for species abundance distributions (community weighted mean), since dominant species might stabilise community weighted composition.

2 | MATERIALS AND METHODS

2.1 | Arthropod dataset

The data set used in this study was compiled from 32 different studies conducted in Switzerland between 1974 and 2018 (Table S1). In total, 51,250 samples were collected during 36 years of data collection (spanning 44 years) across 1367 sites representing six types of land use that reflect various perturbation regimes. We focus on data of arthropod communities sampled with pitfall traps as it represents a relatively standardised method, yielding comparable data for different time periods across different land use types (Table S2 for detailed description of the number of sampled years for each land use type, Figure S1 and Methods S1 for more details about pitfall trap samples). These studies did not require ethical approval or permission for fieldwork.

Classification of sampled habitats into these main land use types followed the standard categorisation for Swiss land use types proposed by Delarze and Goseth (2008; see also Table S3). The three dominant land use types of the study region for which long-term data of arthropods are available are forests (i.e. interiors of forested woody areas), grasslands (i.e. permanent grasslands which are mostly agriculturally managed meadows and pastures), and crops (include different arable crops such as cereals, corn, or vegetables) (see Table S4 for the full list of sampled crops). Furthermore, arthropods were collected in less dominant land use types including wetlands (i.e. areas dominated by vegetation closely associated with

freshwater bodies), linear vegetation elements (i.e. linear ecotone structures with mainly herbaceous and woody vegetation such as forest edges and hedgerows) and ruderal habitats (i.e. herbaceous pioneer vegetation). Although the whole data set was used for completeness and to improve the parameterisation of the covariables in the models, we focus more attention on the three dominant land use types (forests, grasslands and crops), because they represent the main land use types of the study region encompassing most samples in our dataset (~73% of samples). Furthermore, the data for these types of land use covered longer time periods, had fewer temporal gaps, and allowed more robust trend estimates. The sample size consisted of 17,918 samples from forests (from 1974 to 2013), 11,326 samples from grasslands (from year 1985 to year 2008) and 9124 samples from crops (from year 1983 to year 2018). Furthermore, 1694 samples were collected in wetlands (from 1991 to 2007), 5426 samples in linear vegetation structures (from 1976 to 2014) and 5762 samples in ruderal habitats (from 1985 to 2018) (see Table S5 for detailed information on the number of samples per land use type, year and taxonomic group).

Approximately 80% of all sampling sites were located in the Swiss lowlands (below 700m a.s.l.; mean altitude: 513m a.s.l.) (Figure S1). While some studies included sites that were sampled repeatedly for several years (maximum 8years), most studies covered few years and most sites were only sampled in a single year (Table S6), and thus, the effects of site were randomised across years (see Section 2.4.4).

Additionally, we calculated, for each study site and sampled year the mean annual temperature and precipitation, using high resolution maps (1km side grid cell) available from the Federal Office of Meteorology and Climatology MeteoSwiss (https://www.meteoswiss.admin.ch).

2.2 | Arthropod groups and traits

Carabids and spiders are two highly diversified and functionally important groups of arthropods. Most species in these groups are generalist predators, thus playing a crucial role in food webs, and many species can also be important for pest management in agricultural systems. For both taxonomic groups, we analysed long-term changes in four key traits (response traits) that are likely to moderate species' responses to drivers of global change, including changes in land use (Table S7). The selected traits were (Moretti et al., 2017): body size (length in mm), duration of the activity period (period of adult activity in months), tolerance to drought (ordinal factor: steno-hygrophil, hygrophil, mesophil, xerophil and steno-xerophil) and dispersal capacity. Dispersal capacity was assessed for carabids based on wing development type (ordinal factor) as a commonly used proxy of dispersal capacity, that is short-winged, dimorphic, long-winged; while for spiders it was assessed based on expert classification of dispersal capacity (score from 0 to 1, see Gossner et al., 2015). The selected traits are not only considered to play an important role in species sensitivity to anthropogenic change (response traits), but are also considered functionally important (functional traits) (see hypotheses

in Section 1 and Table S7 for an overview of the expected ecological implications of the traits studied). Traits were obtained from several sources, such as published literature (Cardoso et al., 2011; Gossner et al., 2015; Homburg et al., 2014), and trait databases (Fauna indicativa https://www.infofauna.ch/fr/faune-de-suisse/insectes, and European spider trait database https://araneae.nmbe.ch/), considering a wide range of literature on the autecology of species.

To enhance the robustness of trait analyses and to avoid the effect of transient species as well as potential noise in the data introduced by very rare species, singletons were removed (Bihn et al., 2010), resulting in a total of 287 carabid species (18 singletons removed) and 421 spider species (48 singletons removed) included in the final analyses. Because singletons (i.e. species represented by only one individual in the dataset) can potentially affect community means, we tested whether the exclusion of singletons affected the means of the trait community for the four traits and the two taxonomic groups. However, the results were almost identical with and without the inclusion of singletons in the analyses (Pearson correlation test: $r > 0.999$; p-value < 0.001 in all cases). The information about the traits of the carabids was complete, with the exception of two carabid species that lacked the category of wing development. Of the 421 spider species included in the analysis, 18 lack body size values, 43 lack values on the length of their activity period, 135 lack dispersal capacity values, and 169 lack drought tolerance values. Missing trait values were imputed using a random forest approach (Stekhoven & Bühlmann, 2012), starting with traits that had fewer lacking values. Apart from the four traits of interest, we used 16 additional trait variables (Table S8) to ensure a more precise imputation of missing values (Stekhoven & Bühlmann, 2012). The out-of-bag (OOB) error (i.e. estimate of the model's prediction accuracy using the out-of-bag samples, those in the data partition not used to train the model, from the random forest as a validation set) for imputed data was 3.3, 10.5, 0 and 0.6 respectively, which resulted in an overall high accuracy of 99.7% correct trait information. The traits were generally not correlated (Figure S2), except for a negative correlation of body size and dispersal capacity (i.e. wing length type) in carabids (Spearman correlation test: $r = -0.62$, $p < 0.001$), which must be considered when interpreting the results of these two traits in carabids.

To examine the role of species relative abundances compared to changes caused by species turnover alone, we included two centrality measures of community traits: community weighted means, calculated with the *dbFD* function of the *FD* package (Laliberte & Legendre, 2010) in R (which represents relative abundances of species and thus reflecting the observed structure of the community), and community means (which do not consider relative abundances and reflect changes produced by species turnover alone).

2.3 | Change in land use at the landscape level

To study the landscape-scale impact of increased urban area (urbanisation; i.e. impervious areas, including buildings and roads) and loss of woody vegetation (i.e. loss of open forested areas, treelines, clusters of trees, thickets, shrublands, and hedgerows) on arthropod community mean traits, we used a $100\,m \times 100\,m$ cell resolution land-cover classification, obtained from orthophotographs (Arealstatistik Schweiz: the first Arealstatistik map covers the time period 1979–1985, and the last one covers the time period 2013–2018; classifications and nomenclature according to NOLC04- 27 categories). We calculated the change in the number of cells classified as urban or woody vegetated area between 1980 and 2018 considering a 350-m edge length in each direction around each sampling point (49 cells of $100\,m \times 100\,m$). This scale was chosen based on the average mobility ranges attributed to ground-dwelling carabids and spiders (Gallé, 2008; Jeanneret et al., 2003), as well as to minimise overlap of landscape sectors around nearby sampling sites. We defined two classes of magnitude in landscape-level change in land use: high change (more than 2 cells, >4% increase or decrease in urban or woody area, respectively); low change (less than 2 cells, <4% increase or decrease in urban or woody area, respectively) throughout the study period. The threshold was set to allow for a meaningful comparison of the two groups over time (i.e. have enough data points over years in both groups). This method allowed us to set a similar baseline for both categories (that is, starting point) and to analyse how different landscape change trajectories affected arthropod traits over time (i.e. different slopes). For urbanisation (carabid samples as reference), the cut-off point was at the 0.85 quantile ($n = 37,529$ samples with lower urbanisation, mean increase of 0.6%; $n = 6382$ samples with higher urbanisation, mean increase of 11%). For the loss in the area of woody vegetation (carabid samples as reference), the cutoff was at the 0.87 quantile ($n = 38,243$ samples with lower loss of woody vegetation, mean increase of 0.4%; $n = 5658$ samples with higher loss of woody vegetation, mean decrease of 14%) (Figure S3). Note that both landscape change categories included samples from each of the six land use types (Figure S4). For a justification of the landscape-scale land use change factors selected, see Methods S1.

2.4 | Statistical analysis

We performed three sets of analyses to provide complementary responses on changes in the traits of the arthropod community. First, we examined local changes in community traits (at the pitfall trap sample) within each main land use type. Second, we checked the effect of scale by fitting models at the regional scale, where the sampling unit included samples from multiple sites. Finally, we examined the effects of landscape changes due to urbanisation and loss of woody vegetation on the traits of the community of species.

2.4.1 | Local changes of arthropod traits over time and across land-use types

First, to examine whether arthropod traits (body size, length of activity period, drought tolerance and dispersal capacity) changed in

different land use types (forests, grasslands, crops) during the whole assessed period, we examined the individual trajectories of each community trait in each land use type and taxonomic group (carabids and spiders) at a local scale. Therefore, we fitted general linear mixed models, focusing on community means and weighted means of each trait at the level of the pitfall trap sample as a response variable. In total, we considered 43,911 trap samples for carabids and 36,274 trap samples for spiders. The models included trap size (upper edge, continuous), week of the year (categorical), mean annual temperature (continuous) and mean annual precipitation (continuous) as fixed effect covariates. The main variables of interest were: year (continuous), land-use type (categorical) and their interaction, which were included as fixed factors. In addition, site ID, nested within land-use type, and study ID were included in the models as random intercepts, to account for non-independence of measures within land-use type, site, and across studies. Standardised trend measures (i.e. temporal trends) and 95% confidence intervals were calculated for each focal land use type, trait and taxonomic group.

2.4.2 | Regional trait changes over time and across land-use types

To assess the trajectories of carabid and spider community traits on a larger scale, we fitted linear models in which the response variables (i.e. community weighted trait means and community trait means) were calculated from a pool of aggregated pitfall traps. To this end, we aggregated the communities found in 90 randomly selected pitfall trap samples within each year. We used this number of samples to allow community variability across iterations (within land-use type and year), while ensuring a representative number of pitfall trap samples at the same time. We resampled 100 random communities without replacement (i.e. aggregating 90 samples 100 times) within each year and focal land use type. In each iteration, we also calculated covariates that could be potential influencing factors: average Euclidean distance between sampling sites, number of different sites in the subset, number of different weeks represented in the subset, and standard deviation of the weeks. These four variables entered the models as fixed factor covariates along with year, land-use type and their interaction as main explanatory variables. These models were then used to calculate the slopes (temporal trend) and the 95% confidence interval of the slope for each land use type and taxonomic group.

2.4.3 | Effects of landscape-scale urbanisation and change in woody vegetation area on arthropod community traits

To assess the effects of landscape-scale urbanisation and loss of woody vegetation on arthropod community traits, we first classified sites with lower or higher urbanisation and lower or higher area of woody vegetation in their surroundings throughout the study period. Then, we fitted linear mixed-effect models using community weighted and non-weighted trait means at the pitfall trap sample level as response variables. The models included week of the year (factor) as well as year, landscape change type (urbanisation or loss of woody vegetation) and their interaction (year × landscape change type) as fixed factors. Site ID nested within land use type was included in the models as random intercepts. Additionally, the ID of the study entered the model as a random factor. A significant interaction between the type of landscape change and the year would indicate that the trajectories of traits over time depended on the change in land use at the landscape scale. For each taxonomic group (carabids or spiders), landscape change type (urbanisation or loss of woody vegetation) and arthropod trait (body size, length of activity period, drought tolerance and dispersal capacity), we ran a sensitivity analysis to assess the robustness of the results to the effect of a single year. This analysis consisted of running first a full model including all 36 sampling years. Then, to identify particularly important years, we reran the models excluding 1 year each time (leave-one-out jackknife procedure). The *t*-values and *p*-values of the interaction term were then compared across the entire model and all models missing a particular year (Seibold et al., 2019).

Quantitative explanatory variables were scaled to 0 mean and 1 standard deviation. Residuals of all presented models met the assumptions of normality and non-collinearity of independent variables. All statistical analyses were conducted in *R 4.2* (R Core Team, 2021). We used the Satterthwaite method (Type III sum of squares) for calculating degrees of freedom in linear mixed-effects models. Linear mixed effect models were fitted using the *lme4* package (Bates et al., 2015) and plots made using *ggplot2* (Wickham, 2016). In addition, we used *dplyr* (Wickham et al., 2021) to manage and process the dataset, and *MuMIn* (Barton & Barton, 2020) to calculate models' R^2-values.

2.4.4 | Controlling for heterogeneity in the dataset

Pitfall traps were used to sample carabid and spider species at all sites throughout the study period. Pitfall traps are a standardised method and have been widely used to assess the community of ground-dwelling arthropods and their functional traits in different habitats (Martinson & Raupp, 2013; Rivera-Pedroza et al., 2019; Schirmel et al., 2016). The arthropod sampling method across studies and years was relatively homogeneous (Figure S5). Most samples (90%) were collected between Week 15 (mid-April) and Week 39 (end of September), matching the period of highest activity of species of these arthropod groups. Most traps (approx. 90%) were funnel traps, while ca. 10% were cup-shaped pitfall traps (with vertical walls); only in one small study directional pitfall traps (only 545 samples) were used. The median trap size was 15 cm (upper diameter), with 88% of the traps between 10 and 15 cm. Exposure time (that is, trapping period) was typically 7 days (90% of samples; mean ± 1 SD: 7.8 ± 3.6 days). Therefore, the vast majority of the samples were very similar and the differences were distributed randomly throughout the years (Figure S5). Although most of these factors

are not expected to bias the traits of sampled communities, models focusing on temporal trends accounted for week of the year and trap size (highly correlated with trap type) as covariates. In addition, we also verified that there was no significant association between the sampling year and factors such as the exposure trap time, the type of trap and the sampling site (i.e. coordinates) (Figure S5; Tables S9 and S10). In this way, we reduced the possibility of biased conclusions due to the potential heterogeneity of the residual data. Additionally, we included the study ID as a random factor in all models, accounting for variability in sampling effort or other sources of variation between studies.

3 | RESULTS

In total, 1.73 million individuals belonging to 877 species were collected, including 301 carabid species and 576 spider species. On average, there were five carabid species (26 individuals) and four spider species (16 individuals) per pitfall trap sample. There were a few species that were particularly abundant: These were, for example, the carabid species *Poecilus cupreus* (24% of all individuals), *Pterostichus melanarius* (8%) and *Anchomenus dorsalis* (7%), and the spider species *Oedothorax apicatus* (17%) and *Pardosa palustris* (12%). In general, forests tended to harbour larger carabid species with lower dispersal capacity compared to other land use types (Figure S6). The wetlands had carabid communities with longer activity periods and lower tolerance to drought. Spider communities in forests tended to have relatively

lower dispersal capacities and, in wetlands, lower drought tolerances compared to other types of land use (Figure S6).

3.1 | Changes in arthropod community traits at local and regional scales

The weighted mean of the community (CWM) and the mean of the community (CM) of the body size of carabid communities tended to decrease in all types of land use studied (Figure 1), but the trend was particularly strong in crops on local scales (CWM = −0.16; 95% CI = −0.20 to −0.13).

Apart from this general trend, there was substantial variation in long-term temporal changes between land use types and spatial scales. The carabid length of the activity period increased on the local scale in forests (CWM = −0.007; 95% CI = −0.010 to −0.003), and crops (CWM = 0.019; 95% CI = 0.003–0.026), but trends were more variable in grasslands and on the regional scale (Figure 1). The tolerance to drought of carabids was highly variable across all types of land use and scales (Figure 1), while the dispersal capacity (i.e. wing length) did not change consistently across types of land use (Figure 1), but increased significantly (CWM and CM) on both scales (local and regional) in crops (Figure 1).

Spider community traits showed different patterns than those of carabids and were often land-use type dependent (Figure 2). Locally, the mean weighted body size of the spider community was increased
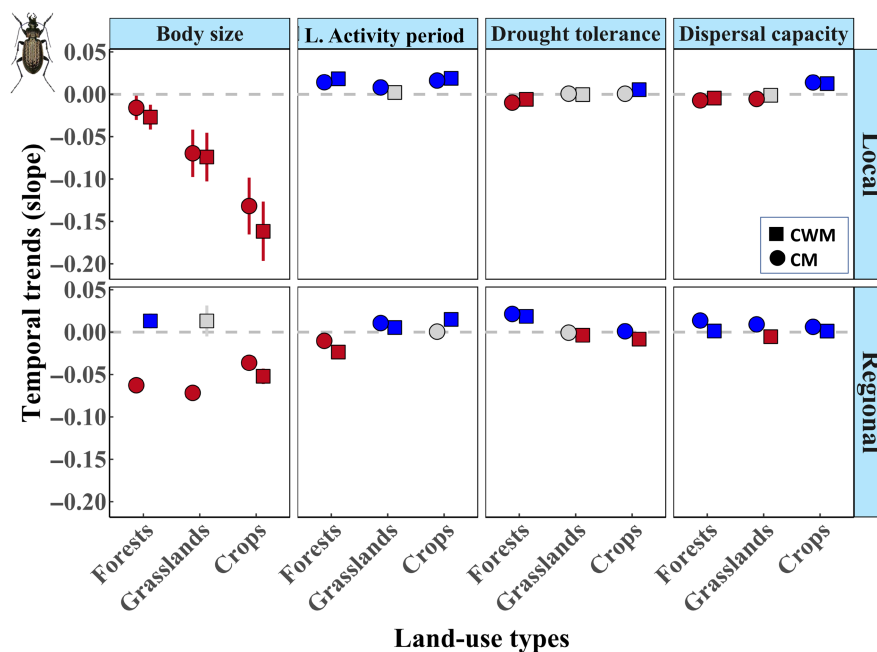

FIGURE 1 Estimated marginal means of linear temporal trends for carabid community traits in dominant local land-use types. Squares represent estimated change in community weighted means (CWM) with 95% confidence intervals. Circles represent expected change in (non-weighted) community means (CM, i.e. only variation due to species turnover) with 95% confidence intervals. Significantly (alpha = 0.05) positive trends (blue), significantly negative trends (red) and non-significant trends (grey) are represented with colours. Upper panels show (standardised) temporal trait changes at the local pitfall trap level for each land-use type. Lower panels show (standardised) temporal trait changes at the regional level. Changes refer to the linear expected change in the standardised response variable every 1SD of the variable year (~10 years for comparability). L. Activity period = length of activity period.

in grasslands (CWM = 0.03; 95% CI = 0.02–0.05), while it decreased in forests (CWM = −0.012; 95% CI = −0.019 to −0.006). The average duration of the activity period (both CWM and CM) tended to decrease in all three focal land use types locally (Figure 2). The CWM of drought tolerance in spiders decreased in the three main types of land use at both scales (Figure 2). The community-weighted dispersal capacity did not change substantially. On the regional scale, the average body size of spider communities (both CWM and CM) increased in forests and CWM in grasslands, but did not change (CM) or decrease (CWM) in crops. The community mean length of activity period decreased in the three focal land use types. However, when accounting for relative abundances of species, the CWM of activity length in spiders consistently increased in the three land-use types (Figure 2). Dispersal capacity did not show substantial or consistent changes on the regional scale either. Temporal trends in the three minor land use types varied (see Figures S7 and S8 for completeness) and are discussed in Discussion S1 in Supporting Information.

3.2 | Urbanisation and loss of woody vegetation at the landscape-scale affect arthropod community traits

Urbanisation and loss of area in woody vegetation were associated with changes in the temporal trajectories of CWM of functional traits of carabid and spider communities (Table 1; Figures 3 and 4).

The results for CM were very similar (Figures S9 and S10), so only the results regarding CWM are presented here. Carabid communities in landscapes with more urbanisation tended to show a decrease in body size. However, the length of the activity period, the tolerance to drought, and the dispersal capacities did not change significantly compared to those communities in landscapes with less urbanisation (Table 1; Figure 3). The landscape-level loss of woody area changed community traits towards larger body sizes, shorter activity periods, higher drought tolerances and decreased dispersal capacities.

The changes in the trait composition of spider communities were more strongly affected by urbanisation (Table 1; Figure 4), resulting in relatively larger body sizes, longer activity periods, lower relative tolerances to drought and higher dispersal capacities (Figure 4). The loss of woody vegetation led to communities with a lower dispersal capacity but did not significantly shape the average body size, activity periods or tolerance to drought of spiders (Table 1; Figure 3).

4 | DISCUSSION

Our study reveals significant long-term changes in the composition of arthropod community traits over the past ~40 years. These changes depended highly on taxa, local land use type, and landscape-scale level changes related to urbanisation and loss of woody area.

In line with our first prediction, we observed a general long-term temporal shift in carabid body size towards communities composed of
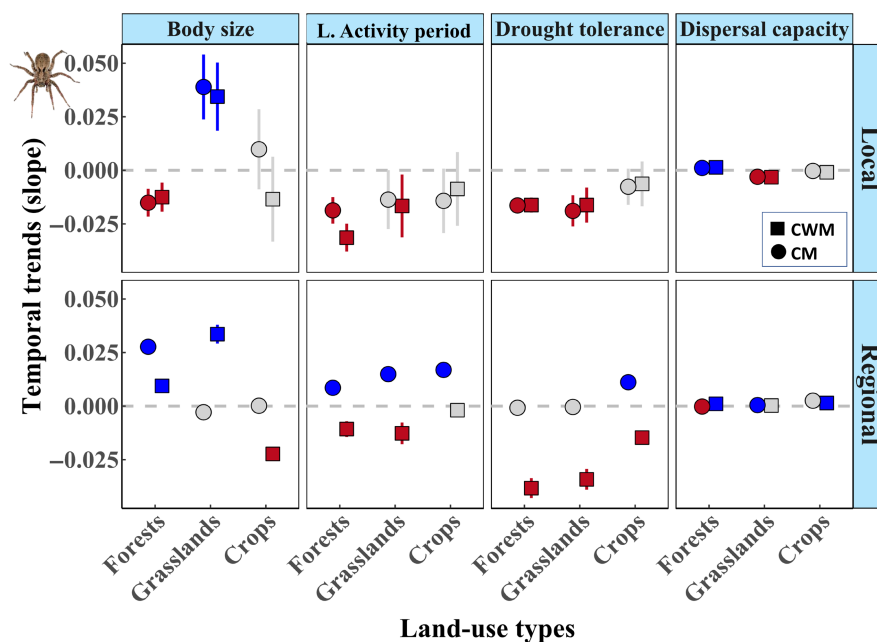

FIGURE 2 Estimated marginal means of linear temporal trends for spider community traits in dominant local land-use type. Squares represent expected change in (CWM) with 95% confidence intervals. Circles represent expected change in (non-weighted) community means (CM, i.e. only variation due to species turnover) with 95% confidence intervals. Significantly (alpha = 0.05) positive trends (blue), significantly negative trends (red) and non-significant trends (grey) are represented with colours. Upper panels show (standardised) temporal trait changes at the local pitfall trap level in each land-use type. Lower panels show (standardised) temporal trait changes at the regional level. Changes refer to the linear expected change in the response variable every 1SD of the variable year (~10 years for comparability). L. Activity period = length of activity period.

TABLE 1 Effect of urbanisation and woody area loss on temporal trends of carabid and spider community traits.

Group	Class	Trait	Estimate (effect of year)	Lower CI	Upper CI	R^2m	R^2c	p
Carabids	Low U	Body size	−0.042	−0.055	0.029	0.9	49.1	**0.036**
	High U		**−0.077**	**−0.112**	**−0.043**			
	Low U	L. Activity period	**0.008**	**0.005**	**0.010**	0.6	40.1	0.152
	High U		0.003	−0.003	0.010			
	Low U	Drought tolerance	**−0.006**	**−0.008**	**−0.004**	1.3	47.5	0.382
	High U		**−0.008**	**−0.012**	**−0.003**			
	Low U	Dispersal capacity	**−0.003**	**−0.005**	**−0.001**	0.3	59	0.763
	High U		−0.002	−0.007	0.003			
	Low WL	Size	**−0.061**	**−0.075**	**−0.049**	3.1	50.6	**<0.001**
	High WL		**0.170**	**0.136**	**0.204**			
	Low WL	Activity period	**0.009**	**0.006**	**0.011**	0.7	40.1	**<0.001**
	High WL		−0.003	−0.009	0.004			
	Low WL	Drought tolerance	**−0.007**	**−0.009**	**−0.006**	1.0	47.5	**<0.001**
	High WL		**0.008**	**0.003**	**0.012**			
	Low WL	Dispersal	**−0.002**	**−0.004**	**−0.001**	0.8	59.8	**<0.001**
	High WL		**−0.016**	**−0.021**	**−0.001**			
Spiders	Low U	Size	**−0.006**	**−0.012**	**−0.001**	5.3	32.0	**0.023**
	High U		0.013	−0.004	0.030			
	Low U	Activity period	**−0.030**	**−0.0351**	**−0.02408**	7.0	26.0	**0.021**
	High U		−0.010	−0.0269	0.00599			
	Low U	Drought tolerance	**−0.018**	**−0.021**	**−0.015**	3.5	31.6	**<0.001**
	High U		**−0.034**	**−0.043**	**−0.024**			
	Low U	Dispersal	0.0002	−5.75e-05	0.0005	3.0	59.3	**<0.001**
	High U		**0.0034**	**2.34e-03**	**0.0045**			
	Low WL	Size	−0.005	−0.011	0.001	4.9	32.4	0.377
	High WL		−0.011	−0.025	0.003			
	Low WL	Activity period	**−0.028**	**−0.034**	**−0.023**	7.0	27.4	**0.046**
	High WL		**−0.043**	**−0.057**	**−0.029**			
	Low WL	Drought tolerance	**−0.018**	**−0.021**	**−0.015**	2.3	28.8	0.168
	High WL		**−0.013**	**−0.021**	**−0.005**			
	Low WL	Dispersal	**0.0004**	**0.0002**	**0.0008**	1.4	60.4	**<0.001**
	High WL		**−0.0021**	**−0.0029**	**−0.0013**			

Note: Estimated effect of landscape changes on temporal trends in community weighted trait means. Low U=lower urbanisation class (<4%); High U=higher urbanisation class (>4%). Low WL=lower woody area loss class (<4%); High WL=higher woody area loss class (>4%). Size=body size. Activity period=length of activity period. D. tolerance=drought tolerance and Dispersal=dispersal capacity. Lower and upper 95% confidence interval (lower CI and upper CI). Marginal (R^2m) and conditional (R^2c) R^2 (% of variance explained by fixed and random factors respectively). p=p-value of the interaction term between the landscape change type (urbanisation or loss of woody area) and year. In bold, significant slopes and interaction terms at an alpha level of 0.05.

smaller species (but context-dependent trends in spiders), especially in more intensively managed and perturbed land-use types such as crops, as well as in landscapes characterised by a high degree of urbanisation. These findings are in agreement with expectations that landscape context can shape local arthropod communities (Tscharntke et al., 2005, 2012), and that frequent perturbations and less stable environments should benefit smaller species, which have been shown to cope better with diminished or more fluctuating resource availability (Eggenberger et al., 2019; Merckx et al., 2018; Peters, 1983),

loss of environmental heterogeneity and reduced availability of microclimatic conditions. Potential underlying mechanisms are related to lower energetic costs and faster development and reduced risk of predation risk of small species (Fenoglio et al., 2021). In fact, the shift to smaller species of ground-dwelling arthropod communities has also been reported in space-for-time substitution studies on the impact of increased land-use intensity (Simons et al., 2016; Tiede et al., 2022; Webb et al., 2010) and urbanisation (Hahs et al., 2023; Martinson & Raupp, 2013). This change is often attributed to species
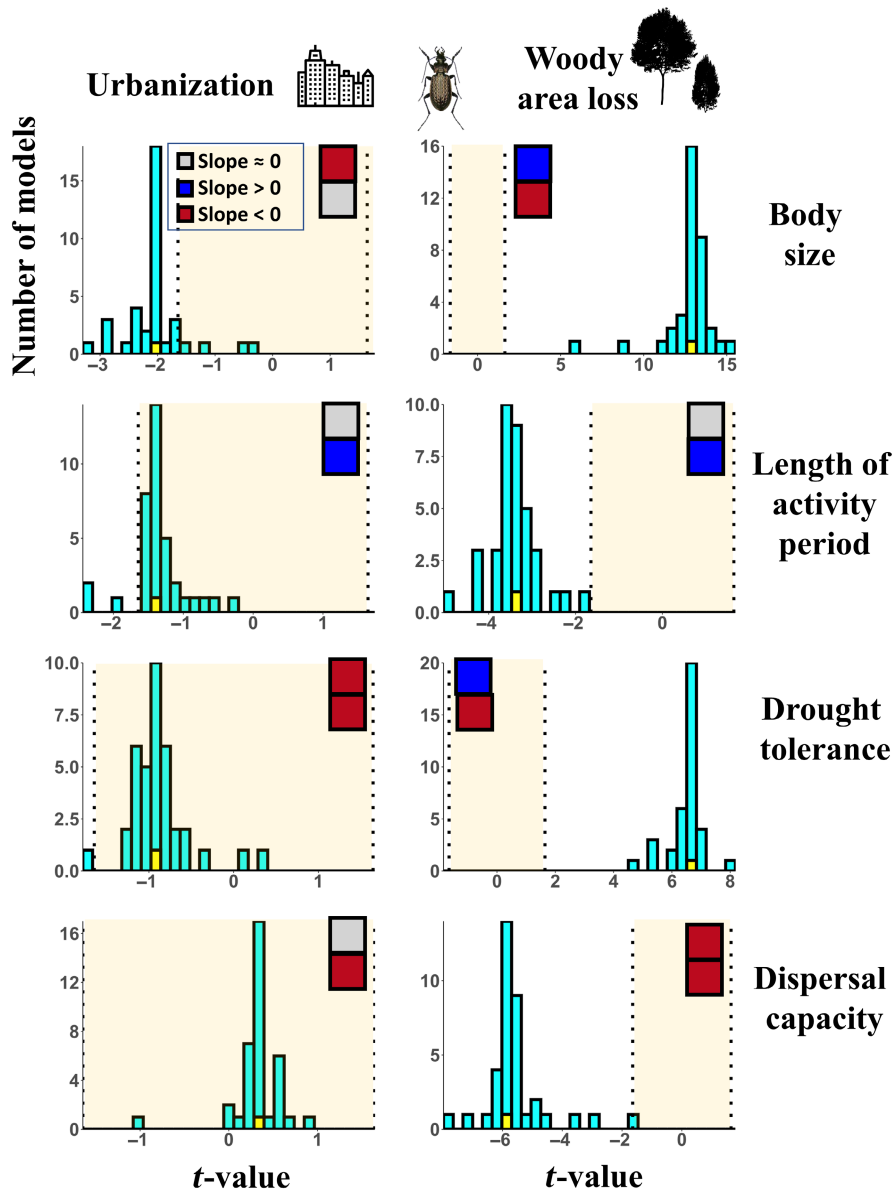
FIGURE 3 Effect of landscape-level urbanisation and woody area loss on the four community-weighted carabid trait means (CWM): body size, length of activity period, drought tolerance, and dispersal capacity. The *t*-value of the interaction term (landscape change class × time) shows differences in trait CWM inter-annual trends across more and less urbanised landscapes (or landscapes with a higher or lower decrease in woody area). A negative *t*-value means a steeper decreasing trend or less pronounced increase of CWM trait values in landscapes highly urbanised or that lost woody area, respectively. The yellow bar represents the interaction *t*-value of the model including all years with data, and the blue ones represent models missing a single year each time (i.e. leave-one-out jackknife procedure). The two dotted black lines determine the area of non-significant differences in trends. Coloured squares represent the slope for each landscape category independently (higher urbanisation or woody area loss = top square, and lower urbanisation or woody area loss = bottom square). Grey for non-significant trends, blue for significantly positive and red for significantly negative trends (alpha = 0.05).

(re-)distributions and local extinctions (Wong et al., 2019) due to environmental filtering. Our results of body size declines in carabid communities associated with high levels of urbanisation corroborate these findings and highlight that such effects do indeed translate into profound long-term temporal shifts towards a smaller average body size of arthropod communities. Thus, our study closes an important gap of knowledge (Terry et al., 2021) incorporating the long-term temporal dimension to changes in arthropod traits as response to temporal landscape-scale changes. The size of species in communities is considered to play a key role in structuring food webs, species interactions and ecosystem functioning (Beukeboom, 2018; Tiede et al., 2022). For this reason, the observed long-term decrease in the mean body size of generalist predators in response to anthropogenic local and landscape change processes likely has important general consequences at the ecosystem level (Han et al., 2022; Planillo et al., 2021). However, it is important to note that these effects can vary across taxonomic groups, as highlighted by our study (see also Hahs et al., 2023).

Our findings provide moderate support for our second prediction (that is, decrease in the duration of activity periods). Spider communities showed decreasing activity periods over the last ca. four decades across forests, grasslands and crops, which was to a large extent driven by a few highly abundant species. In addition, urbanisation and the loss of woody areas favoured carabid communities with shorter activity periods compared to less modified landscapes. This could be explained by the advantage in escaping times of resource scarcity and disturbances (e.g. herbicide use in agricultural or urban areas) in more perturbed areas (Johansson et al., 2020; Leather et al., 1993), which could promote the presence of species that have shorter activity periods. However, we did not find consistent overall negative changes in the weighted mean duration of the activity period, and the length of activity periods increased in spider communities as a response to urbanisation. These results suggest a trade-off in this trait, because more generalist species (here in terms of activity period) might also have

FIGURE 4 Effect of landscape-level urbanisation and woody area loss on the four community-weighted spider trait means (CWM): body size, length of activity period, drought tolerance and dispersal capacity. The *t*-value of the interaction term (landscape change class×time) shows differences in trait CWM inter-annual trends across more and less urbanised landscapes (or landscapes with a higher or lower decrease in woody area). A negative *t*-value a steeper decreasing trend or less pronounced increase of CWM trait values in more urbanised landscapes (or that lost more woody area) compared to those that suffered less urbanisation (or loss of woody area). The yellow bar represents the interaction *t*-value of the model including all years, and the blue ones represent models missing a single year each time (i.e. leave-one-out jackknife procedure). The two dotted black lines determine the area of non-significant differences in trends. Coloured squares represent the slope for each landscape category independently (higher urbanisation or woody area loss=top square, and lower urbanisation or woody area loss=bottom square). Grey for non-significant trend, blue for significantly positive and red for significantly negative trends (alpha=0.05).
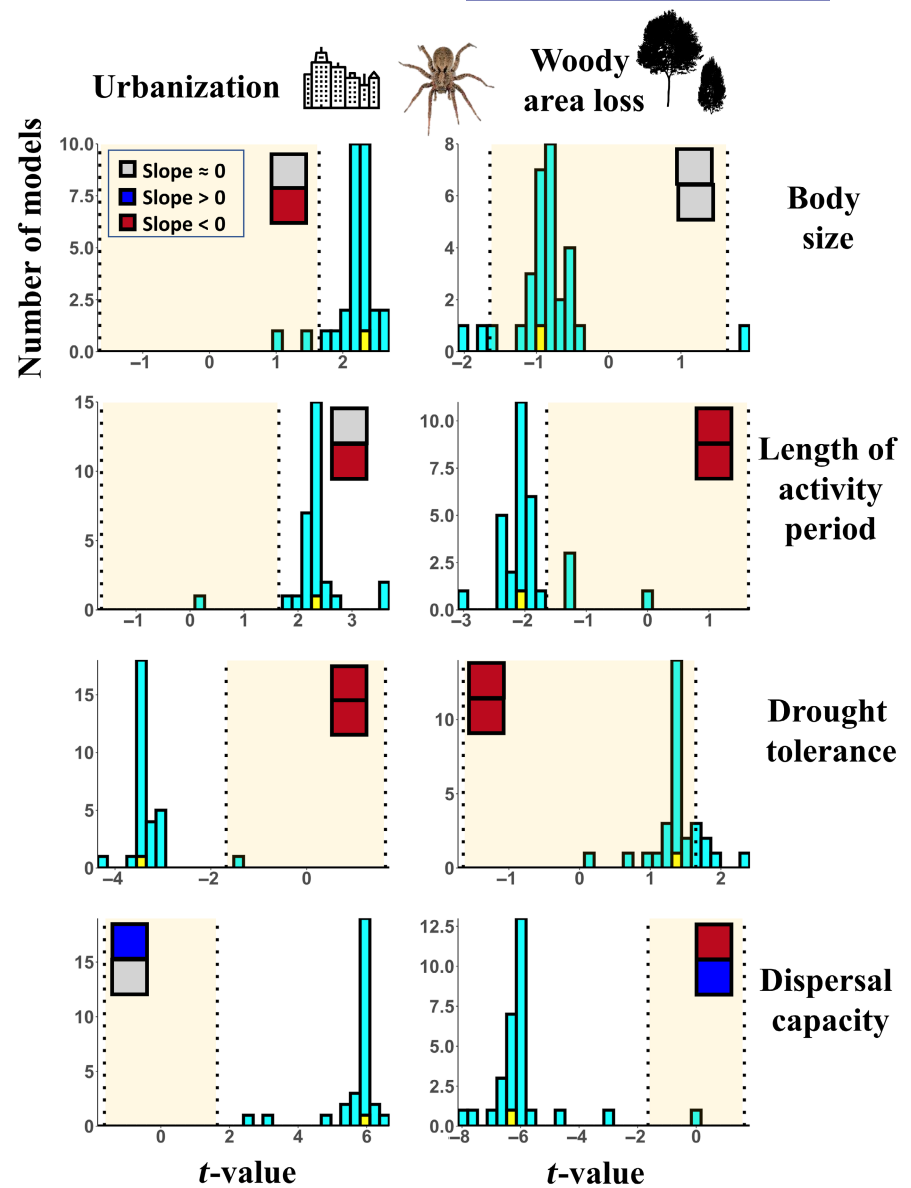
some advantages under fluctuating environmental conditions, that is they can exploit a variety of resources (Gallé et al., 2019; Martinson & Raupp, 2013).

The results provide mixed support for our third prediction (increase in tolerance to drought). Our findings show that in landscapes with higher rates of woody vegetation loss during the past decades, drought tolerance was favoured in carabid communities, which is an expected response to drier, warmer and more variable environmental conditions of open land types (Weldon et al., 2016; Wong et al., 2019). This finding is in line with the expectation of higher drought tolerance in open habitats compared to woody habitats, in which weather extremes are generally more buffered and humidity is often relatively high (De Frenne et al., 2019) However, the trends in drought tolerance in carabid communities were land use and scale dependent. However, in spiders, average drought tolerance tended to decrease in all types of land use, suggesting that drought tolerance is not a limiting factor for spiders in the studied environments.

Although species more tolerant to desiccation and droughts are theoretically better able to colonise drier and warmer environments (Malmos et al., 2021; Weldon et al., 2016), the studied gradient of humidity and temperature could not have been strong enough to detect a general signal at the community level.

Regarding our fourth prediction, we expected that arthropod species with higher dispersal capacities could cope better with more perturbed and fragmented habitats (Perović et al., 2018). Therefore, low dispersal capacity should be associated with higher vulnerability to such land-use modifications and face higher local extinction risks (Tscharntke et al., 2012; Wong et al., 2019). These predictions are partly supported by our study, showing long-term trends towards increased dispersal capacity of carabid communities in crops. Furthermore, our findings support evidence from space-for-time substitution studies (Peng et al., 2020) that spider species are especially sensitive to fragmentation by urban barriers compared to carabids, highlighting long-term changes towards increased dispersal

capacities in spider communities in landscapes urbanising more strongly.

Finally, with respect to our fifth hypothesis, temporal trends in community traits showed similar patterns when accounting for species relative abundances or when only species turnover was considered. However, species turnover alone appears to promote stronger changes in several traits in response to landscape variations, but the persistence of dominant species buffers these changes, thus promoting temporal stability in abundance-weighted community traits. This epitomises how dominant species can have a disproportionately profound impact on community trait compositions regardless of high species turnover, as predicted by the mass ratio hypothesis (Grime, 1998).

In addition to the long-term interspecific trait shifts revealed by our study, it would be a fruitful area of future research to also consider intraspecific variation and how anthropogenic changes may cause intraspecific trait shifts, which was beyond the scope of the present study.

5 | CONCLUSIONS

This study highlights the significant impact of anthropogenic changes in land use on the functional composition of ground-dwelling arthropod communities over the past four decades, revealing pronounced long-term trait changes. The findings indicate that landscape-level changes in terms of urbanisation and loss of woody vegetation such as hedgerows, small forested areas and isolated groups of trees are associated with changes in arthropod key traits, which are dependent on taxonomic groups. For example, urbanisation resulted in a decrease in the average body size of carabids, a decrease in the drought tolerance of spiders, and an increase in the dispersal capacity of spiders at the community level. Furthermore, our findings highlight an overall reduction in the average body size of carabids, particularly pronounced in agriculturally managed systems, that is arable crops and, to a lesser extent, grasslands. The long-term anthropogenic changes in arthropod traits revealed by our study can potentially have cascading effects on other trophic groups of organisms and thus have important implications for the structure of the food web as well as the functioning and stability of ecosystems.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Studies included in the dataset.

Table S2: Number of sampled and gap years.

Table S3: Main habitat types and subtypes that they encompass.

Table S4: Crop species sampled each year.

Table S5: Number of samples collected in each year and land-use type for each taxon.

Table S6: Number of sites that were sampled from one to eight years.

Table S7: Carabid and spider traits considered and their ecological implications.

Table S8: Additional traits used to increase random forest imputation accuracy in spider missing traits.

Table S9: Pearson correlation coefficients between longitude and latitude, and the response variables (trait community weighted means).

Table S10: Pearson correlation coefficients between longitude and latitude, and the response variables (trait community means).

Figure S1: Map of pitfall sampling locations in different habitats across Switzerland.

Figure S2: Spearman correlations between the four traits in carabids (A) and spiders (B).

Figure S3: Landscape change in (A) urban area, (B) arable land and (C) woody area, in 350m radius around each sampling points between 1980 and 2018.

Figure S4: Number of samples in each land-use type and category of landscape change: urbanization (A) and loss of woody areas (B).

Figure S5: Pitfall trap sampling type used across years and land-use types.

Figure S6: Density plot with probability distribution of each trait for (A) carabids and (B) spiders across land-use types.

Figure S7: Estimated marginal means of linear temporal trends for carabid community traits in all land-use types.

Figure S8: Estimated marginal means of linear temporal trends for spider community traits in all land-use types.

Figure S9: Effect of urbanization and woody area loss on four community carabid traits (CM): Body size, length of activity period, drought tolerance, and dispersal capacity.

Figure S10: Effect of urbanization and woody area loss on four community spider traits (CM): Body size, length of activity period, drought tolerance, and dispersal capacity.