Arthropod decline in grasslands and forests is associated with landscape-level drivers

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Recent reports of local extinctions of arthropod species[1], and of massive declines in arthropod biomass[2], point to land-use intensification as a major driver of decreasing biodiversity. However, to our knowledge, there are no multisite time series of arthropod occurrences across gradients of land-use intensity with which to confirm causal relationships. Moreover, it remains unclear which land-use types and arthropod groups are affected, and whether the observed declines in biomass and diversity are linked to one another. Here we analyse data from more than 1 million individual arthropods (about 2,700 species), from standardized inventories taken between 2008 and 2017 at 150 grassland and 140 forest sites in 3 regions of Germany. Overall gamma diversity in grasslands and forests decreased over time, indicating loss of species across sites and regions. In annually sampled grasslands, biomass, abundance and number of species declined by 67%, 78% and 34%, respectively. The decline was consistent across trophic levels and mainly affected rare species; its magnitude was independent of local land-use intensity. However, sites embedded in landscapes with a higher cover of agricultural land showed a stronger temporal decline. In 30 forest sites with annual inventories, biomass and species number—but not abundance—decreased by 41% and 36%, respectively. This was supported by analyses of all forest sites sampled in three-year intervals. The decline affected rare and abundant species, and trends differed across trophic levels. Our results show that there are widespread declines in arthropod biomass, abundance and the number of species across trophic levels. Arthropod declines in forests demonstrate that loss is not restricted to open habitats. Our results suggest that major drivers of arthropod decline act at larger spatial scales, and are (at least for grasslands) associated with agriculture at the landscape level. This implies that policies need to address the landscape scale to mitigate the negative effects of land-use practices.

Much of the debate surrounding the human-induced biodiversity crisis has focused on vertebrates[3], but population declines and extinctions may be even more substantial in small organisms such as terrestrial arthropods[4]. Recent studies have reported declines in the biomass of flying insects[2], and in the diversity of insect pollinators[5,6], butterflies and moths[1,7–10], hemipterans[11,12] and beetles[7,13,14]. Owing to the associated negative effects on food webs[15], ecosystem functioning and ecosystem services[16], this insect loss has spurred an intense public debate. However, time-series data relating to arthropods are limited, and studies have so far focused on a small range of taxa[11,13,14], a few types of land use and habitat[12]—or even on single sites[1,17]. In addition, many studies lack species information[2] or high temporal resolution[2,12]. It therefore remains unclear whether reported declines in arthropods are a general phenomenon that is driven by similar mechanisms across land-use types, taxa and functional groups.

The reported declines are suspected to be caused mainly by human land use[2]. Locally, farming practices can affect arthropods directly by application of insecticides[18,19], mowing[20] or soil disturbance, or indirectly via changes in plant communities through the application of herbicides or fertilizer[21]. Forestry practices can also affect local arthropod

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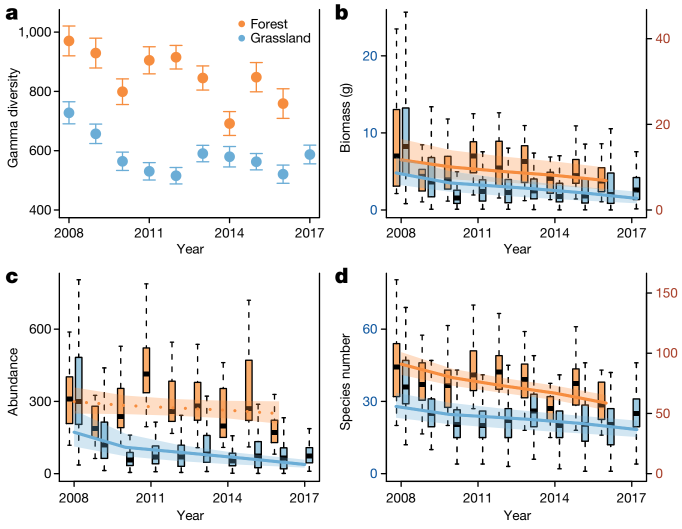

Fig. 1 | Temporal trends in arthropod communities. a–d, Gamma diversity (total number of species across all grassland or forest sites) (**a**), biomass (**b**), abundance (**c**) and number of species (**d**) of arthropods were recorded in 30 forest and 150 grassland sites across Germany. Gamma diversity shows mean incidence-based, bias-corrected diversity estimates (Chao's BSS, that is, the higher value of the minimum doubled reference sample size and the maximum reference sample size among years[29]) for $q = 0$ and 95% confidence intervals derived from bootstrapping ($n = 200$). Non-overlapping confidence intervals indicate significant difference[30]. Box plots show raw data per site and year ($n = 1{,}406$ (grassland) or 266 (forest) independent samples). Solid lines indicate significant temporal trends ($P < 0.05$) based on linear mixed models that included weather conditions, and local and landscape-level land-use intensity as covariates. Shaded areas represent confidence intervals. Boxes represent data within the 25th and 75th percentile, black lines show medians, and whiskers show 1.5× the interquartile range. Data points beyond that range (outliers) are not shown for graphical reasons. Plots for biomass and species number have separate *y* axes for grassland and forest.

communities via changes in tree species composition or forest structure[22]. In addition, local arthropod populations can be affected by land use in the surrounding landscape; for example, through the drift and transport of pesticides and nitrogen by air or water[23,24], through the effects of habitat loss on meta-communities (source–sink dynamics[25]) or by hampering dispersal.

To disentangle the local and landscape-level effects of land use on temporal trends in arthropod communities of grasslands and forests, we used data from the 'Biodiversity Exploratories' research programme that pertain to more than 1 million individual arthropods (2,675 species) (Extended Data Table 1). Arthropods were collected annually at 150 grassland sites by standardized sweep-net sampling in June and August from 2008 to 2017, and at 30 forest sites with flight-interception traps over the whole growing period from 2008 to 2016. An additional 110 forest sites were sampled in 2008, 2011 and 2014 to test for trends across a larger number of sites. Both the grassland and the forest sites cover gradients in local land-use intensity. Land-use intensity was quantified in the form of compound indices that are based on grazing, mowing and fertilization intensity in grasslands[26], and on recent biomass removal, the proportion of non-natural tree species and deadwood origin in forests[27]. To analyse landscape-level effects, we quantified the cover of arable fields, grassland and forest in circles, with a radius between 250 m and 2 km, around each sampling site. We modelled temporal trends in arthropod biomass (estimated from body size; Methods), abundance and the number of species separately for grasslands and forests, and tested for the effects of local and landscape-scale land-use intensity on these trends, accounting for weather conditions. Analyses were conducted for all species together, and for different dispersal and trophic guilds.

The total number of arthropod species across all sites (gamma diversity) was substantially lower in later than in earlier years in both forests and grasslands (Fig. 1). Gamma diversity, biomass, abundance and number of species fluctuated over time but revealed an overall decrease with strongest declines from 2008 to 2010, especially in grasslands (Fig. 1). Year-to-year fluctuations in arthropod biomass, abundance and number of species were partially explained by weather conditions (Extended Data Fig. 1, Supplementary Table 1-1, Supplementary Information section 2). Accounting for weather, fitted trends from our models showed declines in biomass of 67% for grasslands and 41% for forests, declines in species numbers of 34% for grasslands and 36% for forests, and declines in abundance of 78% for grasslands, with no significant change in abundances for forests (−17%) (Fig. 1, Supplementary Table 3-1). In grasslands, declines occurred consistently across all trophic guilds (herbivores, myceto-detritivores, omnivores and carnivores), although the trend for carnivores was not significant (Supplementary Table 1-1). In forests, the patterns were more complex: herbivores showed an increase in abundance and species number, whereas all other trophic guilds declined. Temporal trends of arthropods on the basis of data recorded in 3-year intervals from all 140 forest sites were similar to the trends based on the 30 sites with annual data (Supplementary Table 1-1). Sensitivity analyses that removed or reshuffled years showed that the decline was influenced by, but not solely dependent on, high numbers of arthropods in 2008. Fluctuations in numbers (including the numbers from 2008) appear to match trends that have been observed in other studies[2], which suggests that the recent decline is part of a longer-term trend that had begun by at least the early 1990s (Extended Data Fig. 2, Supplementary Information section 3). Further sensitivity analyses showed consistent declines when data from individual sampling dates were not aggregated per year, and also showed that declines concerned all three regions that we analysed (Supplementary Tables 3-2, 3-3, Supplementary Fig. 3-1).

Linking changes in biomass, abundance and the number of species to one another enables further inferences regarding the mechanisms that drive arthropod declines. In grasslands, both abundant and less-abundant species declined in abundance (Fig. 2), but loss in the number of species occurred mostly among less-frequent species (Fig. 1, Extended Data Fig. 3, Supplementary Information section 4). This suggests that the decline in the number of species in grasslands was attributable mainly to a loss of individuals among rare species. In forests, species that were initially less abundant decreased in abundance, whereas some of the most abundant species—including invasive species and potential pest species—increased in abundance (Fig. 2, Supplementary Table 5-1). The loss of species was, however, irrespective of their frequency (Fig. 1, Extended Data Fig. 3, Supplementary Information section 4). This suggests that the decline of arthropods in forests is driven by mechanisms that negatively affect the abundances of many species, which leads to an overall decline in biomass and the number of species but favours some species that are able to compensate declines in abundance.

The magnitudes of declines in biomass, abundance and the number of species in arthropod communities were independent of local land-use intensity (Supplementary Table 1-1) as well as changes in plant communities (Supplementary Information section 6) at all sites. However, in forests declines in the number of species were weaker at sites with high natural or anthropogenic tree mortality, possibly owing to increased heterogeneity in local habitats (Extended Data Fig. 4). Landscape composition had no effect on arthropod trends in forests (note that forest sites covered only limited gradients of the landscape variables, Extended Data Fig. 5), but it mediated declines in the number of species in grasslands: the magnitude of the declines increased with increasing cover of arable fields, and marginally increased with cover of grasslands in the surrounding landscape (Fig. 3, Supplementary Table 1-1). This suggests that major drivers of arthropod decline in grasslands are associated with agricultural land use at the landscape scale.

The interaction between a species and the landscape around its habitat depends on its dispersal ability, which ultimately determines

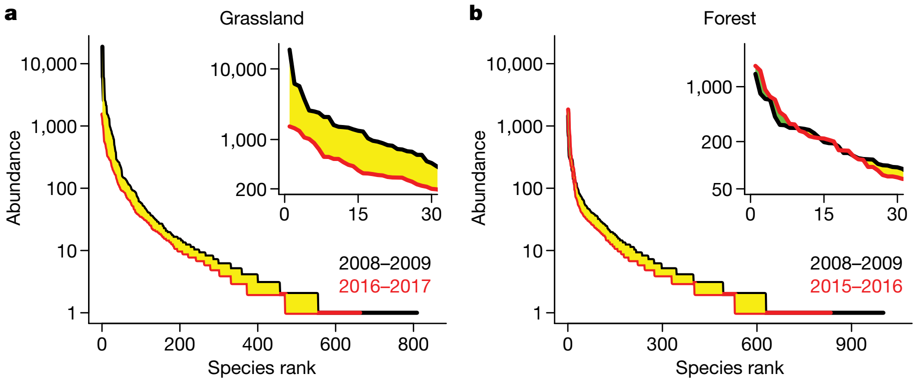

Fig. 2 | Changes in the dominance of species. Rank abundance curves of arthropod communities for the first two (2008–2009) and final two (2016–2017 for grasslands and 2015–2016 for forests) years of the study, from 150 grassland and 30 forest sites. The insets show enlarged curves for the 30 most-abundant species. Data from the first two and final two study years were pooled (abundances are the total number of individuals of a species observed over two years). Declines in abundance are highlighted by yellow shading, and increases in abundance are shaded in green. The *y* axes are log-scaled, but show untransformed values.

its occurrence and persistence[28]. In grasslands, taxa of high and low dispersal ability (Methods) both declined, but an increasing cover of arable fields—although not of grasslands—in the surroundings amplified declines in the biomass of weak dispersers more strongly than it did declines of strong dispersers (Fig. 3, Supplementary Table 7-1). Weak dispersers may experience higher mortality during dispersal, and thus have a lower chance of (re)colonization of a particular site when arable field cover is high. In forests, strong dispersers declined in biomass, abundance and the number of species, whereas weak dispersers increased in abundance and biomass—but less strongly when grassland cover in the landscape was high (Supplementary Table 7-1). This suggests that the drivers behind arthropod declines in forests also act at landscape-level spatial scales.

We showed that arthropods declined markedly not only in biomass but also in abundance and the number of species, and that this affected taxa of most trophic levels in both grasslands and forests. Declines in gamma diversity suggest that species might disappear across regions. Our results also indicate that the major drivers of arthropod decline in both habitat types act at landscape-level spatial scales, but that declines may be moderated by increases in heterogeneity of local habitats in forests. Although the drivers of arthropod decline in forests remain unclear, in grasslands these drivers are associated with the proportion of agricultural land in the landscape. However, we cannot ascertain whether the observed declines are driven by the legacy effects of historical land-use intensification or by recent agricultural intensification at the landscape level; for example, by the decrease of fallow land and field margins rich in plant species, the increased use of pesticides or use of more potent insecticides (Supplementary Information section 3). Time-series data relating to changes in the use of agrochemicals or the presence of fine-scale arthropod habitats would be necessary to answer this question. Furthermore, the extents to which changes in climate have reinforced the observed trends in arthropod biomass, abundance and number of species is unclear (Supplementary Information section 2). Our results show that widespread arthropod declines have occurred in recent years. Although declines were less pronounced during the second half of our study period, there is no indication that negative trends have been reversed by measures that have been implemented in recent years. This calls for a paradigm shift in land-use policy at national and international levels to counteract species decline in open and forested habitats by implementing measures that are coordinated across landscapes and regions. Such strategies should aim to improve habitat quality for arthropods and to mitigate the negative effects of land-use practices not only at a local scale (within isolated patches embedded in an inhospitable agricultural matrix) but also across large and continuous areas.

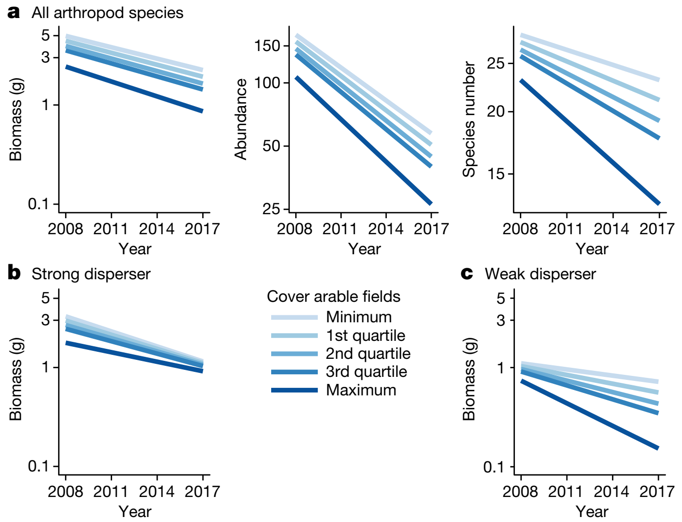

Fig. 3 | Landscape effects on arthropod decline in grasslands. a, Temporal changes in biomass, abundance and the number of species for all arthropod species. **b**, **c**, Temporal change in biomass of species with high (**b**) or low (**c**) dispersal ability, conditional on the cover of arable fields in the surrounding landscape (1-km radius). The decline in biomass increased significantly with the cover of arable fields for weak dispersers, but not for strong dispersers. Slopes were derived from models that included weather conditions and local land-use intensity as covariates. The *y* axes are log-scaled, but show untransformed values.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-019-1684-3.

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Methods

No statistical methods were used to predetermine sample size. The experiments were not randomized and investigators were not blinded to allocation during experiments and outcome assessment.

Study system, land-use measures and weather data

The study was conducted as part of the Biodiversity Exploratories project (www.biodiversity-exploratories.de) in three regions of Germany: (1) Schwäbische Alb in southwestern Germany (460–860 m above sea level (asl)); (2) Hainich-Dün in central Germany (285–550 m asl); and (3) Schorfheide-Chorin in northeastern Germany (3–140 m asl). The three regions differ in climate, geology and topography, but each is characterized by gradients of land-use intensity in grasslands and forests that are typical for large parts of temperate Europe[31].

A total of 150 grassland sites of 50 × 50 m in size (50 per region) and 140 forest sites of 100 × 100 m in size (49 in Schwäbische Alb, 50 in Hainich-Dün and 41 in Schorfheide-Chorin), located within larger management units, were selected from a total of about 3,000 candidate sites by stratified random sampling to ensured that the selected sites covered the whole range of land-use intensity and to minimize the confounding effects of spatial position or soil type[31]. All sites have a long history of the same type of land-use and of broadly similar land-use intensity. Land use is conducted by landowners or tenant farmers (rather than by the scientific consortium) and the start of the project did not cause changes in land use. Local land-use intensity decreased significantly in forests and marginally in grasslands over the course of our study (Supplementary Information section 8). No pesticides were applied at any of the sites, except for application of herbicides in grasslands in five occasions (site number and year: AEG2 2011, HEG2 2013, HEG36 2014, HEG37 2014 and HEG1 2015).

In grasslands, the gradient of land-use intensity ranged from seminatural to intensively managed grasslands. Natural grasslands, which do not require management to prevent succession to forest, are almost entirely absent from western and central Europe. All sites were continuously managed by farmers. Information on management practices, including the level of fertilization (kg N ha^{-1} year^{-1}), grazing (number of livestock units ha^{-1} year^{-1}) and mowing (number of cuts year^{-1}), was assessed annually by standardized interviews with the farmers. Local land-use intensity in grasslands was then quantified as a compound index by summing the standardized intensities (that is, divided by the global mean value) of these three components[26]. We then calculated the mean local land-use intensity for each site over the ten years of our study (2008–2017). The least intensively managed grasslands are often located within protected areas ($n = 47$ sites, including 15 sites in strictly protected areas) and are typically grazed by 40–50 sheep per hectare for about 10 days per year (or more rarely by 1–3 cattle per hectare for 20 days), unfertilized and not mown. Grasslands of intermediate land-use intensity are usually unfertilized (or fertilized with less than 30 kg N ha^{-1} year^{-1}), and are either mown twice a year or grazed by 4 cattle per hectare for about 50 days. The most intensively managed grasslands are typically fertilized (60–120 kg N ha^{-1} year^{-1}) and either mown 2 or 3 (maximum of 4) times a year, grazed by 5–10 cattle per hectare for 100–150 days, or both mown and grazed.

In forests, the gradient of land-use intensity included three broad categories: unmanaged broadleaf, managed broadleaf and managed conifer forest. The least intensively managed forests have been managed to some degree in the past, but are now often located within protected areas ($n = 56$ sites, including 31 sites in strictly protected areas; 14 and 9, respectively, of these sites have annual arthropod data). The naturally dominant tree species at all sites is European beech (*Fagus sylvatica*). The dominating conifer species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), which are native to central Europe but would be absent or rare in the study regions under natural conditions. However, these trees have been cultivated in the study regions for approximately 250 years. On all sites, inventories of living trees, stumps and deadwood were conducted between 2009 and 2011[27]. To obtain a continuous fine-grained measure for local land-use intensity in forests, we calculated a compound index on the basis of three indicators scaled 0–1: recent biomass removal (volume of harvested timber divided by the sum of the volume of living trees, harvested timber and remaining deadwood), proportion of tree species that do not belong to the native vegetation community (volume of standing timber, harvested timber and deadwood of non-native tree species (including spruce and pine) divided by the sum of the volume of all tree species) and deadwood origin (volume of deadwood with saw cuts divided by the total volume of deadwood)[27].

Land-use intensity at the landscape scale was quantified by measuring the proportion of area covered by arable fields, grasslands and forests within circular areas around the centre of our sites. As the scale of effect was unknown, we considered different area sizes with radii 250, 500, 1,000, 1,500 and 2,000 m. We used vector land-cover data from ATKIS Basis DLM (license agreements: GeoBasis-DE/LGB 2017, BG-D 29/17) with ±3 m accuracy of polygon borders, representing conditions between 2008 and 2010. We are aware that land cover is only a coarse measure for land-use intensity at the landscape scale, but information on fine-scaled habitat availability (such as field margins and within-field plant diversity) or details on land-use practices (such as the amount of fertilizers and pesticides used) was not available.

Air temperature was recorded at all 290 sites with hourly resolution starting between early 2008 and early 2009, depending on the site. Gaps within the time series at individual stations were filled on the basis of average linear relationships with neighbouring stations within the three regions. To derive complete time series from winter 2007–2008 onward, the initial time span was filled on the basis of data from the station network of the German Weather Service that surrounds each Exploratory (five stations each). Using 10× space–time cross-validation and a forward feature selection approach, the best individual subset of the 5 surrounding stations for each of the 290 stations to be filled was identified and a multiple linear model was used to predict the missing values. Precipitation for site was derived from the RADOLAN product of the German Weather Service (hourly radar-based precipitation estimates corrected by gauge measurements, with a resolution of 1 km^2 and 0.1 mm/h). From these products, we calculated—for each region and year—the mean temperature, number of frost days (daily minimum temperature <0 °C), number of warm days (daily mean temperature >20 °C) and precipitation sum for winter (from November of the previous year to February), growing period (from March to October) and year (from November of the previous year to October). Gap filling at the start of the time series was conducted in R version 3.5.1[32]. Other computations used the climate-processing software TubeDB (https://environmentalinformatics-marburg.github.io/tubedb).

Arthropod sampling

Arthropods were sampled annually in a consistent and standardized way from all 150 grassland sites from 2008 to 2017 and from 30 forest sites from 2008 to 2016. On the other 110 forest sites, arthropods were sampled by the same method and with the same sampling effort in 2008, 2011 and 2014. In grasslands, all arthropods of the herb layer were sampled twice per year in June and August to represent different phenological windows within the peak season of adult arthropod activity. On the basis of monthly samplings at the beginning of the study, we identified these two months as representing the best trade-off between reducing sampling effort and covering most species. Arthropods were sampled by sweep netting along a 150-m-long transect that comprised 3 of the virtual borders of a site by conducting 60 double sweeps per site[20]. Sweep netting was conducted only on days without rain, with low wind speed and after morning dew had dried. To reduce potential observer bias, personnel were trained and changes in personnel were reduced as much as possible (one change in Schwäbische Alb and Hainich-Dün regions in 2009; two changes in Schorfheide-Chorin region in 2009 and

2010; Supplementary Information section 3). In forests, flying insects were sampled using two flight-interception traps per site located close to two randomly selected corners of each site. Traps consisted of two crossed transparent plastic shields (40 × 60 cm) with funnels opening into sampling jars below and above the shields that were filled with 3% $CuSO_4$ solution and a drop of detergent[33]. Traps operated from March to October and were emptied monthly. All sites are part of larger management units, and therefore no edge effects owning to changes in land-use intensity at site borders are to be expected.

All samples were sorted to the order level in the laboratory. For taxonomic groups that occurred in larger numbers, and for which expert taxonomists were available, adult specimens were identified at species level: for grasslands, these included species in the Araneae, Coleoptera, Hemiptera (both Heteroptera and Auchenorrhyncha; some hemipterans were classified only to family or subfamily level) and Orthoptera, and for forests, these included species in the Coleoptera and Hemiptera (in Heteroptera). Only very few adults in these taxonomic groups could not be identified to the species level (1.1% in grasslands and 0.7% in forests), and these were excluded from the analyses. In grasslands, we additionally counted the number of individuals per order for groups for which no taxonomists were available: these included Acarina, Blattodea, Collembola, Dermaptera, Diptera (which was divided into Brachycera and Nematocera), Ephemeroptera, Hemiptera (Psyllidae and Aphidoidea), Hymenoptera (divided into Apocrita, Symphyta and Formicidae), Isopoda, Lepidoptera, Mecoptera, Megaloptera, Neuroptera, Odonata, Opiliones, Plecoptera, Pseudoscorpiones, Psocoptera, Raphidoptera, Strepsiptera, Thysanoptera and Trichoptera. Information on body length, trophic level and dispersal ability for identified species was obtained from the literature[34,35]. We estimated the biomass of all arthropod specimens that were identified to species level by applying a previously developed[36] general power function: biomass (in g) = $0.305 \times L^{2.62}/1{,}000$ where L is the mean body length of a species in millimetres. All arthropods identified to the species level were assigned to one of four trophic groups (herbivores, myceto-detritivores, carnivores and omnivores) on the basis of their known main food resource as adults. Because typical dispersal distances are unknown for most arthropod species, we classified species according to morphological characteristics and behavioural traits within taxonomic groups (for example, wing development, ballooning or hunting strategy)[35]. Dispersal ability—ranging from 0 to 1 in steps of 0.25—was defined differently for the groups, considering wing dimorphism (for Hemiptera, Coleoptera and Orthoptera), flying ability (Coleoptera) as well as information on migration and ballooning behaviour (Araneae) (details have previously been published[34]). All species with a dispersal ability ≤0.5 were considered to be weak dispersers, and all species with a dispersal ability >0.5 were considered to be strong dispersers.

Vegetation sampling

Plant communities in all 150 grassland sites were recorded in an area of 4 × 4 m between mid-May and mid-June from 2008 to 2017, and in 30 forest sites in an area of 20 × 20 m twice a year (spring and summer) from 2009 to 2016, by estimating the cover of each species. Ellenberg indicator values were taken from a previous publication[37].

Statistical analyses

All analyses were conducted in R v.3.5.1[32].

We performed principal component analyses (PCAs) and pairwise correlation tests including all weather variables. On the basis of the results, and similar to a previous publication[2], we selected mean winter temperature and precipitation during the growing period for subsequent analyses because these variables were weakly correlated and represented both seasons and both temperature and precipitation (Extended Data Fig. 6). Despite considerable temporal fluctuations, mean winter temperature increased and precipitation during the growing period decreased within our study period (Extended Data Fig. 7). PCAs and pairwise correlation tests for landscape-level variables enabled us to select cover of arable fields and cover of grassland as independent predictors because these were weakly correlated across spatial scales, whereas forest cover was correlated to both cover of arable fields and grassland (Extended Data Fig. 6).

We calculated gamma diversity (estimated total number of species) across 150 grassland and 30 forest sites separately for grassland and forest for each year using the 'diversity accumulation curve' framework that extends methods for rarefaction and extrapolation of species richness[29]. We used Chao's BSS based on the frequencies of species: the higher value of the minimum doubled reference sample size, and the maximum reference sample size among years as incidence-based, bias-corrected diversity estimates for $q = 0, 1$ and 2[29]. This approach accounts for slight differences in site numbers between years caused by limited accessibility or failure of traps. With increasing order q, the more frequent species are more strongly weighted ($q = 0$ equals species richness, $q = 1$ equals the exponential of Shannon entropy and $q = 2$ equals the inverse of Simpson diversity), which enables us to assess whether changes in gamma diversity depend on the frequencies of species. Using different reference-sample sizes resulted in consistent results (data not shown). Confidence intervals were calculated by bootstrapping ($n = 200$ bootstraps).

We aggregated data from all arthropods identified to species per site and year to calculate biomass, abundance and the number of species for all species, and separately for each trophic and both of the dispersal groups. For grasslands, we additionally calculated the abundance of all arthropods per site and year, including groups that were not identified to species level. To identify the scale of the effect for landscape-level land-use intensity[38], we conducted a multiscale analysis by correlating arthropod biomass, abundance and the number of species with the cover of arable fields and cover of grassland separately for radii of 250–2,000 m. For this, only data from a random subset of sites with non-overlapping buffers at the 2,000-m scale were used, and this procedure was repeated 100 times. In grasslands, correlations increased initially with increasing radius but started to plateau at 1,000 m (Extended Data Fig. 8). Owing to the higher overlap of buffers of neighbouring sites at larger spatial scales, we thus present results for all grassland analyses at the 1,000-m scale. In forests, the patterns were more complex, but—because of the small range of agricultural land-use variables at small scales (Extended Data Fig. 5) and the higher overlap of buffers of neighbouring sites at larger spatial scales—we also present the results for all forest analyses at the 1,000-m scale.

To test for temporal trends in our arthropod data, we fitted generalized linear mixed models with Poisson errors for count data (abundance and species number; function glmer in package lme4) and linear mixed models with Gaussian errors for biomass (log-transformed; function lmer), separately for grasslands and forests. For forests, we analysed the annual data from 30 sites and the 3-year-interval data from 140 sites separately. Separate models were fitted for trophic groups. Fixed effects included year, weather (mean winter temperature, precipitation during the growing period and their interaction), local land-use intensity and landscape-level land-use intensity (cover of arable fields and cover of grassland within a radius of 1,000 m), as well as interactions between year and local land-use intensity and between year and landscape-level land-use intensities. Models included the site nested in the region as a random effect to account for the nested design and the repeated measures at the site level. Poisson models included an observation-specific random effect to account for potential overdispersion[39]. All continuous predictor variables were standardized to a mean of 0 and an s.d. of 1 before modelling. To test whether changes in the overall number of species were associated with changes in overall abundance, we ran additional models with the number of species as response and log-transformed abundance as covariate. To assess the contribution of individual years to the overall trend, we repeated the models for overall biomass, abundance and number of species, and excluded data from one year each time. In addition, we tested whether the observed effect of year differed from a random expectation by randomizing the order of years 100× for forests and grasslands before modelling.

To test for differences between dispersal groups, we fitted models for biomass, abundance and number of species in which effects of year, local and landscape-level land-use intensity (as well as their interactions) were estimated specifically for each dispersal guild. These models included response values for each group per site and year, and dispersal group (weak or strong) as fixed effect. To test whether observed effects differed significantly between dispersal guilds, we fitted additional models including the three three-way interactions between dispersal guild, year and each of the three land-use variables. All models included the site nested in the region as a random effect to account for spatial arrangement and temporal repetitions per site. Poisson models included an observation-specific random effect to account for potential overdispersion.

In addition to models for data aggregated per site and year, we fitted models for biomass, abundance and number of species at the level of individual observations (two collections per year for grasslands and five collections per year for forests), which could account for seasonal differences and weather conditions at the time of sampling. For forest data from 30 sites, fixed effects included mean winter temperature, mean temperature and precipitation during sampling period, length of sampling period (in days), Julian date of the day on which traps were emptied, local and landscape-level land-use intensity (cover of arable fields and cover of grassland within a radius of 1,000 m), as well as interactions between year and local land-use intensity, and between year and landscape-level land-use intensity. For grasslands, fixed effects included mean winter temperature, precipitation during the growing season and their interaction, mean temperature and precipitation on the day of sampling, Julian date of the day of sampling, local land-use intensity and landscape-level land-use intensity (cover of arable fields and cover of grassland within a radius of 1,000 m), as well as interactions between year and local land-use intensity, and between year and landscape-level land-use intensity. Models included the site nested in the region as a random effect to account for the nested design and the repeated measures at the site level. Poisson models included an observation-specific random effect to account for potential overdispersion[39]. To allow nonlinear effects for day of sampling, we fitted generalized additive models (function gamm4 in package gamm4).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

This work is based on data from several projects of the Biodiversity Exploratories programme (DFG Priority Program 1374). All data used for analyses are publicly available from the Biodiversity Exploratories Information System (https://doi.org/10.17616/R32P9Q) at https://www.bexis.uni-jena.de/PublicData/PublicDataSet.aspx?DatasetId=25786. Raw data are publicly available from the same repository (with identifiers 21969, 22007, 22008, 19686 and 20366), or will become publicly available after an embargo period of five years from the end of data assembly to give the owners and collectors of the data time to perform their analysis. Any other relevant data are available from the corresponding author upon reasonable request.

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Author contributions S.S., J.M. and N.K.S. conceived the idea for the manuscript; M.M.G., N.K.S., S.S., D.A., W.W.W., T.N., S.W., P.S., C.A., J.B., J.V., D.P. and M.F. collected and processed data; S.S., J.M., M.M.G. and W.W.W. defined the final analysis; S.S., N.K.S., C.P., P.S. and M.M.G. analysed the data; S.S. and W.W.W wrote the first manuscript draft and finalized the manuscript. All authors discussed the analyses and commented on the manuscript.

Competing interests The authors declare no competing interests.

Additional information

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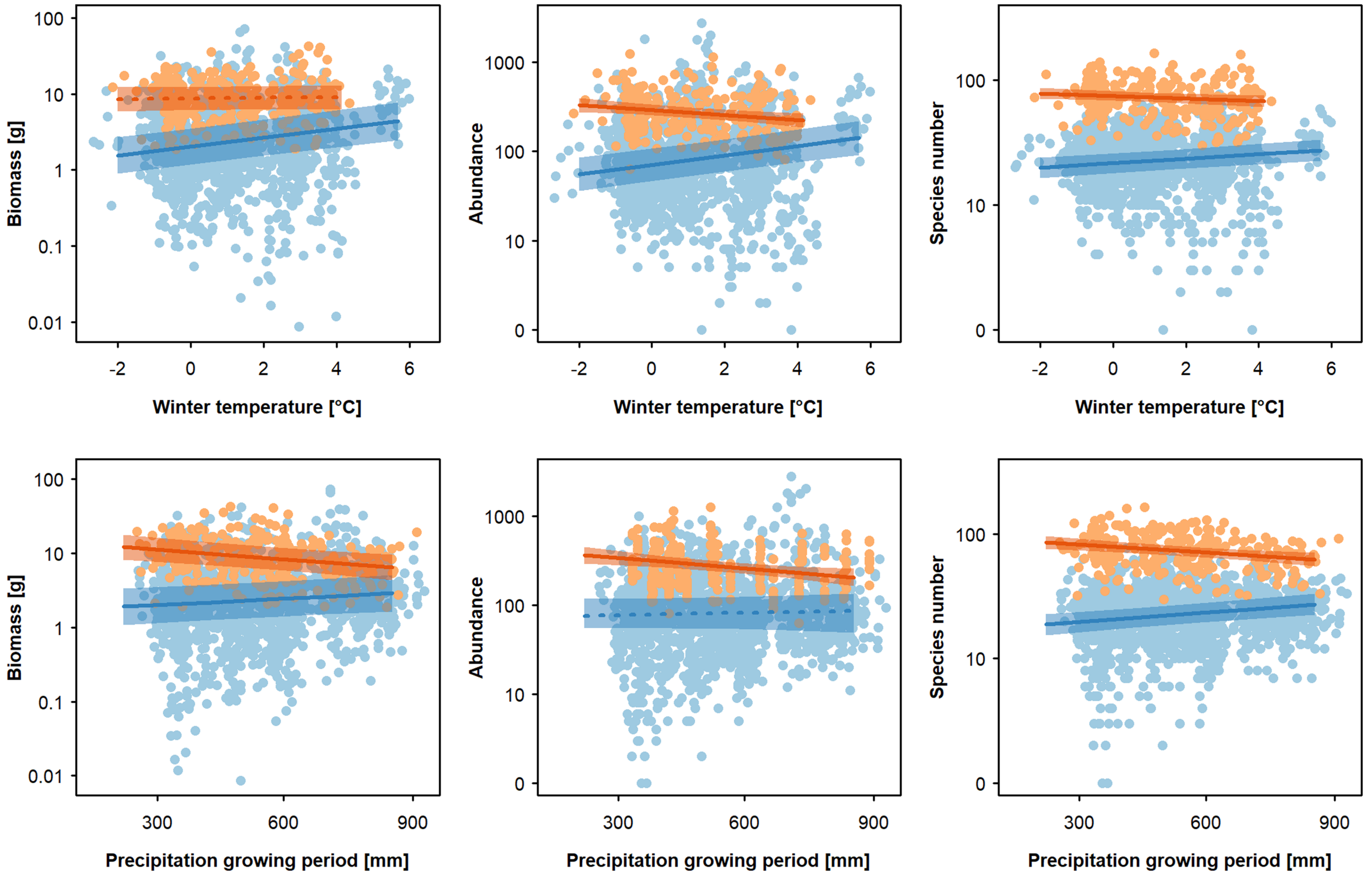
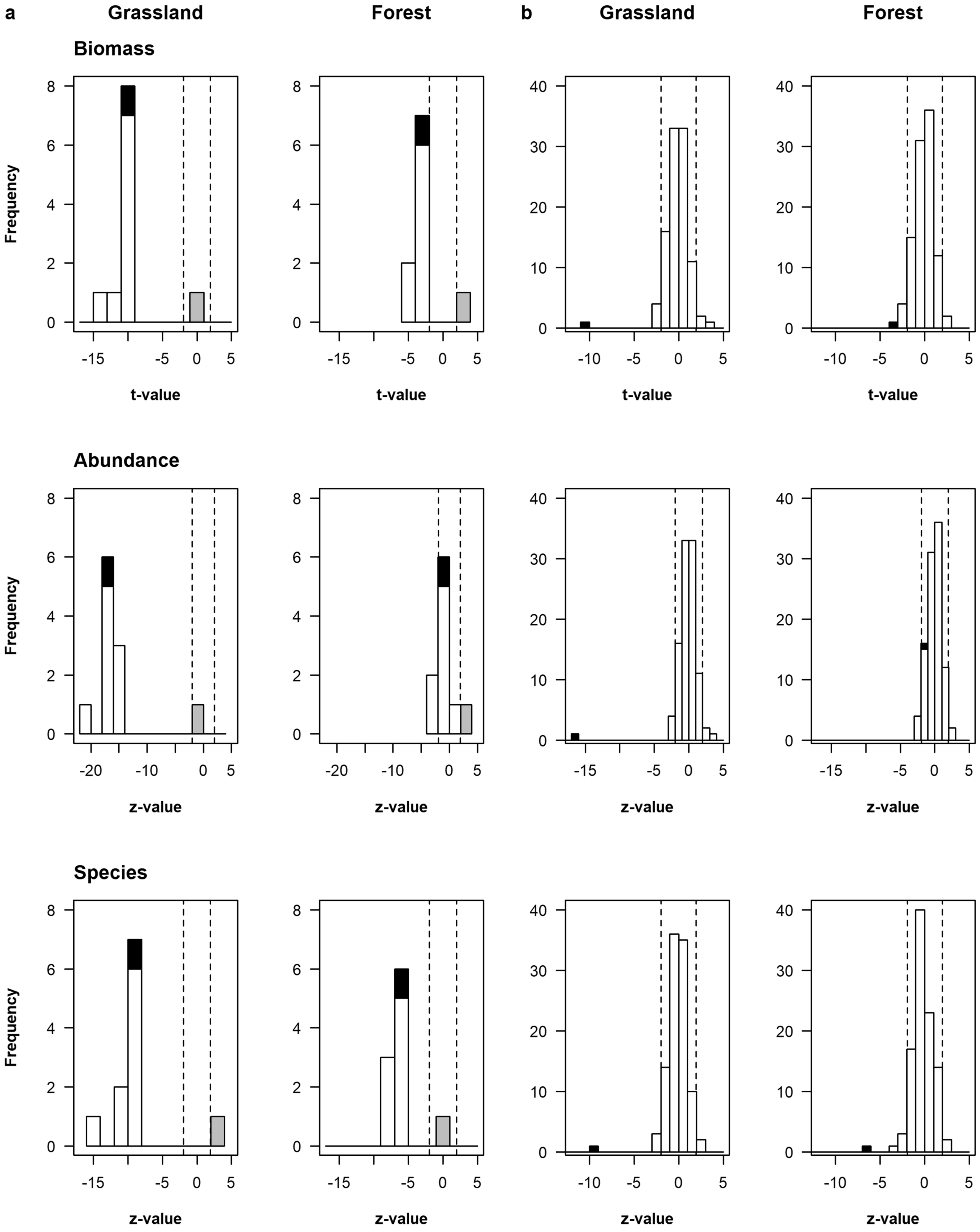
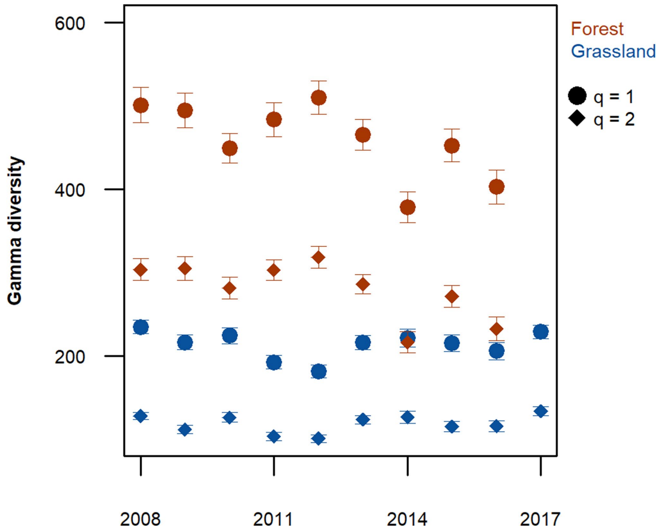


Extended Data Fig. 1 | Effects of weather variables on arthropod numbers. Effects of mean winter temperature (November to February) and precipitation during the growing period (March to October) on biomass, abundance and number of species in arthropod communities in 30 forests (orange) and 150 grasslands (blue) across three regions of Germany. Dots represent raw data aggregated per site and year ($n = 1{,}406$ (grassland) or 266 (forest) independent samples). Dotted lines indicate non-significant ($P \geq 0.05$) and solid lines indicate significant effects of weather variables ($P < 0.05$), based on linear mixed models that included year, local and landscape land-use intensity as covariates. Shaded areas represent confidence intervals. The effects of winter temperature and precipitation differed between forests and grasslands. In grasslands, arthropod numbers increased with increasing winter temperature and with increasing precipitation in the growing period; the effect of precipitation was weaker than the effect of winter temperature, and the effects of both weather variables were weaker than the effect of the year (Supplementary Table 1-1). In forests, arthropod numbers decreased with increasing winter temperature and with increasing precipitation in the growing period; the effects of the two weather variables were similarly strong, but slightly weaker than the effect of the year (Supplementary Table 1-1).

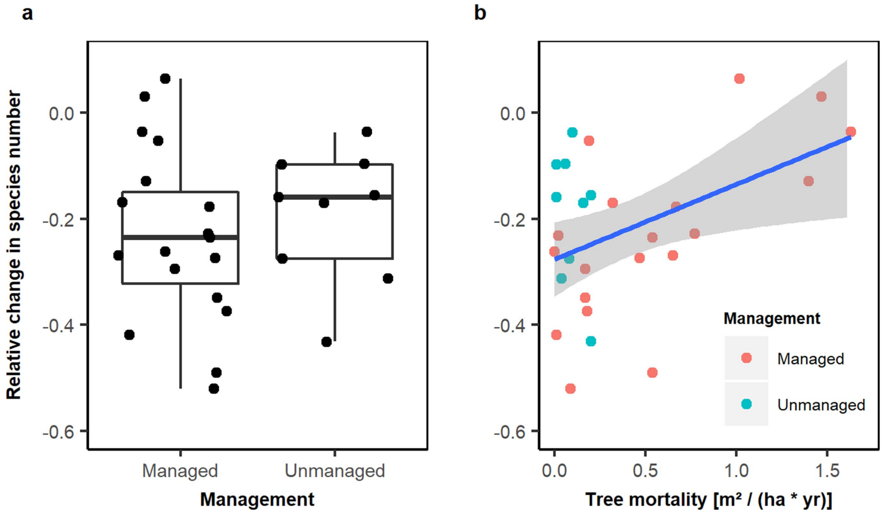


Extended Data Fig. 2 | See next page for caption.

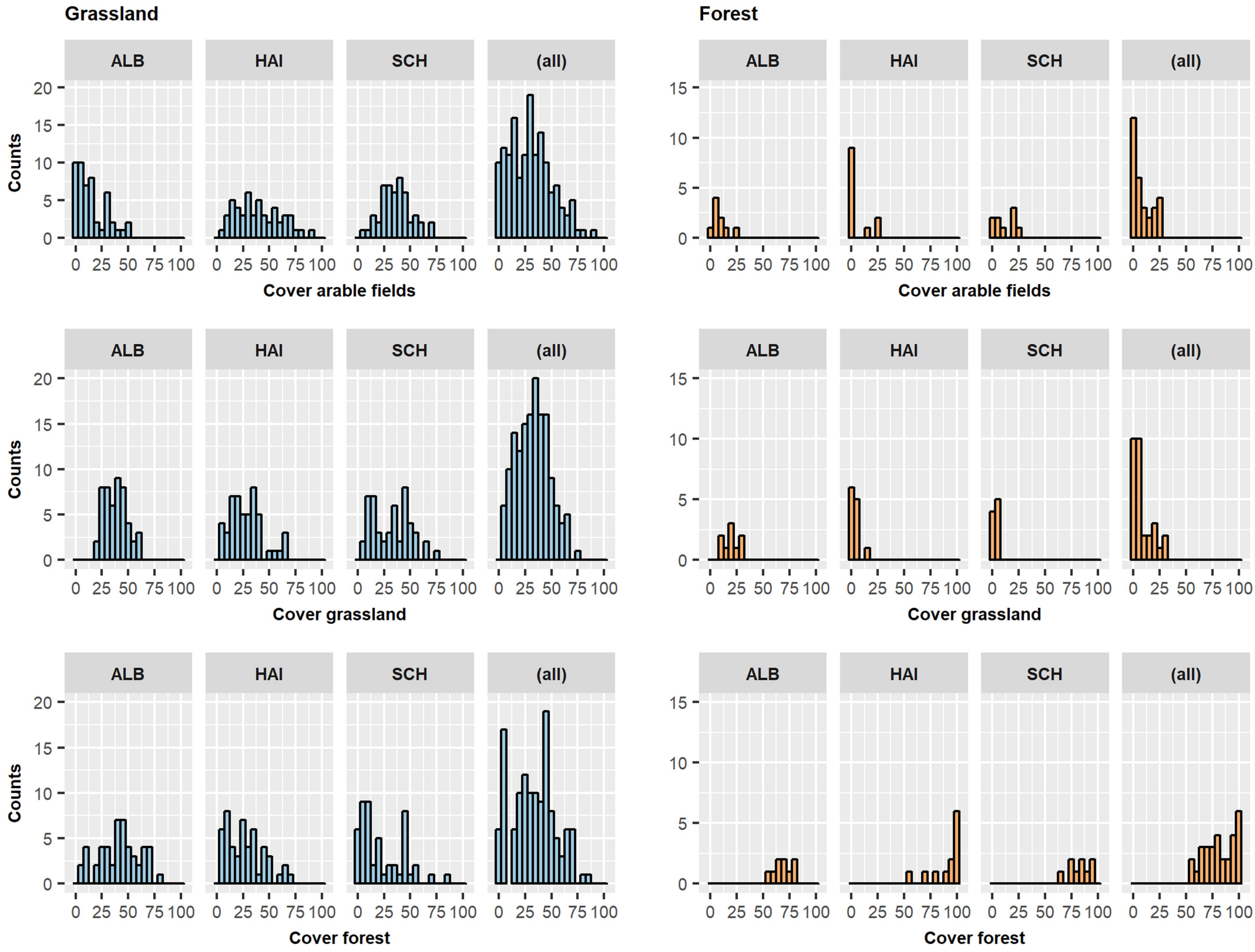
Extended Data Fig. 2 | Contribution of individual years to overall trends. **a**, To assess the contribution of individual years to the overall trend, we repeated the linear mixed models for overall biomass, abundance and number of species, and excluded one year each time. The distribution of *t* and *z* values for the effect of the year from subset models (white), and from the full models including all years (black), are shown (11 models for grasslands and 10 models for forests). Grey bars denote effect of the year 2008 (the year with the strongest effect on overall trend estimates). **b**, In addition, we tested whether the observed effect of year differed from a random expectation by randomizing the order of years 100× for forests and grasslands before modelling. The distribution of *t* and *z* values for the effect of the year from models with randomly ordered years (white) and models with the years ordered correctly (black) are shown (101 models each for grasslands and forests). Vertical dashed lines indicate levels of significance with $P < 0.05$. The results in **a** show that both weaker and stronger temporal trends could be detected when single years were excluded from the analysis, compared to the full model including all years. Results in **b** show that models with the years ordered randomly produced effects of the year that were normally distributed around zero, and only the models with years ordered correctly generated strong temporal trends. For a more detailed discussion, see Supplementary Information section 3.



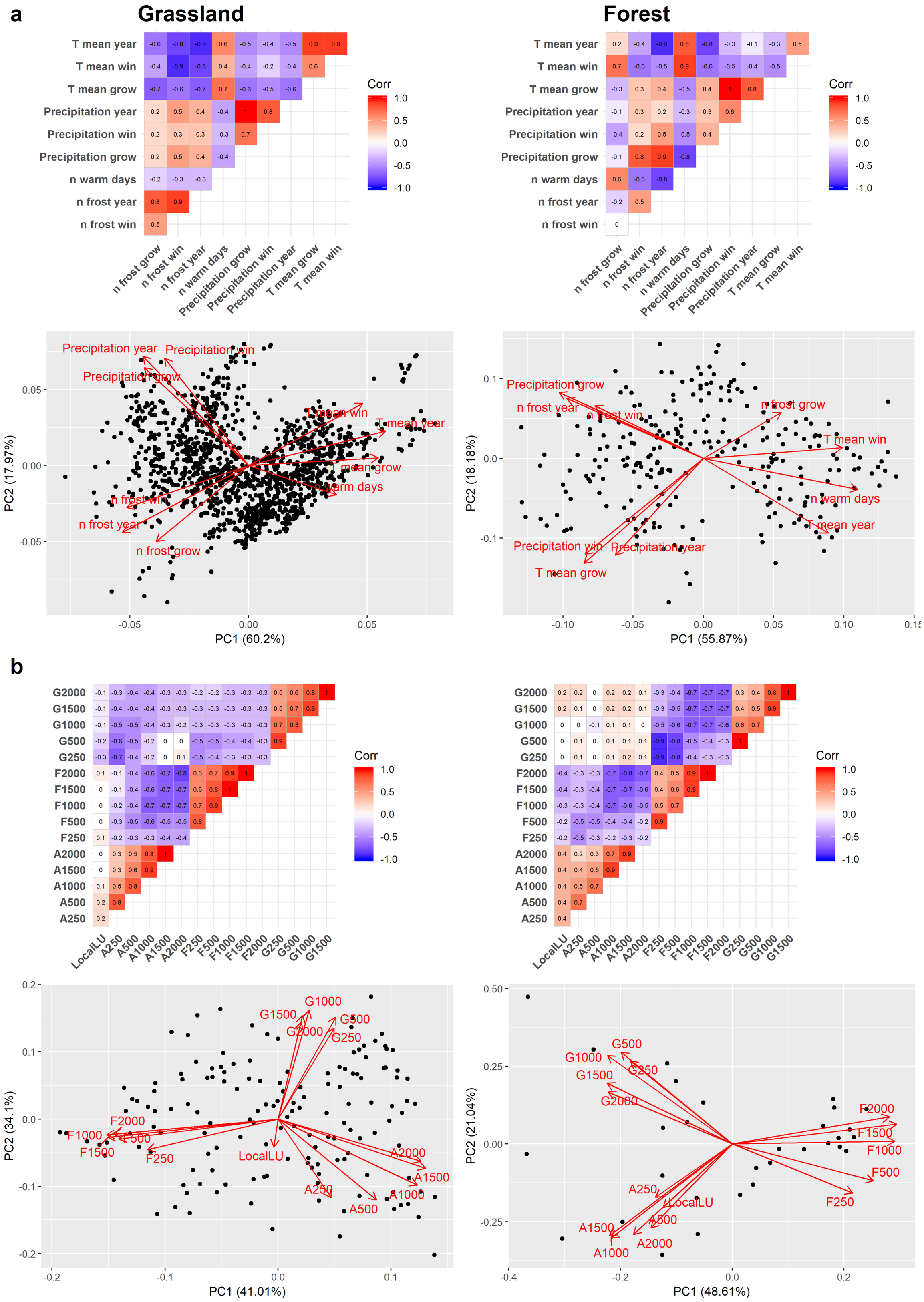
Extended Data Fig. 3 | Declines in gamma diversity of frequent species. Estimated gamma diversity (total number of species across all grassland or forest sites) over time. Symbols and error bars shown mean and 95% confidence intervals for gamma diversity, calculated as incidence-based, bias-corrected diversity estimates (Chao's BSS[29], with 200 bootstrapping runs; Methods) for $q = 1$ and 2 (for $q = 0$, see Fig. 1). With increasing order q, the more-frequent species are more strongly weighted ($q = 0$ equals species richness, $q = 1$ equals the exponential of Shannon entropy and $q = 2$ equals the inverse of Simpson diversity; that is, only dominant species affect the diversity measure). This approach accounts for slight differences in site numbers between years caused by limited accessibility or failure of traps. Non-overlapping confidence intervals indicate a significant difference between two sampling years[30]. Figure 1 shows that gamma diversity declines in both forests and grasslands for $q = 0$. We find that in forests gamma diversity declines when only the more-common species are considered ($q = 1$ and $q = 2$), whereas in grasslands there is no overall decline when only the common species are considered. For a more detailed interpretation, see Supplementary Information section 4.



Extended Data Fig. 4 | Effect of tree mortality on arthropod trends. a, The relative change in the number of arthropod species between the first two and the final two study years was similar for managed (*n* = 19) and unmanaged (*n* = 9) forest sites (*z* = 0.648, *P* = 0.517, derived from a linear mixed model with relative difference in species number as response, harvesting category as fixed and region as random effect). Dots show raw data per site. Boxes represent data within the 25th and 75th percentile, black lines show medians, and whiskers show 1.5× the interquartile range. **b**, When considering actual tree mortality between forest inventories in 2009 and 2016, declines in the number of arthropod species were weaker at sites with higher tree mortality (*z* = 2.536, *P* = 0.011, derived from a linear mixed model with relative difference in species number as response, tree mortality as fixed and region as random effect). Dots show raw data per site. The blue line visualizes the significant relationship between the change in the number of arthropod species and tree mortality based on the linear mixed model, and the shaded area represents confidence intervals. This suggests that changes in habitat conditions and heterogeneity linked to tree mortality—such as increasing canopy openness, herb cover or deadwood availability—moderated declines in the number of arthropod species. More research is needed to identify mechanistic relationships. Tree mortality included both natural mortality and timber harvesting. Forest sites had a stand age of, on average, 116 years (minimum of 30 years and maximum of 180 years) and therefore did not include overmature stands. Owing to stand age and because management was abandoned 20 to 70 years before this study started, natural tree mortality was low even in unmanaged stands. We expect increasingly positive effects of natural tree mortality and associated increased structural diversity and heterogeneity[40] on arthropod trends with increasing stand age, but further research is required. In Germany, harvesting is usually conducted as shelterwood cutting. In our sites, the harvested amount over the course of our study reached a maximum of 1% of the standing volume per year. More intense harvesting systems (such as clear cutting), which lead to less heterogeneous habitat conditions, may not have similar moderating effects on arthropod declines.

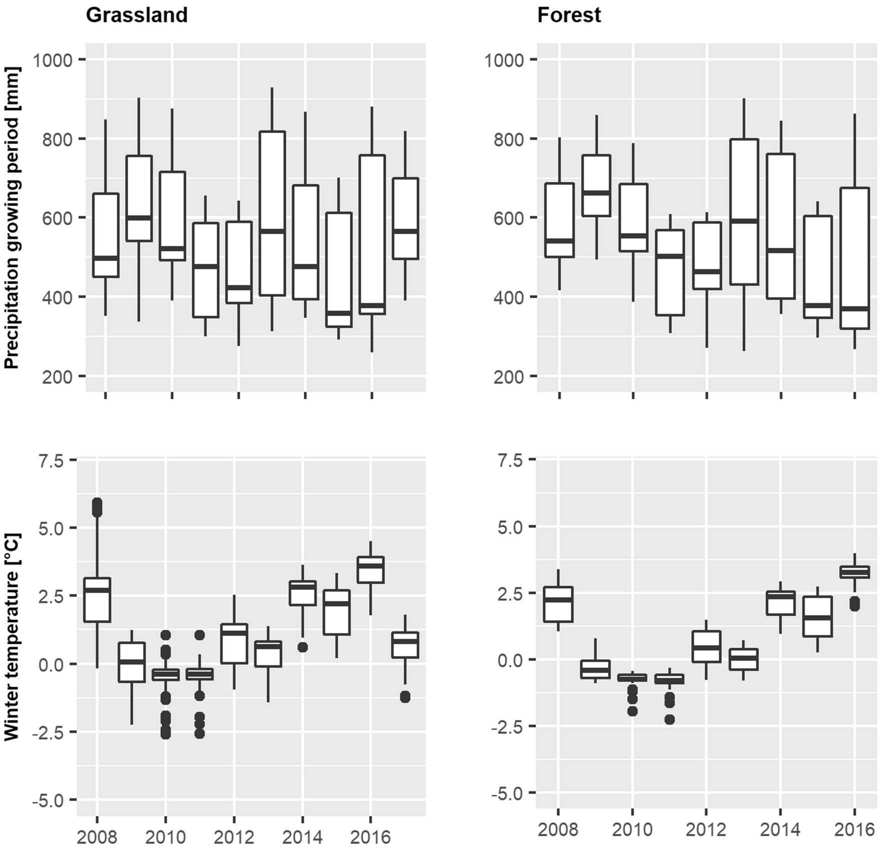


Extended Data Fig. 5 | Distribution of landscape-level land-use variables. Data distribution of the cover of arable fields, grassland and forest within 1,000 m surrounding each of the 150 grassland and 30 forest sites for each region, and for all regions in total. ALB, Schwäbische Alb; HAI, Hainich-Dün; SCH, Schorfheide-Chorin.

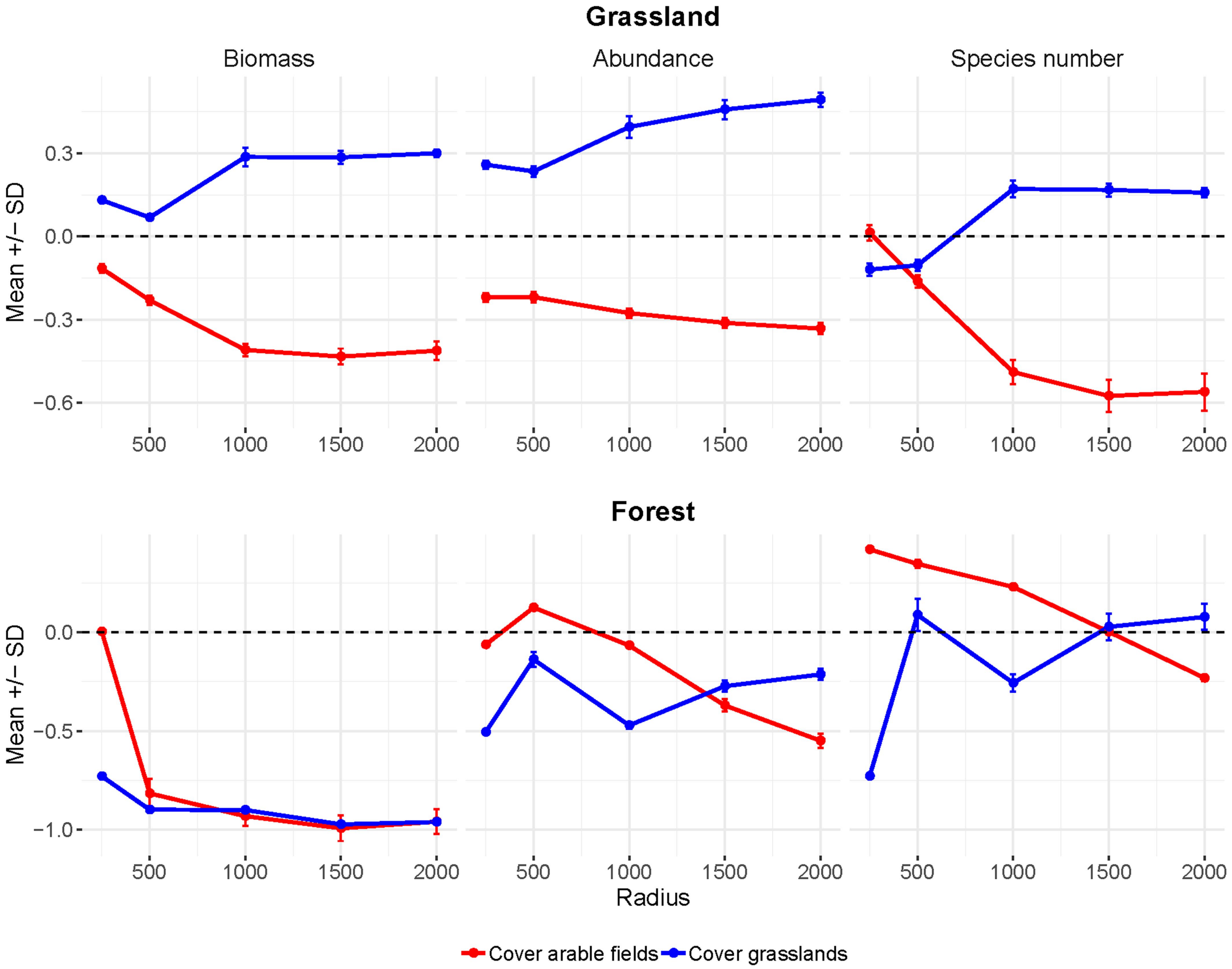


Extended Data Fig. 6 | See next page for caption.

Extended Data Fig. 6 | Correlations among weather and among land-use variables. a, **b**, Coefficients of pairwise correlations and PCAs for weather variables (**a**) and land-use variables (**b**). Temperature-related data are based on observed air temperature by weather stations at each site. Precipitation is derived from gauge-corrected radar observations (RADOLAN, Deutscher Wetterdienst). For each site and year, we calculated mean temperature (*T* mean), number of frost days (daily minimum temperature <0 °C; *n* frost), number of warm days (daily mean temperature >20 °C; *n* warm days) and precipitation sum in mm (precipitation) for three different periods: winter (November of the previous year to February; win), growing period (March to October; grow) and year (November of the previous year to October; year). The number of independent observations for weather variables was $n = 1{,}406$ (grasslands) or 266 (forests). Land-use variables include local land-use intensity (local LU) and cover of arable fields (A), grassland (G) and forest (F) at different spatial scales (250, 500, 1,000, 1,500 and 2,000 m). The number of independent observations for land-use variables equalled the number of sites; $n = 150$ (grasslands) or $n = 30$ (forests). On the basis of correlations and PCA results, we chose mean winter temperature and precipitation during the growing period, as well as cover of arable fields and cover of grassland, as ecologically meaningful and the least-correlated explanatory variables for modelling arthropod data.



Extended Data Fig. 7 | Temporal patterns in weather conditions. Temporal patterns of the sum of precipitation during the growing period (March to October) and mean winter temperature (November of the previous year to February) for 150 grassland and 30 forest sites ($n = 1{,}406$ (grassland) or 266 (forest) independent observations). Boxes represent data within the 25th and 75th percentile, black lines show medians and whiskers show 1.5× the interquartile range. A linear mixed model for each response variable, with year as a fixed effect and the site nested in the region as a random effect, indicate that winter temperature increased (grassland, $z = 10.90$, $P \leq 0.001$; forest, $z = 8.24$, $P \leq 0.001$) and precipitation during the growing period decreased during our study period (grassland, $z = -6.53$, $P \leq 0.001$; forest, $z = -8.44$, $P \leq 0.001$). We are currently not able to quantify whether and how much the observed trends in arthropod numbers were affected by changes in climatic conditions (Supplementary Information section 2).



Extended Data Fig. 8 | Results from multiscale analysis. Mean and s.d. of Pearson's coefficients of correlation between arthropod numbers (biomass, abundance and number of species) and landscape-level land-use variables (cover of arable fields and cover of grassland) for radii of 250–2,000 m around 150 grassland sites and 30 forest sites. Only data from a random subset of sites with non-overlapping buffers at the 2,000-m scale were used. The randomized subsampling of sites with non-overlapping buffers and the calculation of correlations was repeated 100 times (median number of sites per subsample was $n = 18$ (grassland) or 17 (forest)). The 1,000-m scale was used for modelling arthropod numbers for both grassland and forests because (i) the correlation coefficients appeared to plateau at this scale in grasslands, (ii) the range of landscape-level land-use variables at small spatial scales in forests was small and (iii) buffers of neighbouring plots overlapped more extensively at higher spatial scales.

Extended Data Table 1 | Details on arthropod numbers

	Grassland	Forest30	Forest 140	Sum
Abundance				
Identified and unidentified taxa	864,548	80,624	117,731	1,032,279
Unidentified taxa	685,738	NA	NA	685,738
Identified taxa	178,810	80,624	117,731	346,541
Species number	1,309	1,582	1,634	2,675
Biomass[g]	5,637	2,676	4,199	11,642
Weak disperser				
Abundance	29,979	5,744	6,580	
Species number	209	136	148	
Strong disperser				
Abundance	133,710	74,492	110,794	
Species number	946	1,375	1,418	
Carnivores				
Abundance	10,503	9,543	12,611	
Species number	344	531	517	
Omnivores				
Abundance	3,849	21,878	36,900	
Species number	179	354	382	
Herbivores				
Abundance	163,054	20,016	33,252	
Species number	720	295	341	
Myceto-/detritivores				
Abundance	1,403	29,158	34,964	
Species number	64	395	394	

Total biomass, number of individual arthropods and number of arthropod species from 150 grassland and 30 or 140 forest sites. Data are available for each year from 2008 to 2017 for all 150 grassland sites, and from 2008 to 2016 for 30 forest sites. In addition, data from 2008, 2011 and 2014 are available for 140 forest sites (including the 30 sites with annual data). Information regarding the abundance of arthropod taxa that were not identified to the species level was collected only in grasslands and not in forests. Classification as a weak or strong disperser was based on morphological and behavioural characteristics (Methods). Owing to missing information, not all species could be assigned to a dispersal or trophic group.

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n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
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☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
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☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data.
Data analysis	Data analyses were conducted using R version 3.5.1 including the packages vegan (function decostand) , lme4 (function glmer and lmer), reshape2 (function dcast), BiodiversityR (function rankabundance), stats (prcomp), iNext and ggplot2 for graphics; Climate data was processed using the software TubeDB (https://environmentalinformatics-marburg.github.io/tubedb).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data used for analyses are publicly available at the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q) https://www.bexis.uni-jena.de/PublicData/PublicDataSet.aspx?DatasetId=25786. Raw data are publicly available from the same repository (IDs: 21969, 22007, 22008, 19686, 20366) or will become publicly available after an embargo period of five years from the end of data assembly to give data owners and collectors time to perform their analysis.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	To disentangle local and landscape-level effects of land use on the temporal trends of arthropod communities in grasslands and forests, we used our arthropod data from the Biodiversity Exploratories research program, including more than 1 million individuals and 2,700 arthropod species. Arthropods were collected annually during the growing period from 2008 to 2017 by standardized sampling at 150 grassland plots and from 2008 to 2016 at 30 forest plots. An additional 118 forest plots were sampled in 2008, 2011 and 2014 to test the overall trend across a larger number of plots. Both grassland and forest plots cover gradients in local land-use intensity. Land-use intensity was quantified in the form of compound indices based on grazing, mowing and fertilization intensity in grasslands, and on recent biomass removal, the proportion of non-native tree species and deadwood origin in forests. To analyze landscape-level effects, we quantified the cover of arable fields, grassland and forest within a 2 km radius around each sampling plot. We modelled temporal trends in biomass, abundance and species number of arthropods and of different dispersal and trophic guilds separately for grasslands and forests, and tested for effects of local and landscape-scale land-use intensity on these trends, accounting for weather conditions and different spatial scales.
Research sample	The sample unit is the arthropod community of a grassland or forest plot within a given year. It is characterized by measures of biomass, abundance and species number. A sample unit is considered to represent arthropod populations at our study sites which measured 50m x 50m in grasslands and 100m x 100 m in forests. Data from different months and traps per plot were pooled per plot and year.
Sampling strategy	Standardized sweep-net sampling along 3 50m transects were conducted in grasslands in June and August. These periods represent the start and end of the peak season for arthropods Central Europe. Sweep-netting is most efficient to sample arthropods in grassland habitats. In forests, we used 2 flight-interception traps per plot which provide a broad range of flying arthropods. Traps were operated during the complete growing season. All samples were sorted to order level in the lab and all groups for which taxonomists were available were identified to species level. No statistical methods were used to predetermine sample size.
Data collection	Samples were operated in the field and sorted in the lab by trained technicians. Identification was done by expert taxonomists. All people involved are listed in the acknowledgments section.
Timing and spatial scale	Grasslands: annual data collection at all 150 plots in June and August 2008 to 2017 (peak season of arthropods in our study regions) Forests: annual data collection from 2008 to 2016 (April to October) at 30 plots (full growing period represented); in addition, 118 plots were sampled (April to October) in 2008, 2011 and 2014 to test for a larger number of plots whether trends are consistent with results based on annual data from the 30 plots described before
Data exclusions	No data was excluded from the analyses
Reproducibility	Our data were collected as part of a monitoring over several years and which cannot be repeated.
Randomization	Study plots were selected from ~3000 candidate plots. Surveys of initial vegetation and land use were conducted on candidate plots by stratified random sampling to ensured that the selected plots covered the whole range of land-use intensity and to minimize confounding effects of spatial position or soil type.
Blinding	Investigators were not aware of the land-use intensity of the plot were they worked, but they could not otherwise be blinded during data collection and analyses for example with respect to the year a sample came from.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Grasslands: sweep-netting was only conducted when the vegetation was dry and wind speed was low Forests: traps were operated at all weather conditions from April to October
Location	Our data were collected in three German regions: (1) Schwäbische Alb in south-western Germany (420 km², 460–860 m above sea level (a.s.l.)); (2) Hainich-Dün in central Germany (1560 km², 285–550 m a.s.l.); and (3) Schorfheide-Chorin in northeastern Germany (1300 km², 3–140 m a.s.l.).
Access and import/export	Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg (Regierungspräsidium

Access and import/export	Tübingen, file number 55-3/8852.15), Thüringen (Thüringer Landesverwaltungsamt, file number 13.4 64233/08-08SDH) and Brandenburg (Landesumweltamt Brandenburg, file number RO7/SOB-0907).
Disturbance	Activity of investigators was spatially limited to three 50m transects for sweep-netting and short paths to access the flight-interception traps

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	No laboratory animals were involved in the study.
Wild animals	Arthropods of about 2700 different species were collected in the field and killed on-site using CuSO4-solution for flight-interceptions traps and ethanol for sweep-netting. Identification of arthropods requires killing and transport to the lab were microscopes can be used.
Field-collected samples	Samples were stored in 93% ethanol at 7°C except for short time periods during transport, sorting and identification.
Ethics oversight	It could not be ruled out that threatened or protected arthropod species would be collected and killed. Thus, permision was required from the authorities which was granted for scientific reasons. These permits were issued by the responsible state environmental offices of Baden-Württemberg (Regierungspräsidium Tübingen, file number 55-3/8852.15), Thüringen (Thüringer Landesverwaltungsamt, file number 13.4 64233/08-08SDH) and Brandenburg (Landesumweltamt Brandenburg, file number RO7/SOB-0907).

Note that full information on the approval of the study protocol must also be provided in the manuscript.