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RESEARCH ARTICLE

Evidence for regional-scale declines in carabid beetles in old lowland beech forests following a period of severe drought

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Abstract

Context Evidence for declines in insect populations is growing with climate change being one suspected driver. Forests, however, are still underrepresented in the relevant research. Recent droughts (2018–2020) have severely affected forests in Central Europe and have been linked to declines in carabid abundance, biomass as well as changes in species traits at the local scale.

Objective We tested drought effects on forest carabids at regional scale. We additionally investigated whether variability in drought effects could be explained with the initial community composition and the local environmental context.

Methods We used generalized linear mixed models to compare data from 1999 to 2001 and 2020 to 2022 across eleven old beech forest sites of high conservation interest in North-East Germany and investigated changes in carabid abundance, biomass, Hill numbers and selected species traits. We then tested additional community-related and environmental predictors to explain spatial variability in changes in biomass.

Results We found significant declines in biomass of 65% and in abundance of 51%. There were no significant changes in Hill numbers. We found consistent evidence that declines affected especially larger and less mobile species. Declines and changes in species traits also occurred in strictly protected old-growth beech forests. Among environmental predictors, landscape composition explained local variability in biomass declines best with stronger decline at forest sites with less forest area in their vicinity.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-024-01920-1.

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Conclusions Our findings reveal large-scale declines in forest carabids in the context of recent droughts and highlight the exceptional role of landscape composition in this regard. Future insect conservation strategies need to incorporate the landscape context and potential exposure to extreme weather.

Keywords Biosphere Reserves · Climate change · Drought · *Fagus sylvatica* · Global environmental change · Insect decline · Old-growth forests · UNESCO World Heritage

Introduction

There have been concerning reports about declines in insect populations affecting a variety of taxonomic groups and habitats (e.g. Dalton et al. 2023; Seibold et al. 2019; van Klink et al. 2020; and see Didham et al. 2020a for a selection of further studies). Moreover, several suspected drivers contributing to declines have moved into the focus of research (Habel and Schmitt 2018; Wagner et al. 2021; Weisser et al. 2023). For instance, recent studies have linked insect trends to weather anomalies (Bauerfeind and Fischer 2014; Ewald et al. 2015; Evans et al. 2022; Welti et al. 2022; Müller et al. 2023). Consequently, climate change is among the suspected drivers of population declines (Didham et al. 2020a; Halsch et al. 2021; Wagner et al. 2021; Harvey et al. 2022), especially in the context of recent droughts and heatwaves in Europe (2018–2020), which have been unprecedented for centuries (Hari et al. 2020; Rakovec et al. 2022; Schumacher et al. 2022; Zachariah et al. 2023; Treydte et al. 2023).

Despite increasing research efforts, drivers and long-term trends of insect populations in forest ecosystems remain largely understudied (Staab et al. 2023; Blüthgen et al. 2023). Some of the few available studies thus far found notable declines (Seibold et al. 2019; Harris et al. 2019; Barendregt et al. 2022; Staab et al. 2023). Therefore, there remains an urgent need to learn more about exactly where and why certain groups of insects are declining to better understand the nuances in population trends. Some of the suspected causes of declines in open landscapes, such as industrial agriculture or urbanization, play a lesser role in European forests. However, the effects of anthropogenic climate change on forests are becoming increasingly clear (Oakes et al. 2014; Seidl et al. 2017; Senf et al. 2018). For instance, recent periods of drought have severely affected forests in Europe, leading to growth declines and increased mortality (Senf and Seidl 2021; Schnabel et al. 2022; Spiecker and Kahle 2023). Recent droughts have probably also had severe effects on forest insects (Pureswaran et al. 2018; Cours et al. 2023; Blüthgen et al. 2023), but these have hardly been investigated to date.

Large proportions of the insect biodiversity and biomass of temperate forests can be found in the litter and upper soil layers (Schowalter 2017). Here, carabid beetles (Coleoptera: Carabidae), a family of mostly predatory beetles, make up a considerable proportion of the epigeic fauna and play an essential role in invertebrate food webs (Magura 2002). They are sensitive to environmental changes and thus are often used as bio-indicators (Rainio and Niemelä 2003; Kotze et al. 2011). Many of the species found in temperate forests are adapted to relatively stable, cool and humid environments (Fitzgerald et al. 2021; Irmler 2007; Koivula et al. 1999; Müller-Motzfeld 2001). In line with this, several experimental studies (Williams et al. 2014; Jouveau et al. 2022) and observational studies (Šustek et al. 2017; Šiška et al. 2020) found a high sensitivity of forest carabids towards droughts. A recent study by Weiss et al. (2024) revealed declines in carabid abundance in a small forest area in North-East Germany, which were linked to the recent period of drought. They found even greater declines in biomass and larger, less mobile, and predatory species seemed to be particularly affected by these declines. However, there remains a general lack of knowledge about how recent droughts have affected forest insects such as carabids on a larger spatial scale. Investigating this knowledge gap would also improve the understanding of environmental factors for insect trends in general.

In this study, we investigated changes in forest carabids in the context of recent severe droughts (2018–2020) at the regional scale. For that purpose, we analyzed data from 1999 to 2001 and 2020 to 2022, collected at eleven old lowland beech forest sites in North-East Germany, the same region from which the findings of Weiss et al. (2024) originate (Fig. 1). Drought conditions similar to those described by Weiss et al. (2024) also prevailed at the regional level, suggesting that there might have been

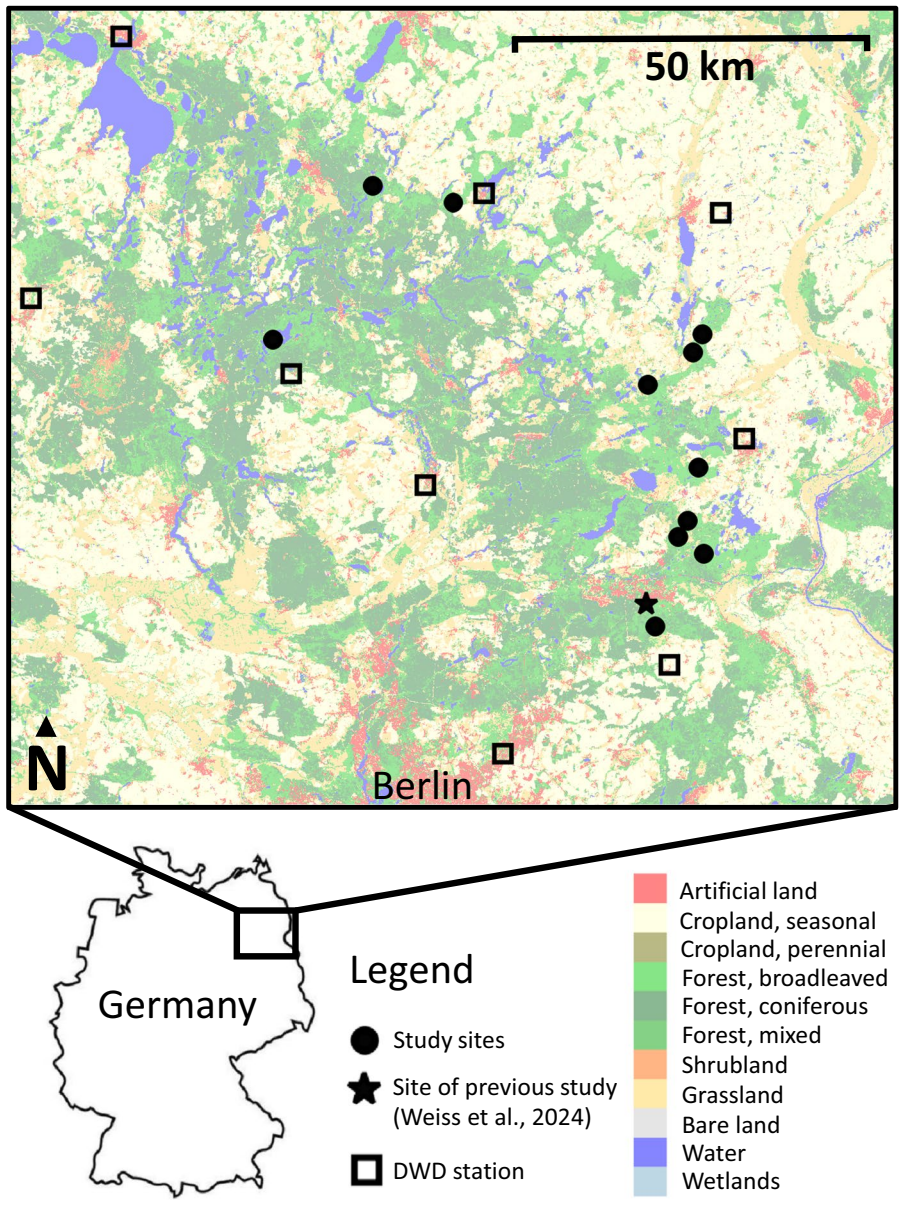

Fig. 1 Map of the study area. Study sites are shown as filled circles and DWD stations used to source meteorological data as squares (four stations outside the shown area). The study site of Weiss et al. (2024) is highlighted as star. Land cover classes are based on Pflugmacher et al. (2019). Only 9 of 14 meteorological stations of which we used data are located within the mapped area

declines in forest carabid communities exceeding the local scale (Fig. S1, Table S1, Method S1). We therefore investigated if there had been regional-scale declines in carabid abundance, biomass and diversity as well as changes in the relative abundance of species traits, expecting changes corresponding with the findings of Weiss et al. (2024). In addition, we examined the variability of potential biomass declines at the local scale as the effects of drought on the carabid community might vary among sites. Forests have the capacity to buffer heat and retain moisture (Haesen et al. 2021; Gohr et al. 2021; Floriancic et al. 2023). However, this capacity can be influenced by factors such as local water availability, stand structure, forest fragmentation, or edge effects (Davis et al. 2019; Koelemeijer et al. 2022; Mann et al. 2023). Moreover, disturbance effects in insect communities are often determined by their initial composition (Kotiaho et al. 2005), which might additionally vary among different sites.

We tested the following hypotheses at the regional scale:

1) Severe drought leads to declines in carabid abundance, biomass, and taxonomic diversity; effects on carabid biomass are most pronounced.
2) Larger, predatory species with poorer dispersal abilities are affected more strongly by declines.
3) Drought effects (i.e. changes in biomass) are variable due to differences in the initial community composition and the local environmental context.

Methods

Study area

The study area is located in the North-East German Lowland (Fig. 1). It represents the center of the natural distribution range of lowland beech (*Fagus sylvatica*) forests (Bohn et al. 2000). The eleven study sites of this study were chosen as representative selection of managed and unmanaged beech forests of old stand age and comparable environmental site conditions (Winter 2005). Today, all sites have a stand age of approximately 120–140 years or older (Fig. S2, Table S2) and mainly fall under the definition of old-growth beech forests (Dieter et al. 2020; Bolte et al. 2022). Five of the sites are strict reserves with no timber use before or during the period of study and meet the stricter definition for old-growth beech forests (> 180 years) used by the Biodiversity Strategy of the European Union (European Commission 2020; Meyer et al. 2023). Two of these sites (Serrahn and Grumsin) have been declared UNESCO World Heritage Sites, two others (Heilige Hallen and Fauler Ort) represent the oldest known lowland beech forests without timber use in Germany (Winter 2005). The remaining six areas are extensively managed to promote natural processes and structures according to the guidelines of Winter et al. (2020). The majority of the sites (seven, including Grumsin) are part of the Schorfheide-Chorin Biosphere Reserve, while Serrahn is part of the Müritz National Park. There were no general changes in the landscape at regional level and at individual sampling sites, where the share of agricultural areas and forests in the surrounding landscape remained stable during the period of study (Fig. S3). In the period after 1999, the annual precipitation and mean temperature ranged from 386 to 868 mm and from 7.3 to 10.9 °C, respectively (Weigel et al. 2023).

Beetle sampling

In 1999–2001 Winter (2005) sampled carabid beetles at the eleven forest sites described above. We relocated the original sampling locations (with a tolerance of < 2 m) using the GPS locations and tree survey maps of Begehold et al. (2016). From 2020 to 2022 we re-sampled the original locations using the exact same methods, which we describe in the following: Single pitfall traps were placed at five to ten sampling locations at each of the eleven sampling sites resulting in 79 trap locations in total. The number of sampling locations per site varied among sites and sampling years due to logistical constrains and conservation reasons. The sampling locations were initially (1999–2001) determined by randomly selecting intersection of a 100 × 100 m grid. Only at one site were traps placed closer together maintaining a minimum distance of 30 m, which can still be considered sufficient to ensure spatial independence of the individual traps (Zhao et al. 2013). Sampling was conducted from mid-April to early November each year. In all years, pitfall traps were emptied fortnightly, yielding 15 samples per trap and sampling year. In a few cases, traps were collected after a shorter or longer exposure time for practical reasons. Each of the eleven study sites was sampled for at least one whole season (April–November) during each period (1999–2001 and 2020–2022), while nine of the sites were sampled for two or three season during at least one of the periods to better account for interannual variation during modeling (Fig. S4).The pitfall traps consisted of a 400 ml honey jar featuring an extended PVC rim plate for increased standardization and reduction of the 'digging-in effect' (Digweed et al. 1995; Boetzl et al. 2018). They were placed in a piece of PVC pipe and covered with a metal roof leaving a gap of approximately 2 cm. Each trap contained 200 ml of trapping fluid (50% solution of monoethylene glycol and water). We provide an illustration of the trap design in the Supporting Information (Fig. S5).

After collection, the carabid beetles were determined to the species level according to Müller-Motzfeld (2006 and earlier editions) by T.K. and D.P. in 1999–2001 and by F.W. and T.K. in 2020–2022. We calculated the biomass for all the samples using the size-weight equations of Szyszko (1983) and Booij et al. (1994) following the approach proposed

by Weiss and Linde (2022) based on the mean sizes provided in Müller-Motzfeld (2006). We took information for the other selected species traits (wing morphology and feeding guild) from carabids.org (Homburg et al. 2014a, b, accessed in 2020). In some cases, we complemented unavailable trait information based on Müller-Motzfeld (2006). We provide the compiled trait information in the Supporting Information (Table S3).

In 2020–2022, a considerable number of traps were affected by disturbances caused by wild boars (*Sus scrofa*), invasive racoons (*Procyon lotor*) and invasive slugs (*Arion vulgaris*), all possibly searching for sources of water during drought. If minor disturbances were visible but traps contained insects (14% of samples in 2020–2022), samples were considered for pooling community samples for diversity metrics, but excluded for modeling quantitative trends (e.g. abundance, biomass). This discrimination was not made for data from 1999 to 2001, as these sources of disturbance were neglectable then. We generally excluded all samples from traps heavily disturbed by rainfall or destroyed by wildlife. This affected approximately 8% of all samples in 1999–2001 and 4% in 2020–2022.

Meteorological data

We extracted publicly available meteorological data from the German Weather Service (DWD) for 14 meteorological stations in and around the study area from 1974 to 2022 (DWD 2023, Table S4). Data on daily precipitation and temperature were only available for eight stations for the whole period. We used ordinary least squares (OLS) regression with measured data from these eight available stations (continuous) and 'month' (categorical, only in temperature models) as predictors to back-cast periodically missing daily precipitation sums and daily mean temperatures for the remaining six stations. In the next step, we used inverse distance weighting (IDW) ('gstat' package, Pebesma and Graeler 2023) to interpolate daily precipitation and mean temperatures for the eleven study sites.

Statistical analyses

To investigate changes in insect communities, it is usually preferable to use time series that provide longitudinal data from consecutive years without gaps. In this study, we investigated changes in the carabid community by comparing data from 1999 to 2001 and 2020 to 2022. Generally, comparing data from relatively short periods is prone to time selection bias and so-called 'snapshot effects', especially when interannual fluctuations are strong (Didham et al. 2020b). Comparing two periods of multiple years avoids this problem and allows for more reliable trend estimates (Schuch et al. 2012; Harris et al. 2019). All the statistical analyses were conducted using R v.4.4.0 (R Core Development Team 2024). The 'glmmTMB' package (Brooks et al. 2022) was used for fitting generalized linear mixed models (GLMMs), and the 'DHARMa' framework (Hartig and Lohse 2022) was used for evaluating the model fit. We used the 'ggeffects' package (Lüdecke et al. 2023) to predict and plot all the effects.

Modeling changes in abundance and biomass

We used GLMMs of the negative-binomial family (O'Hara and Kotze 2010; Stoklosa et al. 2022) and of the zero-inflated gamma family to model abundance and biomass, respectively (Eq. S1 and S2). We included data from only undisturbed fortnightly samples to ensure maximum quantitative standardization and to minimize false zeros (see Blasco-Moreno et al. 2019). This resulted in 1071 samples from 1999 to 2001 and 1350 samples from 2020 to 2022 collected. The abundance and biomass of single samples served as response variables, and period (1999–2001 or 2020–2022) was the main categorical predictor. We used the mean temperature (continuous) and sum of precipitation (continuous) of each fortnightly sampling interval as additional fixed effects to account for sampling errors due to short-term weather fluctuations (Saska et al. 2013). The values were scaled separately within each sampling interval to avoid collinearity with sampling interval. The sampling year, sampling interval and trap location nested in site were used as crossed random intercepts. For the biomass GLMM, we used period as an additional zero-inflation term. Relative changes for abundance and biomass were additionally bootstrapped (1000 iterations) to estimate confidence intervals.

Modeling changes in taxonomic diversity

To investigate changes in taxonomic diversity, we aggregated community samples by pooling data per individual trap and year for all sampling locations where data was available throughout the whole season (April–November). We also included data from samples that had a longer or shorter exposure or were disturbed but still yielded a viable sample (Fig. S6). In some cases, gaps in sampling occurred due to missing samples. However, Sapia et al. (2006) showed that a 'pulsating' sampling scheme with gaps between sampling but coverage throughout the whole season still yields accurate estimates of taxonomic diversity. Single metrics often fail to detect changes in taxonomic diversity reliably (Pozsgai et al. 2016; Hillebrand et al. 2018; Edmonds et al. 2024). We therefore used the framework of Hill numbers (Hill 1973) to describe taxonomic diversity using species richness (q0) and the inverse Simpson (q2), which is less sensitive to rarer species than is q0, and evenness (q2/q0 Jost 2010). Hill numbers were calculated for standardized coverage (Chao and Jost 2012) with the functions *iNEXT* and *estimateD* from the 'iNEXT' package (Hsieh et al. 2016, 2022). We excluded all community samples with an abundance of ≤ 15 individuals and standardized them to an estimated coverage of 72% to limit extrapolation to < 2*sample size (Chao et al. 2014). This resulted in 70 community samples from 1999 to 2001 and 79 community samples from 2020 to 2022 collected at 55 different locations that were sampled in both periods. We then fit Gaussian GLMMs for q0 and q2 and a beta GLMM for evenness (Geissinger et al. 2022) with period (categorical) as a single fixed effect (Eq. S3–S5). We included crossed random effects for sampling year and trap location nested within the site.

Modeling changes in species traits

We assessed changes in community composition using different species traits. For this purpose, we assessed each trait for separate samples based on individuals and for community samples based on occurring species. The data selection process for the two approaches was analogous to that used for modeling abundance/biomass and taxonomic diversity, respectively. We calculated the community weighted mean (CWM) of size for each sample serving as a model response and fitted a Gaussian GLMM with period (categorical) as a single predictor (Eq. S6). We included crossed random intercepts for sampling year, sampling interval and trap location nested in site (analogous to the abundance/biomass models). We calculated community means (CM) for each community sample (pooled for trap and year; see previous section) and based on species occurrence. This served as a response variable in a Gaussian GLMM with period (categorical) as a single predictor (Eq. S7). Here, we included crossed random intercepts for sampling year and trap location nested in site (analogous to the taxonomic diversity models). Wing morphology was coded as a binary response variable (1 = winged/0 = shortwinged or dimorphic). We then fit a binomial GLMM modeling the probability of ability to fly (1 = winged) for individuals of each sample and for occurring species of each community sample (Eq. S8 and S9). The fixed and random effects were analogous to the GLMMs for size. The same approach was used to model changes in feeding guild (1 = predator/0 = herbivore or omnivore) (Eq. S10 and S11).

Exploring spatial heterogeneity of trends and testing potential predictors for variability in local drought effects

In addition, we fit all the above-described GLMMs with 'site' (categorical) as an additional fixed effect (instead of a random intercept), including an interaction with period, to assess site-level changes (Eq. S12). We used this approach to explore the variability of local trends as well as to identify sites with extreme changes that could have disproportionate influence on estimated regional-scale trends. Moreover, we tested potential correlations (Spearman) among site-level changes and geographic coordinates to test for any spatial patterns in the changes that might bias the mean estimates. Blowes et al. (2022) showed that metrics such as abundance, species richness and evenness are often related and show related trends at local scale, we therefore also tested for correlations (Pearson) among the different investigated metrics at site-level.

To test how the local context might determine the severity of drought effects we then tested a set of variables representing the initial carabid community (1999–2001) and environmental conditions as

additional predictors in the biomass model (Table 1 and S5). Variables regarding the carabid community were initial CWM of size and initial probabilities of sampling a winged or predatory individual as estimated by the respective GLMMs. Environmental variables featured canopy cover of the main tree layer (plot and site scale), forest edge (plot and site scale), landscape composition (i.e. share of forest and wetlands), mean annual precipitation and protection status (all at site scale). We provide references for justification and information about the calculation for each variable in Table 1. We scaled all variables except protection, which was binary, and then added these variables individually as additional fixed effect with interaction with temporal change (period) (Eq. S13). We compared the resulting models regarding effect size of the interaction, corrected Akaike's Information Criterion (AICc) compared to the initial biomass model (ΔAICc) and calculated Akaike's weights based on AICc for all model candidates. We tested for correlations (Spearman) among all additionally tested predictors.

Results

Abundance and biomass

We sampled 10,799 carabid beetles (6113 in 1999–2001 and 4686 in 2020–2022). We found that mean abundance across sites decreased significantly ($p = 0.018$) by 51% [0.95 CI (− 73%, − 9%)] between the two periods (Fig. 2, Table S6). There was substantial variability between sites, with local declines ranging from 17 to 74%. Biomass decreased significantly ($p = 0.003$) by 65% [0.95 CI (− 81%, − 36%)], with site-specific declines ranging from 51 to 76% (Fig. 2, Table S7). Specifically in the two UNESCO World Heritage sites Serrahn and Grumsin we found respective declines of 38% and 18% in abundance and 55% and 72% in biomass (Table S17). There were no strong associations (i.e. $-0.7 < r < 0.7$) between changes in abundance and biomass as well as with changes in the other metrics (Fig. S18). We found no indication for spatial patterns in the changes in abundance and biomass that might bias the mean estimates (Fig. S19).

Taxonomic diversity

The samples contained 58 carabid species: 49 species in 1999–2001 and 41 species in 2020–2022 (Table S3). 32 species were caught in both periods. There were no significant changes in Hill numbers, between 1999 and 2001 and 2020 and 2022 across sites (Fig. 3, Tables S8–S10). However, site-specific changes appeared to be very heterogeneous ranging from − 4.2 to + 2 for q0, − 2 to + 1.9 for q2 and − 0.1 to + 0.2 for evenness (Fig. 3, Table S17). Generally, there were strong correlations among local changes of all Hill numbers (Fig. S18).

Species traits

Across sites, we found a significant ($p = 0.031$) decrease in mean individual size (CWM) of 1.7 mm [− 9.8%, 0.95 CI (− 18.2%, − 0.7%)] (Fig. 4, Table S11). There was substantial variation in site-specific changes, ranging from a decrease of 5.2 mm to an increase of 2.2 mm (Table S17). However, there were only two sites where the CWM increased. CWM size was the only metric, for which local changes showed an association with geographic location (latitude, $r = -0.66$, Fig. S19). The probability of sampling a winged individual was generally low (< 0.1) but increased significantly ($p = 0.045$) by a mean of 0.02 for 2020–2022 (Fig. 4, Table S13). Site-specific changes represented mostly increases (with four exceptions) but revealed one site with an extreme increase of 0.17, which most likely affected across-site estimates. The probability of sampling a predatory individual was generally very high (~ 0.995) and did not change significantly across sites (Fig. 4, Table S15). This was largely reflected in the estimated site-specific changes. However, there were two sites with strong increases. Changes in species-based traits generally reflected changes also observed in individual-based traits, but with lower significance—most likely due to a lower sample size in species-based metrics (Tables S12, S14 and S16).

Potential predictors of variability in local drought effects

Three of the tested predictors (initial CWM size, edge length, landscape composition; see Table 1) led to an improvement in AICc by − 8.8, − 1.9 and

Table 1 Overview of the different variables that we tested as additional fixed effects (interaction with temporal change) in the biomass model

Variable	Calculation	References
Initial CWM size (site scale)	CWM of size as estimated by the site-specific GLMM for CWM of size for the period of 1999–2001	Cours et al. (2023): Larger, predatory species might be affected more severely by droughts
Initial probability of winged individual (site scale)	Respective probability as estimated by the site-specific GLMM for the period of 1999–2001	Rainio and Niemelä (2003): Larger, poorly dispersing carabid species are usually more sensitive to disturbances
Initial probability of predatory individual (site scale)	Respective probability as estimated by the site-specific GLMM for the period of 1999–2001	Kotiaho et al. (2005): Community response to disturbance depends on initial trait composition
Canopy cover (site scale)	Mean canopy cover of the top tree layer based on a fine-scale assessment of Begehold et al. (2016) from 2012	Davis et al. (2019), De Frenne et al. (2021): Canopy cover affects the microclimatic buffering capacity of forests
Canopy cover (plot scale)	Canopy cover of the top tree layer at each sampling location based on a fine-scale assessment of Begehold et al. (2016) from 2012	
(Forest) edge length (site scale)	Total length of forest edge within a 1000 m radius around the centre of the sampling site. Inferring from the 0.5 hectare definition for forests of the WHO, we defined used open areas ≥ 0.5 hectares to define forest edges	Arroyo-Rodríguez et al. (2017, De Frenne et al. (2021):Forest edges affect forest microclimate Magura et al. (2001): Edge effects modulate the relative abundance of (potentially drought-sensitive) forest specialists
Distance to (forest) edge (plot scale)	Distance from the individual trap location to the next forest edge. Inferring from the 0.5 hectare definition for forests of the WHO, we defined used open areas ≥ 0.5 hectares to define forest edges	
Landscape composition (site scale)	Share of forest, wetlands and waterbodies based on land cover data from 2015, (Pflugmacher et al. 2019) measured in a 1000 m radius around the centre of each study site	Gohr et al. (2021): Forests and wetlands mitigate extremes in land surface temperature
Mean (local) precipitation (site scale)	Mean annual precipitation for the period 2001–2022 based on interpolated meteorological data	Vicente-Serrano et al. (2010): SPEI is a purely relative drought index and only represents relative drought severity. It does not account for spatial variability of absolute precipitation Davis et al. (2019): Local water availability affects the microclimatic buffering capacity of forests
Protection	Binary variable stating if a study site was a strict reserve (1) or if it was extensively managed (0)	Winter (2005), Winter et al. (2005), Begehold et al. (2016): Protected forest sites were old-growth forests, many of which with especially high structural diversity Fuller et al. (2008): Old-growth deciduous forests is important habitat for forest specialist carabids Frey et al. (2016): Old-growth forests may better conserve forest micro-climate during extreme weather

We provide histograms for all variables in Fig. S7

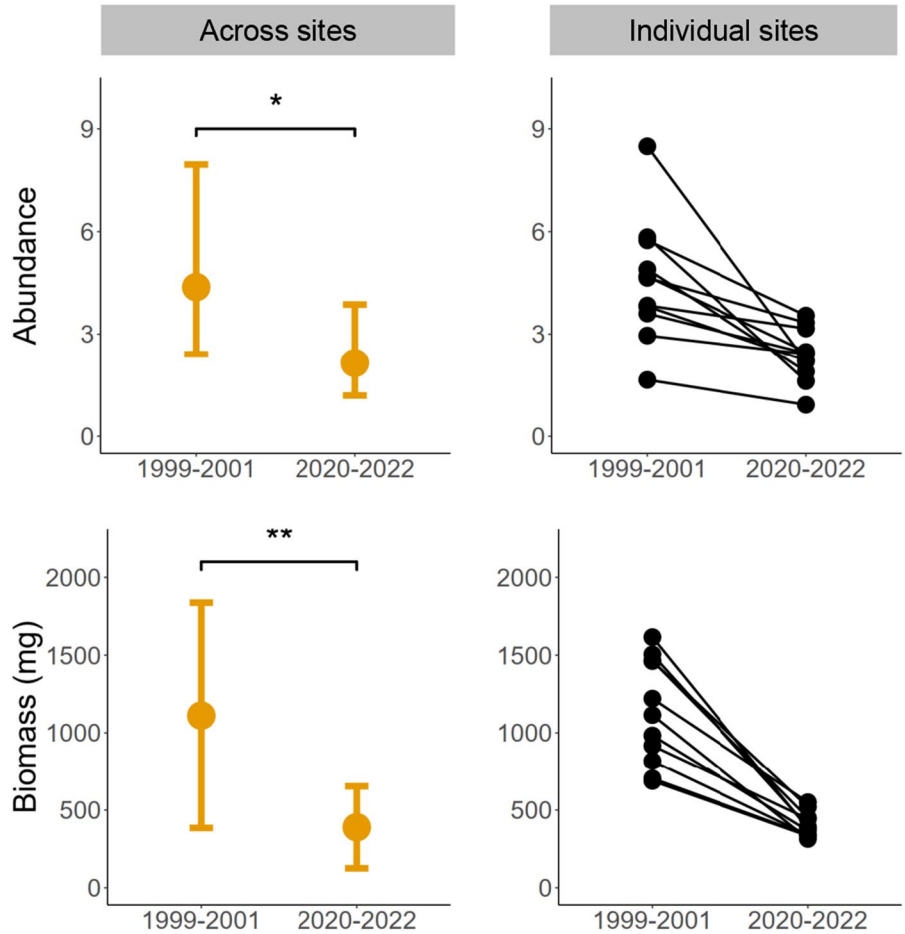

Fig. 2 Carabid abundance (top) and biomass (bottom): Estimated changes between 1999 and 2001 and 2020 and 2022 across all sites (left) and for specific study sites (right). Prediction were made with all other (scaled) fixed effects set to 0 and for marginal effects only. Dots represent estimated means, error bars (left plots) represent 0.95 confidence intervals. Significance codes: **p = 0.001–0.01, *p = 0.01–0.05, n.s. p > 0.05

− 17.6, respectively. (Fig. 5). The inclusion of forest edge length led to an improvement in AICc, likely due to a significant correlation of forest edge length and landscape composition (r = − 0.62, Fig. S20). Moreover, AICc mainly supported the model accounting for landscape composition, while giving some support to the model accounting for initial CWM size (i.e. ΔAICc compared to the best model < 10, Burnham and Anderson 2004). This corresponded with Akaike's weights, which identified the model including landscape composition as the likeliest (0.988), followed by the model including initial CWM size (0.012) and giving no weight to all other models. A greater share of forest and wetlands mitigated declines to some extent, while larger initial CWM size led to stronger declines in biomass. We provide summary tables for all model candidates in Supporting Information (Tables S18–S27).

Discussion

We found strong evidence for regional-scale declines in carabid communities of old lowland beech forests in the North-East of Germany between 1999 and 2001 and 2020 and 2022, which we attribute to recent periods of drought. Biomass declined more strongly and consistently than abundance, and declines were generally more pronounced for larger, less mobile species. On the local scale, the severity of biomass declines did not depend on the protection status of the individual sampling site but was significantly influenced by landscape composition and the initial CWM size of the carabid community in 1999–2001.

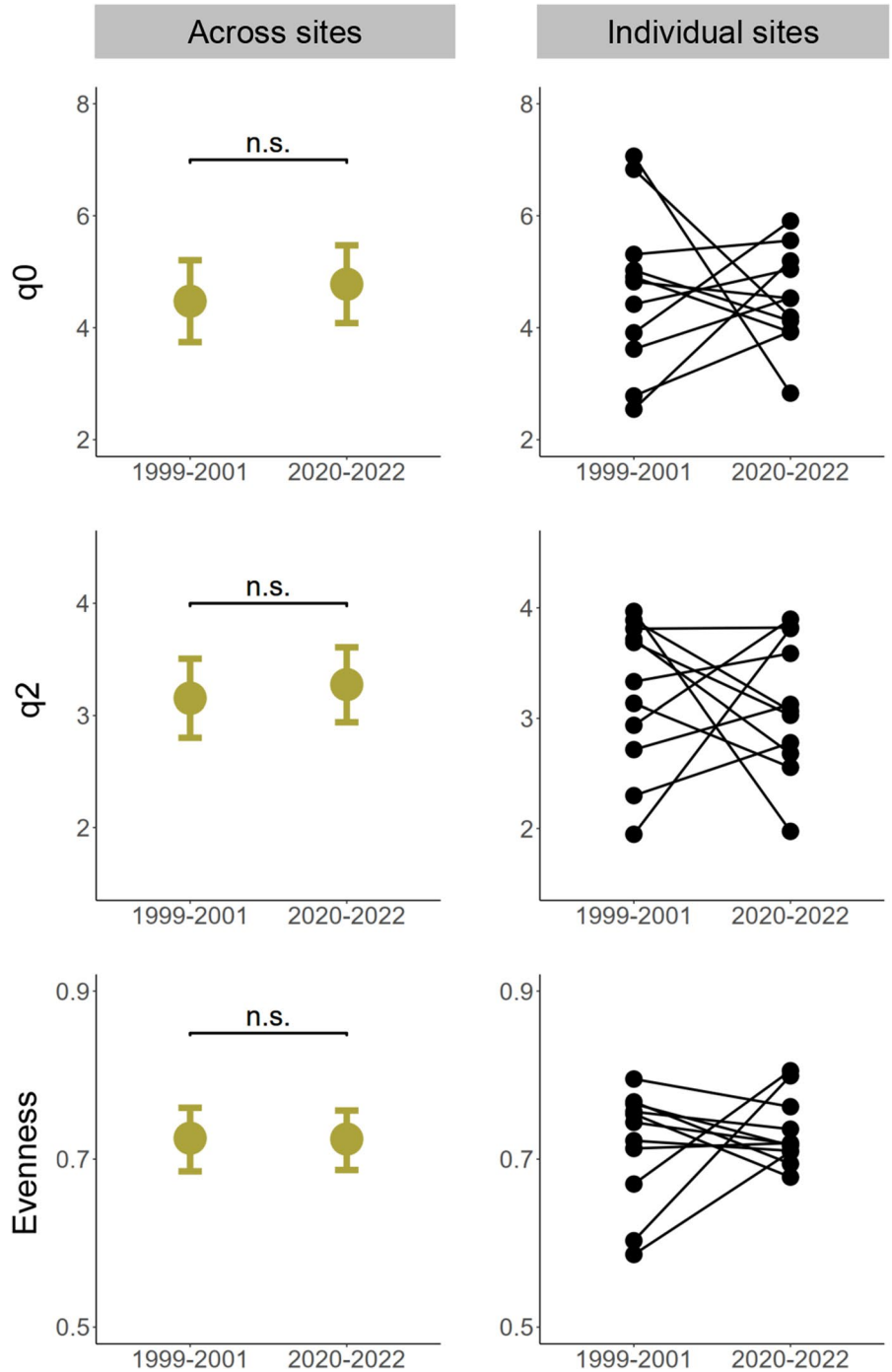

Fig. 3 Hill numbers: Estimated changes between 1999 and 2001 and 2020 and 2022 in q0 (top), q2 (middle) and evenness (bottom) across all sites (left) and for specific study sites (right). Dots represent estimated means, error bars (left plots) represent 0.95 confidence intervals. Significance codes: **p = 0.001–0.01, *p = 0.01–0.05, n.s. p > 0.05

Regional declines in carabid abundance and biomass, but not taxonomic diversity

Comparing the periods 1999–2001 and 2020–2022, we observed declines of 51% [0.95 CI (− 73%, − 9%)] in carabid abundance and 65% [0.95 CI (− 81%, − 36%)]] in biomass at the regional level. We found substantial heterogeneity when considering changes at the study sites, but they were consistently negative for both metrics (Fig. 2). Having only

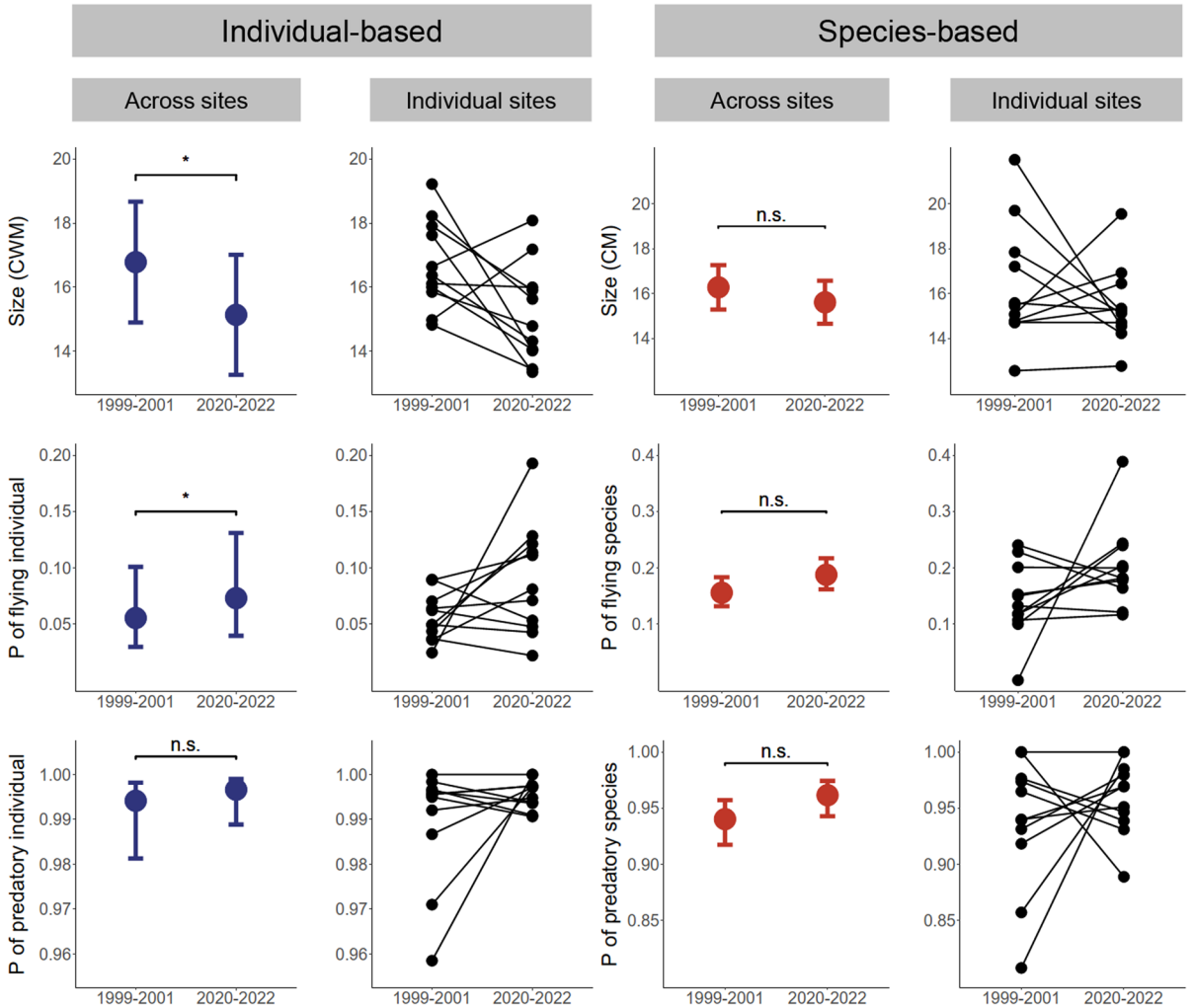

Fig. 4 Species traits: Estimated changes between 1999 and 2001 and 2020 and 2022 in Size (top), wing morphology/ability to fly (middle) and feeding guild/predators (bottom), each based on individuals and occurring species and across all sites and for specific study sites. Dots represent estimated means, error bars (left plots) represent 0.95 confidence intervals. Significance codes: *p = 0.01–0.05, n.s. p > 0.05

two narrow periods to compare data generally limits detailed insights about trends and raises the question of potential confounding factors. On the other hand, there were no regional-scale changes in the landscape, such as land-use change or increasing fragmentation, which could explain these changes (Fig. S3). Management regimes of the study sites did not change during the period of study (compare Winter 2005). While natural forest succession and smaller management interventions at some sites represent potential confounding factors, these would have contributed to the variability in local changes but could not have caused consistent declines at such a spatial scale. This leaves climatic factors that affected the whole region, such as the recent drought period, as the likeliest cause.

Our results generally support the findings of several other studies of drought effects on forest carabids (Williams et al. 2014; Šustek et al. 2017; Šiška et al. 2020) and highlight declines in biomass over those in abundance as also found by Weiss et al. (2024). Generally, the declines in biomass described in this study might still be underestimating true declines. We calculated biomass based on

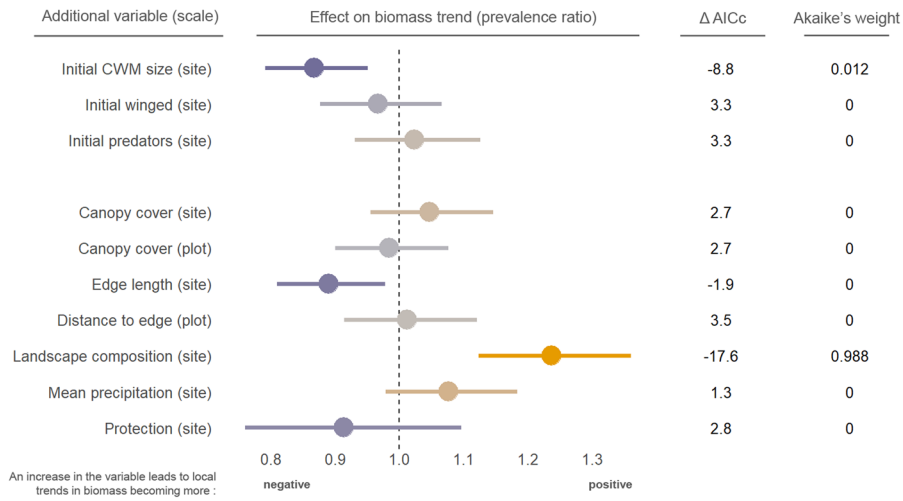

Fig. 5 Results from testing additional predictors and their effects on biomass trends. 'Scale' states the spatial resolution of the predictors. The points indicate the respective variable's effect on biomass trends expressed as prevalence ratio (i.e. 1 = no effect). Bars highlight the 0.95 confidence interval of the respective effect on biomass trends. ΔAICc values state the respective model's difference in AICc compared to the initial biomass GLMM and Akaike's weights were calculated based on AICc

average beetle sizes reported in the literature using the same sizes in 1999–2001 and 2020–2022. Sizes of adult beetles, however, largely depend on conditions during larval development with heat and drought leading to smaller adult beetles (Huk and Kühne 1999; Tseng et al. 2018).

We did not find consistent changes in taxonomic diversity, which contrasts the findings of other studies with regard to drought responses of forest carabid communities (Williams et al. 2014; Šustek et al. 2017; Jouveau et al. 2022). This might be because most of these studies did not standardize diversity metrics. Accordingly, Weiss et al. (2024) who also used Hill numbers, did not find a clear link between drought conditions and taxonomic diversity of forest carabids. Morecroft et al. (2002) observed that during a drought, a similar number of carabid species decreased and increased, offsetting the effects on taxonomic diversity.

Larger species with poorer dispersal abilities disproportionately affected

We observed a significant decrease in the CWM of size and a marginally significant increase in flying individuals at the regional level. Our findings indicate changes in the relative abundance of these traits and generally support the idea that recent droughts especially affected larger, less mobile carabid species. Furthermore, we found stronger evidence for changes in individual-based traits than in species-based traits (i.e. lower p-values, greater consistency at the local level). This suggests that changes in trait composition are due to changes in abundance of more common species rather than species turnover. Larger, poorly dispersing species are typically associated with stable habitats such as old forests (Müller-Motzfeld 2001) and have been reported to be generally more sensitive to environmental changes and disturbances (Rainio and Niemelä 2003; Homburg et al. 2014b; Qiu et al. 2023). While large carabid species might be affected through a change in prey availability and size (Rudolf 2012), species with poorer dispersal ability (i.e. short-winged) might take more time to re-colonize areas

after disturbance (Homburg et al. 2013; Nardi et al. 2022). In carabid species, adult beetle size and wing morphology are often correlated (e.g. Homburg et al. 2019). The more distinctive results regarding size, suggest that these might also drive changes regarding the dispersal ability in this study. We did not find significant consistent changes in feeding guilds, as proposed by other studies (Brandmayr and Pizzolotto 2016; Kirichenko-Babko et al. 2020; Jouveau et al. 2022; Weiss et al. 2024). However, there were generally few non-predatory (i.e., omnivorous, herbivorous) species, and their abundance was very low at the study sites during both periods.

Landscape composition as strong predictor for local changes in biomass

We tested if differences in the initial community composition and the local environmental context could explain the local variability of drought effects on carabid beetles. Above all, we found landscape composition to be a meaningful predictor for the severity of biomass declines observed in this study. Sites that featured less forest (incl. waterbodies and wetlands) within a 1 km-radius showed greater declines in biomass (Fig. 5). Gohr et al. (2021) reported that these types of landscape cover effectively offset extreme temperatures at a similar spatial scale. According to Mann et al. (2023), the size of the forested areas, which is indirectly reflected in our landscape composition variable, also plays a decisive role in this mitigation capacity. Several studies agree that canopy cover (Davis et al. 2019; De Frenne et al. 2021; Haesen et al. 2021) and edge effects (Arroyo-Rodríguez et al. 2017; De Frenne et al. 2021; Koelemeijer et al. 2022) determine forest microclimate. Consequently, these parameters could also regulate drought effects on carabids. Yet, we found little to no indication that canopy cover or forest edge determined changes in carabid biomass at plot or site scale. Protection status could not explain difference in local declines of carabid biomass. However, it is worth noting that we only sampled data from extensively managed or strictly protected sites of old stand age and that drought impacts on carabids in intensively managed beech forest sites of younger stand age may be different.

Community responses to disturbances such as drought may vary with the respective community's trait composition (Kotiaho et al. 2005). We observed that initial CWM size of carabids in 1999–2001 could explain some of the spatial variability of biomass trends indicating stronger declines at sites that initially featured larger carabid beetles. This finding supports the notion that declines especially affect larger species (Brandmayr and Pizzolotto 2016; Nolte et al. 2019; Qiu et al. 2023; Weiss et al. 2024). Again, this suggests that size, rather than wing morphology, may be the key trait for the effects of drought in ground beetles.

Finally, it is crucial to note that the number of independent sites (n = 11) in this study was relatively low and that these were not initially selected to cover consistent gradients of the selected variables. Therefore, estimated effects, CIs and p values should be interpreted with caution. Although our results provide important indication, we emphasize the importance of further research. Future studies should further investigate how local pre-conditions affect drought effects on forest insects (hypothesis 3) with the aim to quantify and disentangle effects using a targeted study design.

Underlying ecological processes

It remains difficult to determine exactly through which processes carabid beetles are affected by drought. Carabids could be affected directly through changes in microclimate. For instance, some carabid species have been found to be negatively affected by low soil moisture (Tyszecka et al. 2023). A higher risk of desiccation might present a direct threat to carabid beetles of all species and life stages, but especially to eggs and larvae (Huk and Kühne 1999; Pozsgai and Littlewood 2014; Tseng et al. 2018; Magura et al. 2021). In addition, higher temperatures can reduce the fertility and reproductive success of insects (Sales et al. 2021). Exposure to drought as larvae can lead to morphological deformations in adult beetles ultimately affecting reproductive success (Huk and Kühne 1999; Tyszecka et al. 2023). In accordance with those observations, we also found morphological deformations in numerous adult carabids of different species in 2020–2022, which could potentially result from droughts (Fig. S21). However, as we did not collect any respective quantitative data, further research is required to confirm this link.

Moreover, carabid beetles could be indirectly affected via trophic interactions (Cours et al. 2023). Wise and Lensing (2019) proposed that reduced soil moisture first affects fungal communities and subsequently cascades up trophic levels. Carabids might respond to lower abundances of drought-sensitive prey such as Gastropoda (Irmler 2007; Šiška et al. 2020). At the same time, process could additionally work top-to-bottom; for example, when omnivorous mammals and birds increasingly search the relatively soft soil and litter layers in deciduous forests for invertebrates during drought periods (Baubet et al. 2003). Ultimately, the observed declines and size shifts in the carabid community could both indicate and lead to broader changes in food webs with potentially far-reaching consequences (Rudolf 2012; Eisenhauer et al. 2023).

Implications for conservation and management

Beech forests are the natural vegetation for large parts of Europe (Bohn et al. 2000; Giesecke et al. 2007). Especially old beech forests play an important role in biodiversity conservation (Springer et al. 2024 [preprint]). They are, as most forests in Central Europe, under increasing pressure due to climate change (Martinez del Castillo et al. 2022; Leuschner et al. 2023) and have been particularly affected by recent droughts (Meyer et al. 2020; Rukh et al. 2023; Weigel et al. 2023). This study, together with that of Weiss et al. (2024), provides first evidence that the insect communities in these forests were also severely affected. These results emphasize climate change with increasing weather extremes as one major threat for insect populations of temperate forests (Harris et al. 2019; Evans et al. 2022; Blüthgen et al. 2023). Furthermore, this study found declines in extensively managed as well as in some of Germany's most protected beech forest areas, such as UNESCO World Heritage sites. This underlines potential limitations of local protection for the conservation of insects under progressing climate change (Warren et al. 2018; Rashid et al. 2023). Future efforts to protect insects should take even greater account of the landscape context and exposure to potential drivers of decline. Without climate change mitigation and adapted conservation approaches, progressing climate change will most likely lead to further declines and changes in the carabid communities of lowland beech forests.

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Author contributions F.W., S.W. and A.L. conceived the research. F.W., S.W., D.P. and T.K. collected the data. F.W., S.W. and D.P. curated, processed and validated the data. F.W., S.W., D.P. and T.K. developed and refined the methodology. F.W. conducted all statistical analysis and created all figures. S.W. acquired funding in 1999–2001, A.L. and F.W. acquired funding in 2020–2022. S.W. administrated the project in 1999–2001. F.W. administrated the project in 2020–2022. A.L. supervised the research and provided resources. F.W. wrote the initial manuscript draft and all authors reviewed the manuscript.

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Data availability Data and metadata are available at PubData (https://doi.org/10.48548/pubdata-118).

Code availability R code is available at https://gitlab.com/fabioweiss/beech_carabids_landscapeecology.

Declarations

Ethics approval Insect research should always carefully consider the use of lethal methods (see Lövei et al. 2023). For reasons of quantitative comparability, this study, however, relied on lethal sampling methods. All carabid species are protected

under German law and some of the study sites have limited accessibility due to their conservation status. We sampled Carabid beetles and accessed sites under special permits of the environmental agency of Mecklenburg West-Pomerania (permit 661.34.4.5.7-10/20), the environmental agency of Brandenburg (permit SNN1-FF 31.03.20), and the Müritz National Park administration. Bycatch was minimized, where possible, and kept for educational purposes.

Competing interests The authors declare to not have any competing interests.

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