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Long-term drought triggers severe declines in carabid beetles in a temperate forest

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Evidence for widespread declines in arthropods is growing and climate change is one of the suspected drivers. Recent droughts in Europe were unprecedented in the previous centuries and we are only beginning to understand the impacts on ecosystems. We analysed a 24-year dataset of carabid beetles from a temperate forest area in northeast Germany and investigated linear and non-linear trends in carabid abundance, biomass, diversity and species traits. We were especially interested if and how these were linked to droughts at different temporal scales using the standardized precipitation evapotranspiration index (SPEI). We found significant linear declines in abundance and biomass with annual rates of −3.1% (0.95 CI [−5.3, −1]) and –4.9% (0.95 CI [−9.4, −1.6]), respectively. Non-linear trends were closely related to the SPEI when considering the climatic water balance of the previous six years and showed severe declines between 2015 and 2022 (−71% abundance, 0.95 CI [−84, −61] / −89% biomass, 0.95 CI [−97, −59]). However, there remained a significant annual background-decline of −2.1% (0.95 CI [−5.7, −0.2]) and −3.1% (0.95 CI [−6.5, −0.1]), respectively, which occurred independently of drought. We observed negative trends in standardized carabid diversity metrics and a shift in species assemblage that were less directly linked to droughts. Declining and drought-sensitive species tended to be larger predators with low dispersal abilities. This study is among the very first to investigate the impacts of the current unprecedented drought on forest insects in central Europe. Our findings add to the concerning amount of evidence for widespread declines in arthropods while pointing towards weather anomalies and climate change as one important driver.

Keywords: biodiversity, climate change, drought legacy, ground beetles, insect decline, standardized precipitation evapotranspiration index (SPEI)

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Introduction

Doubts about a large-scale decline in insects are fading with more and more evidence accumulating (Blüthgen et al. 2023, Weisser et al. 2023). The patterns of decline, however, seem to be heterogeneous across taxonomic groups, habitats and realms (Outhwaite et al. 2020, van Klink et al. 2020, 2022, Wagner et al. 2021a). While calls for action are growing louder (Forister et al. 2019, Cardoso et al. 2020, Harvey et al. 2020, 2022) there remain important questions about the 'how' and 'why' of declines (Weisser et al. 2023). Drivers appear to be diverse (Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021b) and many of them seem to have synergistic effects (Neff et al. 2022). Climate change and specifically droughts have been repeatedly named as one of the main threats for insect populations (Wagner 2020, Halsch et al. 2021, Wagner et al. 2021b). However, our knowledge about drought effects on insects in mostly limited to experimental findings (Gely et al. 2020, Uhl et al. 2022) and observational studies testing this potential driver using long-term data remain a research gap (Rumohr et al. 2023).

Forest ecosystem have received relatively little attention in regard to long-term trends and a potential declines of insects (Blüthgen et al. 2023, Staab et al. 2023). At least in Europe, forests represent relatively stable ecosystems that are often perceived as being less exposed to anthropogenic pressure. Additionally, intact forests can mitigate effects of climate change such as droughts by buffering heat extremes and retaining moisture (Davis et al. 2019, Gohr et al. 2021, Floriancic et al. 2023). Nevertheless, forest ecosystems are increasingly under pressure by climate change (Oakes et al. 2014, Seidl et al. 2017, Senf et al. 2018, Martinez del Castillo et al. 2022). Recent droughts in 2003 and in 2018/2019 had significant negative impacts on European temperate forests (Senf et al. 2020, Senf and Seidl 2021, Schnabel et al. 2022, Rukh et al. 2023) and were followed by another drought in 2022, which has recently been described as unprecedented in 500 years (Schumacher et al. 2023, Henley 2022).These events potentially had large effects on biodiversity in general (Archaux and Wolters 2006) and on insects in particular (Pureswaran et al. 2018, Gely et al. 2020, Cours et al. 2023, Blüthgen et al. 2023). Previous studies on long-term trends (Seibold et al. 2019, Staab et al. 2023) and drought effects (Gely et al. 2020, Sallé et al. 2021, Cours et al. 2022) in forests have mostly focused on insects of the tree layer. Although soil arthropods globally account for approximately four times as much biomass compared to their above ground counterparts (Rosenberg et al. 2023), their ecological importance is often overlooked (Decaëns 2010).

In temperate forests, the forest floor and soil harbours large proportions of the insect biodiversity (Schowalter 2017) considerably contributing to key processes such as decomposition (Ulyshen 2016, Wise and Lensing 2019) or nutrient cycling (Carrillo et al. 2011, Woelber-Kastner et al. 2021). The diverse family of carabid beetles (Cleoptera: Carabidae) plays a prominent role as an essential part of the food web of forest floors. They often act as top-level predators regulating other invertebrates such as springtails (Collembola), slugs and snails (Gastropada), worms (Annelida and Nematoda) and other arthropods including their eggs and larvae (Thiele 1977, Renkema et al. 2014), while being an important food source for vertebrates such as birds and mammals themselves (Cleary et al. 2011, Jaskuła and Soszyńska-Maj 2011).

As for many other insect taxa there is evidence for declines in carabid beetles, e.g. from the Netherlands (Hallmann et al. 2020), the UK (Pozsgai and Littlewood 2014) or Germany (Skarbek et al. 2021). Populations in temperate forests, however, appear to be relatively stable (Brooks et al. 2012, Homburg et al. 2019). On the other hand, many of the carabid species found in temperate forests are closely adapted to the relatively stable, cool and humid conditions and rely on these conditions throughout their lifecycle – especially during larval development (Loreau 1987, Müller-Motzfeld 2001, Irmler 2007, Fitzgerald et al. 2021). Thus, some studies predict them to be heavily affected by climate change and changing precipitation patterns in the future (Williams et al. 2014, Müller-Kroehling et al. 2014, Brandmayr and Pizzolotto 2016). Severe droughts might affect carabid beetles directly through changed abiotic conditions or indirectly through bottom-up effects by changing food availability (Wise and Lensing 2019, Blüthgen et al. 2023, Cours et al. 2023). However, the way individual species respond extreme weather likely depends on species traits such body size, mobility or feeding guild (Homburg et al. 2014b, Qiu et al. 2023).

This study is among the first to investigate insect trends in the light of recent severe droughts. We used a 24-year time series of carabid beetle samples from a temperate forest in northeast Germany to investigate trends in abundance, biomass, diversity and traits and how they were affected by droughts. Specifically, we tested the following hypotheses:

1) Carabid beetles in the study area are not affected by any continuous long-term declines, but recent drought-related declines in abundance, biomass and diversity.
2) Carabid species representing certain traits are more often affected by drought-related declines.

Material and methods

Study area and data

Eberswalde University for Sustainable Development has been sampling carabid beetles at different forest plots (n = 13) in the course of annually taught classes since 1995. From 1999 on, this has been done with highly standardized methods. The study plots were located in a forest area close to Eberswalde, Germany (52°82'N, 13°79'E, Fig. 1), which is part of a larger unfragmented forest area of approximately 300 km^2 in a heavily forested region. All plots were in a managed forest area and sampled a mixture of different dominant tree species (for details see the Supporting information). There were strictly no management interventions on the majority of plots during the duration of the study, while all other

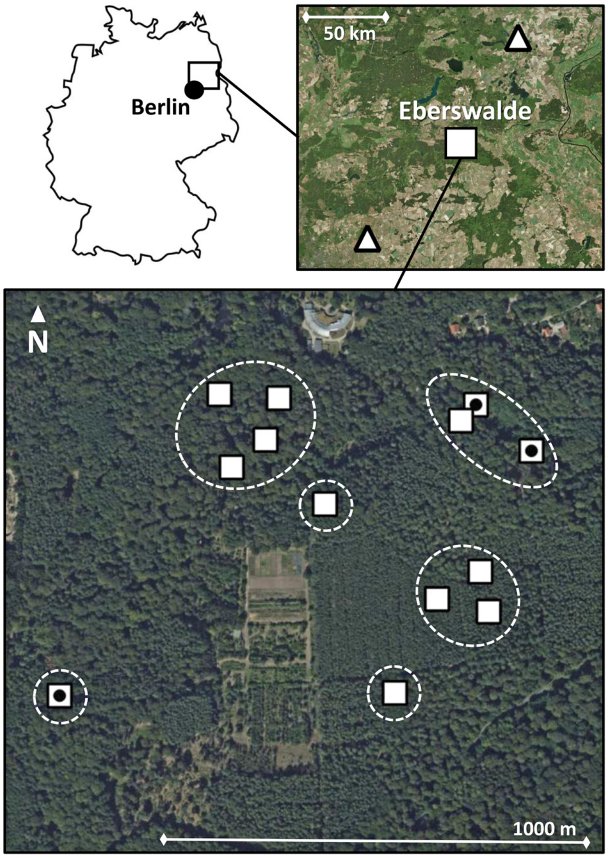

Figure 1. Location of the study area (top) and layout of the plots (bottom). Triangles (top right) mark the meteorological stations (DWD) of which data was used. Squares mark the 13 forest plots (with four pitfall traps each), arranged in either a square (blank) or a transect (dot). Dashed circles indicate how plots were grouped for the 'site' variable.

plots were managed extensively with infrequent selective cutting (with the dominant tree layer remaining intact and only minimal soil disturbance). There were no larger-scale management interventions prior to or during the study period. In 2018, a storm event led to small-scale windthrows (single trees) on two of the plots. There were no agricultural areas in the closer proximity ruling out potential effects of pesticide drift (Staab et al. 2023, Ulyshen and Horn 2023). Carabid beetles were caught between the beginning of May and the end of July each year. The sampling was done with pitfall traps consisting of a 400 ml glass jars with an opening width of 7.5 cm and extended PVC rim plate positioned in a piece of PVC pipe. Boetzl et al. (2018) provide a detailed description and evaluation of this trap design. The traps contained 200 ml of trapping fluid (4% solution of formaldehyde and water) and had metal covers. There were four traps on each plot, setup as either square or transect (Supporting information) with a distance of 20 m between traps. During annual sampling, the traps were emptied three times, usually after four weeks (28 days), however, the exact duration of sampling sometimes varied. After collection, samples were taken to the laboratory and sorted by taxonomic groups. Carabid beetles were determined to species level according to Müller-Motzfeld (2004). Not all plots were sampled each year and we only included data of plots that were sampled in three years or more (Supporting information). We excluded all samples from traps that had been compromised by factors such as flooding or damage. We then only included data from plots with four intact pitfall traps per monthly sampling interval. A lower number of traps might affect sampling efficiency of the remaining traps (Brown and Matthews 2016).

We chose the standardized precipitation evapotranspiration index (SPEI, Vicente-Serrano et al. 2010) as measure of drought. The SPEI is a relative index based on temperature and precipitation data and can be calculated on different temporal scales. Using a moving window approach, monthly SPEI values take into account the climatic water balance (CWB) of a variable time period (months) previous to the respective month. We used daily meteorological measurements of the two closest stations of the German Weather Service (DWD 2023, Fig. 1), which were first averaged between the two stations and then averaged on a monthly basis. We calculated the monthly potential evapotranspiration according to Thornthwaite (1948) using the *thorntwaite* function of the 'SPEI' package (Beguería and Vicente-Serrano 2023) to calculate the CWB. Monthly SPEI values were then calculated using the *spei* function ('SPEI' package) on six different temporal scales (12, 24, 36, 48, 60 and 72 months) and data from 1 Jan 1961 to 1 Dec 2022 were used as reference for standardisation. We aggregated SPEI values with three different time lags (0, 1 and 2): For these, we averaged monthly SPEI values for the carabid beetle sampling season (March to July of the sampling year), for the whole year before sampling (March of the previous year to February of the sampling year), and for the whole year two years previous to sampling (March two years previously to February of the previous year). The procedure is illustrated in Fig. 2.

Modelling abundance and biomass

Linear regression analysis is the simplest and most commonly used method to estimate population trends (White 2019). We fitted a negative-binomial generalized linear mixed model (GLMM) with abundance as response variable and years (continuous) as main predictor to investigate linear trends. We included several covariates to account for sampling history (Welti et al. 2021). We added a quadratic term for number of days of trap exposure (continuous) (Schirmel et al. 2010, Kotze et al. 2012), a term for sampling month ('may', 'june', 'july'; categorical) (Kotze et al. 2012), a term for average temperature during sampling (continuous) (Honěk 1997, Saska et al. 2013), a term for sum of precipitation during sampling (continuous) (Saska et al. 2013, Wang et al. 2014). We used a random intercept for trap ID specific for year (as the numbering of the traps was not consistent throughout years) nested in plot nested in site to account for the spatial structure of sampling (Fig. 1). An additional crossed random intercept for year (factor)

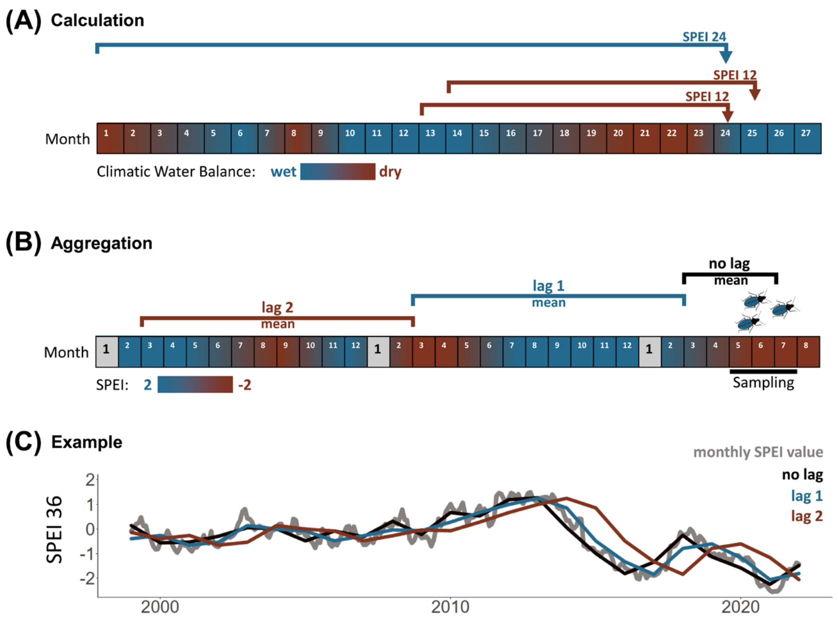

Figure 2. Methodological scheme which was used to calculate and aggregate SPEI-variables: (A) monthly SPEI values were calculated at different temporal scales (e.g. 12 and 24 months) taking into account the CWB of the previous months. (B) Monthly SPEI values were aggregated with different time lag in relation to sampling data. (C) Example of monthly SPEI values and differently aggregated SPEI variables for SPEI 36 as used in this study.

was used to account for temporal pseudoreplication and year effects (Chaves 2010, Knape 2016, Daskalova et al. 2021, Weiss et al. 2023a). We also fitted a negative-binomial generalized additive mixed model (GAMM) to investigate non-linear trends, which followed the same structure as the GLMM with the only difference that the main predictor (year) was fitted with a smoothing term. The dispersion parameter of the negative-binomial distribution was defined as estimated in the GLMM. Following the approach of Knape (2016), we fitted the GAMM first without random intercept for year to determine the appropriate dimension of k for the smoothing term and then refitted the model with random intercept and fixed k. To investigate the effect of drought we then performed a model selection adding SPEI at six different temporal scales and three different time lags as additional fixed effect to the GLMM, yielding 19 candidate models (the previous GLMM and 18 models with different SPEI variables). The model with the lowest AIC was subsequently used to account for drought effects (if $\Delta\text{AIC} > 2$ compared to the initial GLMM, Burnham and Anderson 2004).

$$\begin{aligned}\text{Abundance GLMM: } & \text{Abundance} \sim \text{Year} + \text{Sampling effort}\\ & + I(\text{Sampling effort}^2) + \text{Sampling month} + \text{Temperature}\\ & + \text{Precipitation} + (1|\text{year}) + (1|\text{Site/plot/trapID}),\\ & \text{Family} = \text{nbinom2}\end{aligned}$$

$$\begin{aligned}\text{Abundance GAMM: } & \text{Abundance} \sim s(\text{year}, k = 7, \text{fx} = \text{TRUE})\\ & \text{Sampling effort} + I(\text{Sampling effort}^2)\\ & + \text{Sampling month} + \text{Temperature} \quad + \text{Precipitation}\\ & + (1|\text{year}) + (1|\text{Site/plot/trapID}),\\ & \text{Family} = \text{negbin}(\text{theta} = 6.93)\end{aligned}$$

We calculated biomass with size-weight equations of Szyszko (1983) and Booij et al. (1994) following the approach proposed by Weiss and Linde (2022). Average species sizes needed for the calculation were based on minimum and maximum sizes stated in Müller-Motzfeld (2004). Biomass was modelled the same way using a GLMM and a GAMM. However, we used Gaussian models (instead of negative-binomial) with transformed (cubic root) values of biomass. Otherwise, the models for biomass followed the same structure as described above. We also performed a model selection with SPEI variables using the same approach as for abundance.

$$\begin{aligned}\text{Biomass GLMM: } & \text{Biomass}^{1/3} \sim \text{Year} + \text{Sampling effort}\\ & + I(\text{Sampling effort}^2) + \text{Sampling month} + \text{Temperature}\\ & + \text{Precipitation} + (1|\text{year}) + (1|\text{Site/plot/trapID}),\\ & \text{Family} = \text{Gaussian}(\text{link} = \text{identity})\end{aligned}$$

$$\text{Biomass GAMM: Biomass}^{1/3} \sim s\left(\text{year}, k = 8, \text{fx} = \text{TRUE}\right)$$

$$+ \text{Sampling effort} + I(\text{Sampling effort}^2)$$

$$+ \text{Sampling month} + \text{Temperature}$$

$$+ \text{Precipitation} + \left(1|\text{year}\right) + \left(1|\text{Site/plot/trapID}\right),$$

$$\text{Family } = \text{Gaussian}\left(\text{link} = \text{identity}\right)$$

In studies of insect communities, single species might mask or obscure trends in the community as a whole, so their exclusion from the community-based analysis might be useful (Gandhi et al. 2008, Schuch et al. 2012). We fitted all abundance, biomass and diversity models excluding *Nebria brevicollis* , which was the second to most sampled species (~ 19% of all sampled individuals). *Nebria brevicollis* is known to display extreme fluctuations between years (Nelemans et al. 1989). With 37% of all sampled individuals of this species in just eight samples, it introduced considerable amount of variance into our models potentially masking trends and other effects. As a safety measure, we fitted abundance and biomass models also for data including *N. brevicollis* as well as for data adjusted for pitfall trap sampling bias (Engel et al. 2017).

Modelling taxonomic diversity

While single diversity metrics often fail to detect temporal changes (Pozsgai et al. 2016, Hillebrand et al. 2018), multi-metric approaches are more suitable for capturing temporal trends in biodiversity (Blowes et al. 2022). Following an approach suggested by Roswell et al. (2021) we used standardized richness (Hill-series: ^{0}D, Hill 1973), standardized Simpson (Hill-series: ^{2}D) and standardized evenness (Hill-series: ^{2}D/^{0}D, Jost 2010), all standardized by coverage to account for different sampling effort (Chao and Jost 2012). Furthermore, we considered temporal species turnover. We aggregated samples per plot and year (Kotze et al. 2011), while only including plot-years with four intact traps in all three sampling intervals. This resulted in 143 diversity samples of 13 plots between 2001 and 2022. We then extrapolated/rarefied the samples to equal coverage of 0.86 and calculated species richness (Hill number ^{0}D) and the inverse Simpson index (Hill number ^{2}D) using the 'iNEXT' package (Hsieh et al. 2016, 2022). Hill-series diversity metrics are all special cases of the same equation (Hill 1973) with different sensitivity towards rare species (with ^{0}D more sensitive than ^{2}D). We chose a coverage 0.86 to limit extrapolation to $< 2 \times$ sample size (Chao et al. 2014). We calculated evenness as the ratio ^{2}D/^{0}D (Jost 2010). Species turnover, which is effectively temporal beta-diversity (Shimadzu et al. 2015), was based on observed species and we calculated it using the Jaccard Index comparing annual samples and reference periods. For this analysis we only included data of plots that were sampled in at least five years. We used the first two years available for each plot as reference years. Subsequently, species turnover of the following years was calculated as mean of two Jaccard-values of the respective year and each reference year (taking values between 0 and 1 = very similar). We then excluded reference plot-years as they would automatically take the value 1 and therefore force a negative trend upon inclusion. This resulted in 111 turnover samples from nine plots between 2003 and 2022 (with reference years between 2001 and 2005). We modelled linear trends in diversity metrics with GLMMs of the Gamma family (species richness and Simpson) or beta family (evenness and turnover, Geissinger et al. 2022) using year (continuous) as single fixed term, while including crossed random intercepts for year (factor) and plot nested in site. We also fitted GAMMs for all diversity metrics to explore non-linear trends. Here, Gaussian error distributions were more appropriate in all cases. Furthermore, we tested the effect of drought on diversity metrics by performing a model selection with SPEI-variables following the same routine as described before.

$$\text{Diversity GLMM(s): Diversity metric}^* \sim \text{Year}$$

$$+ \left(1|\text{year}\right) + \left(1|\text{Site/plot}\right),$$

$$\text{Family} = \text{Gamma}\left(\text{link} = \text{'log'}\right) \text{ or beta\_family}\left(\text{link} = \text{logit}\right)$$

$$\text{Diversity GLMM(s): Diversity metric}^* \sim s\left(\text{year}, k =, \text{fx} = \text{TRUE}\right)$$

$$+ \left(1|\text{year}\right) + \left(1|\text{Site/plot}\right),$$

$$\text{Family} = \text{Gaussian}\left(\text{link} = \text{'identity'}\right)$$

Modelling species trend and investigating traits

Moreover, we fitted separate linear trend models (GLMMs) for all species recorded in three or more years. On three occasions, we merged relatively rare species (*Pterostichus diligens, Pterostichus quadrifoveolatus, Pterostichus rhaeticus*) with very similar, more abundant species (*Pterostichus strenuus, Pterostichus oblongopunctatus, Pterostichus nigrita*, respectively) as there was the increased probability of misidentification between those species in early sampling years potentially creating statistical artefacts. For each species, we added zero-counts for all sampling intervals during which the species was not recorded. However, we excluded all plots in which the species had not been recorded at all. Depending on the overall abundance of the individual species these dataset were prone to large amounts of zero counts. We then performed an automated model selection based on AIC; testing different trend models and choosing between Poisson and negative-binomial (O'Hara and Kotze 2010), checking and accounting for zero-inflation (Brooks et al. 2017), and checking and accounting for temporal autocorrelation (Dornelas et al. 2013). Species sampling abundance aggregated per year and plot was modelled as response, while we used year (continuous) as main predictor and mean temperature and sum of precipitation (Saska et al. 2013) averaged for the respective sampling season as covariates. Further, we included crossed random intercepts for year (factor) and plot nested in site. In a second GLMM we used SPEI (at the spatial scale most meaningful in the total abundance model) as main predictor instead of year. As different species have shown to react with varying delay to droughts (Šustek et al. 2017, Šiška et al. 2020) time lag of this SPEI-variable was chosen by lowest AIC. To determine if year and SPEI were meaningful predictors, we compared both GLMMs with the respective null model (no main predictor, only covariates) using AIC. In the case $\Delta\text{AIC} > 2$ (Burnham and Anderson 2004) we considered temporal trends or drought effects meaningful. There was no meaningful effect in either of the GLMMs in species with overall sampling abundance < 35. In those species we assumed the probability of non-meaningful trends/effects due to data deficiency greater than the probability of non-existent trends/effects. We therefore preceded with 27 species that had an overall sampling abundance ≥ 35. We conservatively recognized just three classes of trends: 'declining' (meaningful negative trend), 'increasing' (meaningful positive trend) and 'no trend' (no meaningful trend); and drought effect as 'declining with drought' (meaningful positive effect), 'increasing with drought' (meaningful negative effect) and 'no effect' (no meaningful effect). As SPEI of < 0 represents dry conditions a 'positive' effect actually meant that abundance was negatively affected by droughts.

Finally, we investigated the intersection of classified species trends and drought effects and delay of declines with drought with species traits. The six selected traits were body size, wing-morphology, feeding guild, humidity preference, latitudinal centre of distribution range and local abundance. Body size and wing-morphology are two very prominent and readily available traits, which often show distinctive patterns between carabid communities of different habitats. Larger, flightless (brachypterous) species are usually more abundant in stable ecological conditions (Homburg et al. 2013, Cours et al. 2023) and are predicted to decline with progressing climate change – especially in forests (Qiu et al. 2023). Predatory species have been found to be affected by droughts (Kirichenko-Babko et al. 2020, Jouveau et al. 2022), while herbivorous and omnivorous species might generally benefit from climate change (Brandmayr and Pizzolotto 2016). We were also interested if the species' preference for humid conditions (Šustek 2004) reflect their tendency to be declining and affected by droughts. Further, we expected species with a relatively more northern centre of their distribution range to be more susceptible to effects of climate change (McCarty 2001, Chen et al. 2011, Jaworski and Hilszczański 2013). Finally, we investigated if declines and drought effects are limited to relatively rare species or if they affected locally abundant species as well (Habel and Schmitt 2018).

We compiled data on six carabid traits from different sources. Body size (mm), wing development (winged, dimorphic, short-winged), and latitudinal centre of distribution (latitude) were taken from carabids.org (accessed 15 Dec 2020; Homburg et al. 2014a). Feeding guild (herbivores, general predators, snail-predators, Collembola-predators) was based on carabids.org trait data and complemented using own field observations. Preference for humidity (scale 1–8) was taken from Šustek (2004), complemented based on information (shared habitat) from Müller-Motzfeld (2001). Local abundance (sum of sampling abundance) was based on own data. We used plots and visual inspection to explore how the different species traits were distributed among classified trends, drought effects and delays of declines with drought.

Data handling and processing, statistical analyses and visualisation of results were done using R ver. 4.3.1 (www.r-project.org). We fitted all GLMMs with the 'glmmTMB' package (Brooks et al. 2023) and all GAMMs with the 'gamm4' package (Wood and Scheipl 2020). Residual variance and temporal autocorrelation were inspected for all models using the 'DHARMa' package (Hartig and Lohse 2022). We scaled and centred all continuous variables (except the response). Mean daily precipitation and mean daily temperature were scaled for each sampling interval separately to avoid collinearity issues. In all other cases, scaling was done before splitting up data (e.g. for modelling species trends) to ensure a consistent scale throughout (Desquilbet et al. 2021). In the AIC-based model selection we fitted all candidate models with maximum likelihood instead of restricted maximum likelihood (Fox et al. 2015). We ran a sensitivity analysis for abundance and biomass models to test the robustness of estimates by iteratively excluding data of single plots and years and refitting the models (Weiss et al. 2023a). Predictions for all GLMMs and GAMMs (incl. plotted 0.95 CIs) were made for fixed effects only using *ggpredict* function from the 'ggeffects' package (Lüdecke et al. 2023) with all scaled covariates set to 0 and sampling interval set to 'June'. 0.95 CIs for decline rates were bootstrapped with the *bootMer* function of the 'lme4' package (Bates et al. 2022) for the GLMMs based on 1000 iterations. In case of GAMMs the 'smoothing bias' may cause problems bootstrapping and changes between 2015 and 2022 were bootstrapped based on additional GLMMs for this period. We provide more details on study area, data availability, meteorological data processing, calculation of SPEI in the Supporting information.

Results

Abundance and biomass

From 1999 to 2022 we collected 1866 abundance and biomass samples from 13 plots consisting of 24 167 carabid beetles representing 88 species. The overall abundance of carabid beetles declined significantly at a mean rate of −3.1%/year ($p = 0.005$, 0.95 CI [−5.3, −1]) when estimated as linear trend. The GAMM revealed a non-linear trend with an initial slight decline followed by a slight increase before declining steeply from 2015 to 2022 (−70.5%, 0.95 CI [−83.8, −61.1]) amounting to an overall mean annual decline rate of −5.6% (geometric mean) from 1999 to 2022. Model selection determined SPEI (calculated for 72 months with time lag 2) as meaningful and highly significant predictor for carabid abundance ($p < 0.001$), reducing effect size and significance of the predictor year. Yet, there remained significant background decline of −2.1% ($p = 0.029$, 0.95 CI [−5.3, −1]) annually. Predictions based on annual SPEI values closely resembled the non-linear trend estimated by the GAMM (Fig. 3). Sensitivity analysis showed that these results were not considerably affected by the exclusion of single years or plots.

Trends in biomass generally followed the same patterns (Fig. 3) with an estimated linear decline of −4.9%/year ($p=0.006$, 0.95 CI [−9.4, −1.6]) and a non-linear trend (mean annual rate −8.1%, geometric mean), also showing a steep decline from 2015 to 2022 (−88.7%, 0.95 CI [−97.5, −59.4]). As for abundance, 72-month-SPEI with time lag 2 was the most meaningful additional predictor ($p=0.001$), while there remained a significant negative trend of −3.1% ($p=0.038$, 0.95 CI [−6.5, −0.1]) annually independent of the SPEI variable. Again, predictions based on annual SPEI values closely resembled predictions of the GAMM even reaching a similar marginal R^2-value (0.148 and 0.151, respectively). Biomass trends and SPEI coefficients proved stable during sensitivity analysis.

When fitting these models with data including *N. brevicollis* or data adjusted for pitfall trap sampling bias generally patterns remained the same. Temporal trends in abundance were less pronounced compared to the main models, while temporal trends in biomass remained approximately at the same level. Explained deviance expectedly decreased considerably with including *N. brevicollis*, while p-values partly increased. In all cases SPEI 72 lagged by two years remained a highly significant predictor. We provide detailed results for these models in the Supporting information.

Taxonomic diversity

Standardized richness (Hill number ^{0}D) showed a weak non-significant negative linear trend. The non-linear trend estimated by the GAMM showed a weak decline until 2013 followed by a slight recovery. SPEI 72 with lag 1 performed best during model selection and indicated a slight increase of standardized richness with drought ($p=0.021$), while the background decline became significant ($p=0.034$) as well. Standardized Simpson (Hill number ^{2}D) declined significantly over time ($p=0.008$). The GAMM did not detect any non-linear trend over time and none of the SPEI variables was a meaningful predictor. Standardized evenness (^{2}D / ^{0}D) showed a significant ($p=0.028$) linear decline of similar magnitude. The non-linear trend follow a hump-shape with a slight increase until 2009 followed by a decline. SPEI 60 with no lag was the most meaningful predictor indicating a decrease of standardized evenness with drought ($p=0.013$), while the background decline became non-significant. Temporal species turnover significantly increased (Jaccard similarity decreased) from 2003 to 2022 ($p < 0.001$). The GAMM showed a decline in similarity that came to a halt around 2009 and then declined even more sharply. SPEI was not a meaningful predictor for species turnover. Trends in diversity metrics are illustrated in Fig. 4.

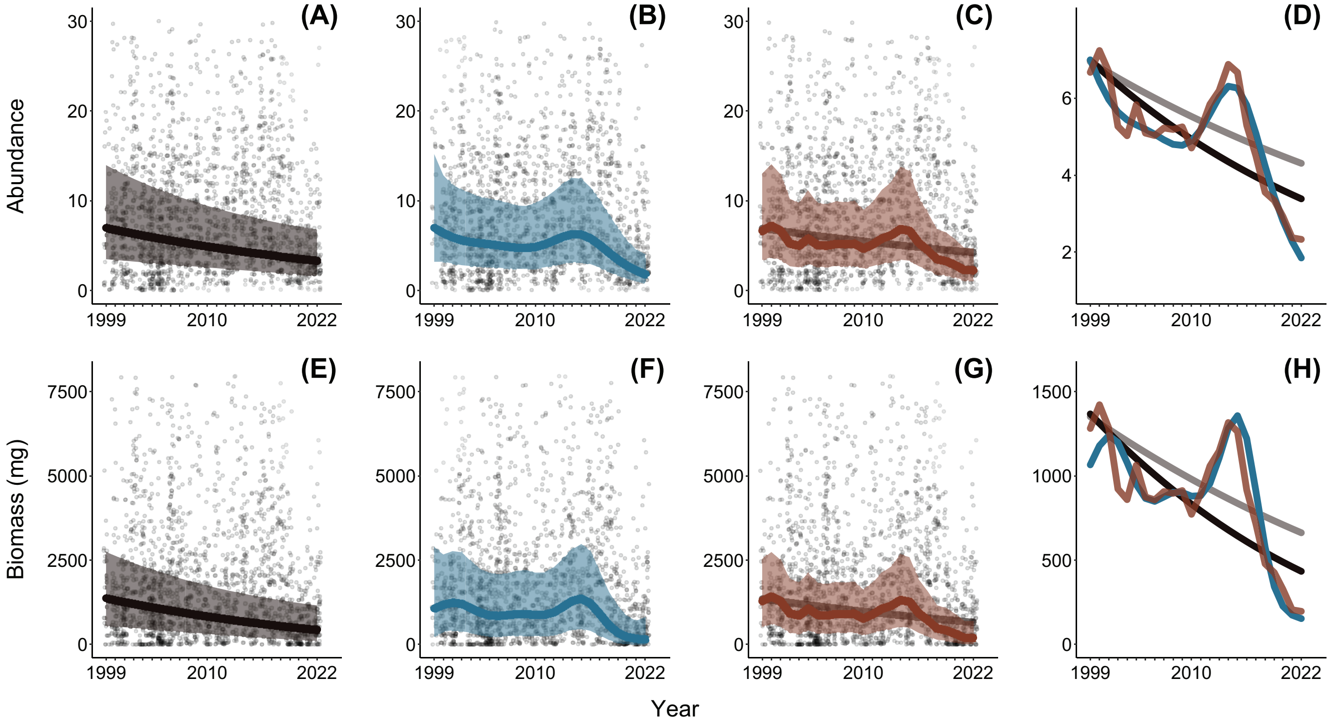

Figure 3. Trends in overall abundance (top) and biomass (bottom) of carabid beetles (excluding. *N. brevicollis*): linear trend (A), (E), non-linear trend (B), (F) and linear trend accounting for the effect of SPEI based on annual values (red) and estimated backround trends with fixed SPEI (grey) (C), (G), and respective trends plotted together for closer comparison (D), (H). Shaded areas represent 0.95 confidence intervals and dots represent sampled values.

Species trends and traits

Of the 27 evaluated species eight declined in abundance (most severely: *Carabus hortensis* and *Pterostichus melanarius*), while two increased (*Notiophilus rufipes* and *Badister lacertosus*) (Supporting information). Ten species were negatively affected by droughts and one species responded positively to droughts (*Carabus granulatus*). There was some overlap between declining and drought-sensitive species (n = 4), while there was no species increasing while positively responding to droughts. Both, declining and drought-sensitive species tended to be larger and short-winged (brachypterous) or dimorphic. Declining species were with one exception (*Harpalus rufipes*) predators and species negatively affected by drought were exclusively predators. Declines and negative drought effects also affected abundant species. There were no apparent patterns in humidity preference and latitudinal centre of distribution range with declining and drought-sensitive species (Fig. 5). Of those ten species negatively affected by drought eight species showed, contrary to community-level results, no delay in drought effects (no lag). Two species were affected by drought with a two-year delay (lag 2) (*Pterostichus oblongopunctatus/quadrifoveolatus* and *Patrobus atrorufus*).

We provide detailed model summaries, results of the model selections and sensitivity analysis in the Supporting information.

Discussion

Non-linear abundance and biomass trends are linked to long-term drought

We found significant linear declines in both carabid abundance and biomass of −3.1 and −4.9% annually, respectively, since 1999. Other long-term studies on carabid beetles from north Germany (Homburg et al. 2019) and central Germany (Zajicek et al. 2021) found no significant quantitative declines. However, these studies used no or only little data recorded after 2017, the time in which we observed the most severe declines. We found drought represented by the SPEI (particularly the 72-months SPEI with a two-year delay) to be a strong predictor for overall abundance and biomass with dry conditions having negative effects. This explained non-linear trends and a large proportion of observed declines. These results are strongly supported by GLMM-predictions based on SPEI values which closely resemble non-linear trends estimated with GAMMs (Fig. 3) and by several experimental and observational studies, which reported negative droughts effects in forest carabids (Williams et al. 2014, Šustek et al. 2017, Jouveau et al. 2022).

We found that the SPEI accounting for the CWB of the past six years most accurately predicted drought impacts on carabid beetles in the study area. The 2003 drought was only weakly reflected by the 72-month SPEI, while the period from 2018 featured unprecedentedly low SPEI values (Fig. 6) indicating a long-term shortage of water. Accordingly, we found large declines concurring with the 2018/2019 drought and with no recovery until 2022. In contrast, local minima in abundance and biomass between 2005 and 2009 (Fig. 3, 6) may be linked to the 2003 drought but are far surpassed by recent declines. In line with these findings, several studies reported that the impacts on forest ecosystems during the 2003 drought were superseded by those of the drought in 2018/2019 (Buras et al. 2020, Schnabel et al. 2022, Rukh et al. 2023). Forests have the capacity to mitigate the direct effects of extreme weather and shorter-term droughts (Davis et al. 2019, Gohr et al. 2021). However, long-term droughts, especially in conjunction with heat waves as in 2018/2019, exceed this mitigation capacity creating a positive feedback loop of soil water depletion and reduced cooling through evapotranspiration (Allen et al. 2015, Buras et al. 2020). Consequently, this increasingly exposes all components of the ecosystem to extreme conditions.

Despite the SPEI accounting for non-linearity and large portions of the declines in abundance and biomass, time (i.e. 'year') remained a significant predictor with negative effect in the models fitted with SPEI as predictor. Droughts, although being a main driver, are probably not the only cause for declines in our study area. Suspected drivers such as pesticides (Nocera et al. 2012, Barendregt et al. 2022), land-use change/habitat loss (Habel and Schmitt 2018, Sánchez-Bayo and Wyckhuys 2019) or intense management (Grodsky et al. 2018, 2020, Staab et al. 2023) were not present in the study areas. Nevertheless, we found concerning background declines of −2.1 and −3.1% annually for carabid abundance and biomass, respectively. Although these trends are significant it is noteworthy that the respective p-values are relatively close to 0.05 and CIs almost include a decline rate of 0%. Hence, there remains some uncertainty about these background declines.

Further, it is important to note that our methodology might underestimate declines in biomass as we based calculations on carabid sizes taken from literature. However, adult beetle sizes are subject to change as they depend on condition during larval development (Ernsting and Huyer 1984, Pozsgai and Littlewood 2014, Magura et al. 2021). Unfavourable conditions due to extreme weather such as droughts and heat will likely lead to smaller (i.e lighter) adult beetles. Tseng et al. (2018) found that especially the body sizes of larger carabid species have declined systematically in the last 100 years, which they linked to climate change. Such decreases in size might lead to additional declines in biomass undetected by this study and our results are likely conservative estimates.

Mostly linear declines and shifts in biodiversity

We observed exclusively negative trends in biodiversity metrics (Fig. 4); note that *N. brevicollis* was also removed for these part of the analyses. However, trends in taxonomic diversity were less directly linked to droughts represented by different SPEI variables. Species turnover showed the strongest trend with decreasing similarity to earlier reference years, which

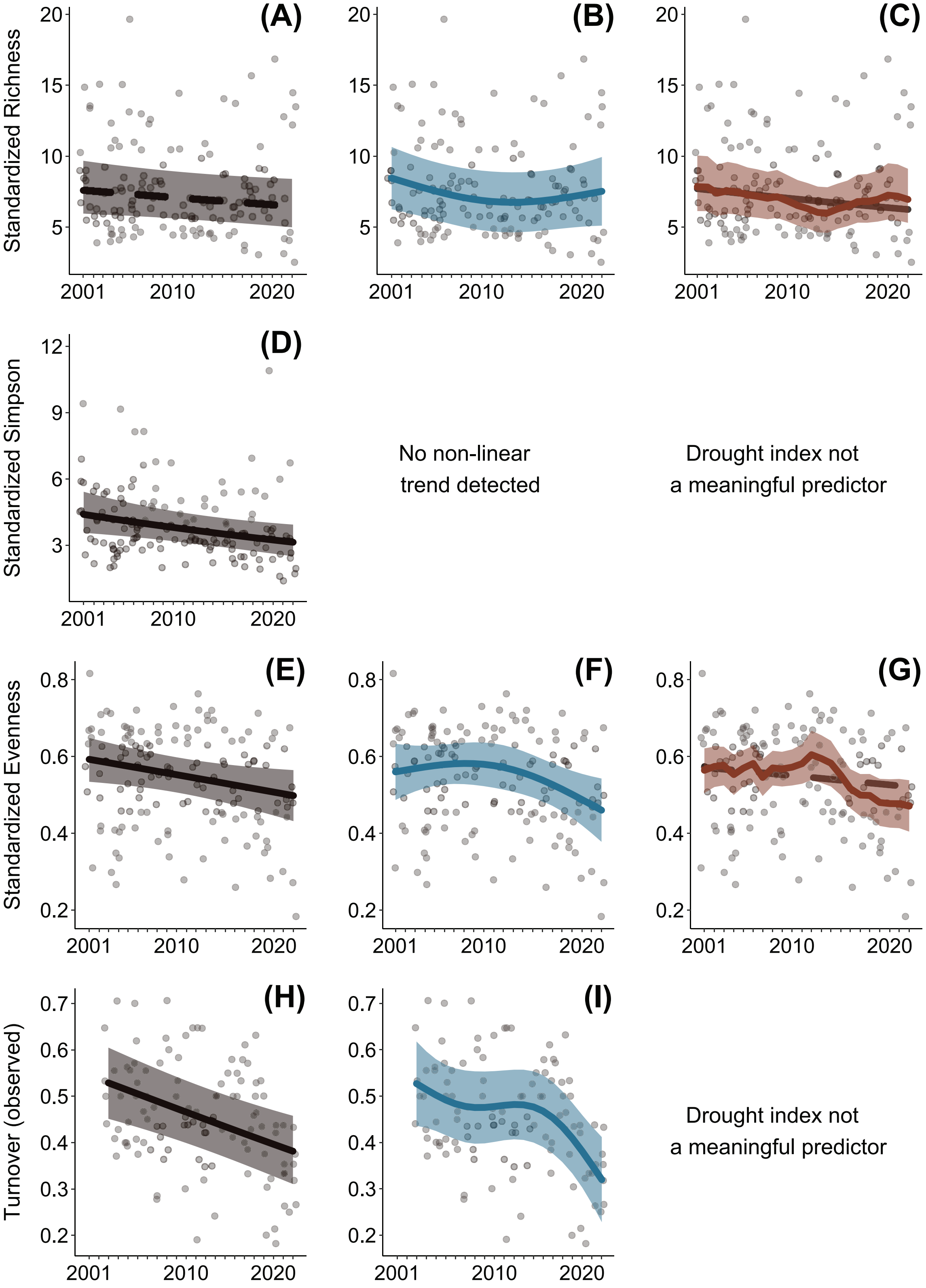

Figure 4. Predicted trends of standardized richness (A)–(C), standardized Simpson (D), standardized evenness (E)–(G) and observed species turnover expressed as Jaccard similarity (H)–(I). Different plots show linear trends (black), non-linear trends (blue) and linear trends accounting for the effect of SPEI based on annual values (red) as well as estimated background trends (grey). Shaded areas represent 0.95 confidence intervals and dots represent values of the respective metric. Dashed lines indicate non-significant trends.

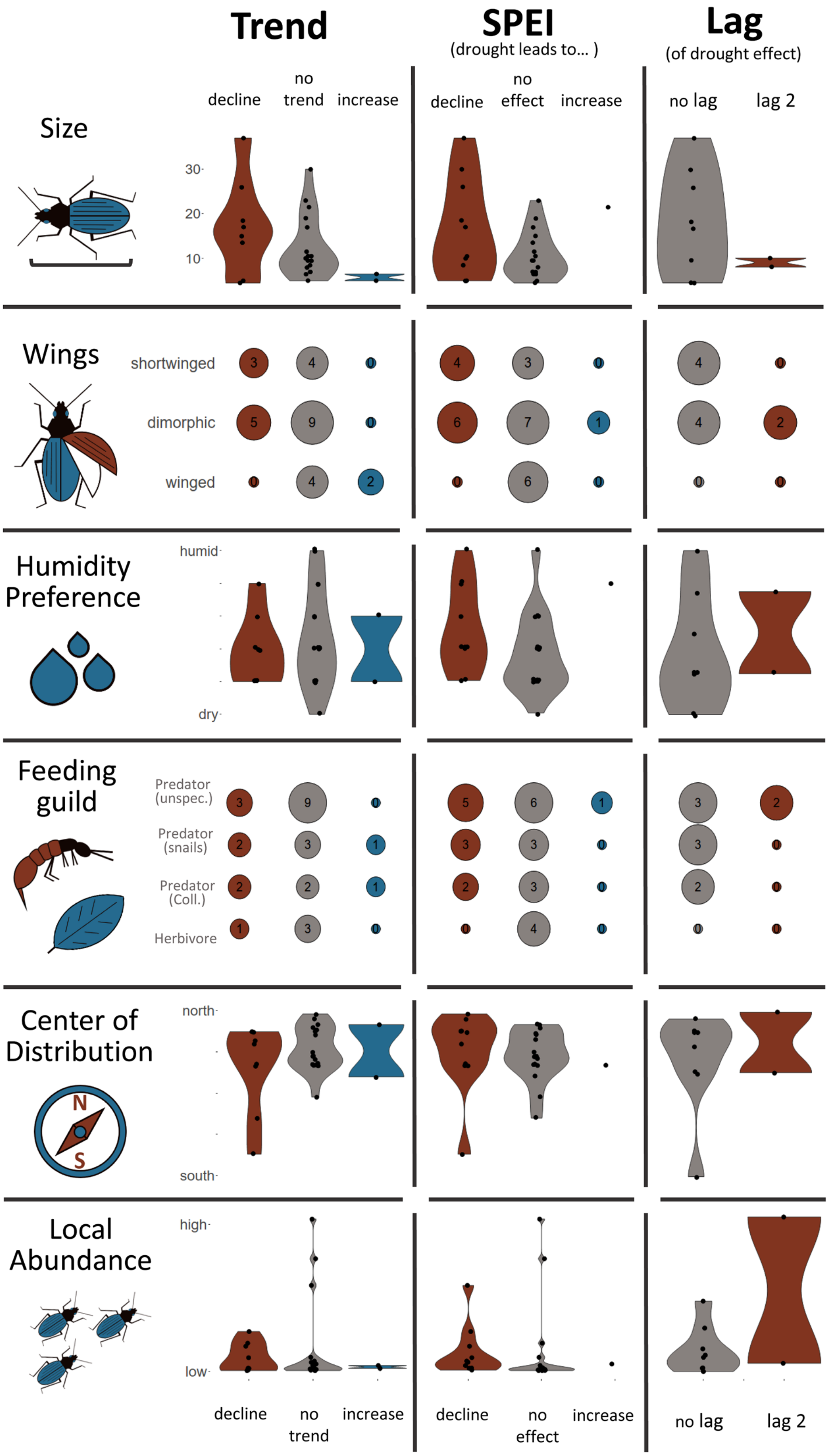

Figure 5. Classified trends (left column), drought effects (middle column) and delay (lag) of declines with droughts (right column) plotted against six species traits (rows). Distribution of trends, drought-effects and delays are visualized with violin plots for traits with continuous scale and with circles for traits with categorical levels.

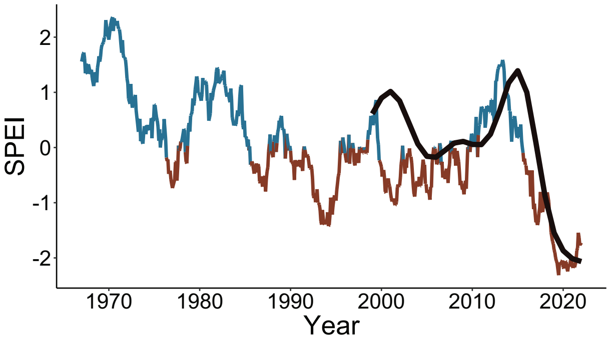

Figure 6. Relative monthly SPEI 72 values for the study area since 1967 with positive (wet) values in blue and negative (dry) values in red. The black line represents the overall biomass trend (GAMM) of carabid beetles found in this study since 1999. Biomass was scaled to match the scale of SPEI, refer to Fig. 3 for comparison of actual scale.

intensified in recent years. Due to turnover being based on observed species (i.e. not being a standardized metric) it is difficult to determine how much of this trend is related to the negative trend in abundance and the therefore lower detection probability of species. However, the strength and very low p-value ($p < 0.001$) of the trend suggests that turnover was actually increasing. A stronger decline and a smaller respective p-value of standardized Simpson compared to standardized richness indicates that diversity among common species is declining stronger than among rarer species. Standardized richness even slightly increased with drought suggesting that changed conditions may have facilitated the occurrence of generalist and open-land species (Gandhi et al. 2008) and overcompensated the loss of other species. Standardized evenness was the only metric that was negatively affected by droughts pointing towards uneven drought effect on different species.

Species trends and traits

Overall, we observed more declining than increasing species (8 versus 2) – a pattern also found by other long-term studies on European carabids (Brooks et al. 2012, Pozsgai and Littlewood 2014) and apparently being a global trend in insects (Sánchez-Bayo and Wyckhuys 2021). Of the two increasing species, *Notiophilus rufipes* has been described as thermophile species in the process of spreading through Europe by Müller-Kroehling et al. (2014). *Badister lacertosus*, on the other hand, is usually assumed to prefer cooler and moister habitats (Brygadyrenko 2015). However, both species are relatively small and winged providing an important advantage for survival under variable conditions as they are potentially able to re-colonize areas from remaining suitable habitat (Thiele 1977, Homburg et al. 2013). We found that declines affected both common and less common species, which were larger on average and exclusively short-winged or dimorphic. This observation is consistent with greater declines in biomass than abundance. Moreover, all declining species (with one exception) were predators. Nolte et al. (2017, 2019) identified reduced dispersal abilities, large body size and predatory feeding behaviour as strong predictors for extinction risk in forest carabids. Similar patterns in decline regarding body size, wing morphology and feeding guild were predicted by Brandmayr and Pizzolotto (2016) as well as Qiu et al. (2023) in the context of climate change, but not found although being investigated in several long-term studies (Homburg et al. 2019, Hallmann et al. 2020, Zajicek et al. 2021). A recent study by Staab et al. (2023) found declines in flying forest insects in Germany, also specifically in abundant, large-bodied, predatory species. Our findings add to the existing evidence that overall declines in insects can be very heterogeneous at species level (Outhwaite et al. 2020, Crossley et al. 2021, Wagner et al. 2021a).

Although declining species and species declining with drought were generally not the identical, they displayed very similar patterns regarding species traits. Again, larger and exclusively predatory and short-winged or dimorphic species were affected. Droughts seem to specifically impact predatory carabid species (Kirichenko-Babko et al. 2020, Jouveau et al. 2022), potentially through drought-mediated changes in prey availability. Wise and Lensing (2019) proposed that bottom–up processes mediate drought effects in the leaf litter arthropod community of temperate forests. Contrary to our expectation, we found no indication that species that usually prefer higher humidity (sensu Šustek 2004) were more often declining or affected by drought conditions. Moreover, there were no patterns regarding the latitudinal centre of distribution range (potentially reflecting adaption to abiotic conditions).

In contrast to our findings regarding overall abundance and biomass, most the species declining with drought were affected without delay (no lag), while only two species were affected with a two year delay (lag 2) (Fig. 5). One of these species was *Pterostichus oblongopuntatus*, the third-most-sampled species in this study, explaining the stronger signal for a two-year delay on the community level. A delay of up to two years in response to changed climatic conditions is typical but variable between carabid species (Irmler 2007, Šustek et al. 2017, Šiška et al. 2020, Skłodowski 2023). Especially carabid larvae are sensitive to microclimatic conditions and might be especially affected by high temperatures and reduced soil moisture which increase the risk of desiccation (Pozsgai and Littlewood 2014, Tseng et al. 2018, Magura et al. 2021). Diverse lifecycles could lead to complex drought legacy effects and differently delayed changes in adult beetle abundance (Matalin 2007). Irmler (2007) as well as Šiška et al. (2020) attribute delays of predatory carabids to the changed availability of prey such as Annelida or Gastropoda, which are sensitive to microclimate (Kirchenbaur et al. 2017, Singh et al. 2019).

Climate change as driver of declines

Human-induced climate will lead to a rise in temperatures and significant alteration in the spatio-temporal distribution of precipitation (Caretta et al. 2022). This will cause more frequent and severe extreme weather events such as droughts (Hari et al. 2020, Vicente-Serrano et al. 2020). Leading meteorological institutions recently confirmed the onset of El Niño in 2023 (National Oceanic and Atmospheric Administration

2023, World Meteorological Organization 2023a). They forecast an additional increase in temperature and the occurrence of severe droughts in the following years. First reports already suggest 2023 to be another exceptional year with the hottest June and September ever recorded (Copernicus 2023, World Meteorological Organization 2023b, Zachariah et al. 2023). Our findings indicate that this combination of severe and repeated droughts can lead to a quantitative collapse in forest carabid beetles. This aligns with recent evidence identifying climate change and especially extreme weather anomalies as major threads to insects in the temperate zone (Harris et al. 2019, Evans et al. 2022, Welti et al. 2022, Müller et al. 2023). Our study highlights the importance of long-term data, which are essential for understanding non-linear trends. Due to our rigorous methods, the high explanatory power of drought for observed trends and the concurrence with major drought events described in the literature we are confident that our findings are valid at a larger spatial scale. However, it is difficult to predict quantitative long-term trends (especially overall abundance) as shifts in species assemblage might change community-level responses to climate change. We expect further declines, especially in large-bodied predatory species in the future, which potentially also affects forests with relatively high water availability (Schnabel et al. 2022). Additionally, drought effects could intensify through increasing climate-habitat interactions.

Forest carabids are mostly predators with specializations for different prey and play essential roles in the food web of temperate forests. Declines of individual species and shifts in relative species abundance most likely indicate changes in lower trophic levels as well as induce changes in both lower and higher trophic levels. This potentially leads to cascading effects in the food web and will have considerable effects on the ecosystems of temperate forests. There still remain large knowledge gaps about how global environmental change affects ground- and soil-dwelling insects (in forests and other habitats). So far, these exceedingly important groups for ecosystem function have received comparatively little attention in the insect decline literature. We need further studies that test drought effects on insects on a larger scale, that aim at disentangling processes through which droughts affect carabid beetles and other soil invertebrates and that investigate legacy effects during post-drought periods. In the context of advancing climate change, there is also an urgent need to better understand the resilience of different ecosystems to weather and climate extremes.

Conclusion

We found that drought measured at long-term scale explained non-linear trends and large portions of decline in abundance and biomass of carabid beetles in a forest area. However, we also observed a concerning quantitative background decline and declines in different diversity metrics (including increased turnover) that were not or less directly linked to drought (hypothesis 1 partially supported).

Species that were generally declining or negatively affected by drought tended to be large, less mobile predators (hypothesis 2 supported). This study is among the very first to investigate the impacts of the current severe drought in central Europe on forest insects. Our findings add to the concerning amount of evidence for widespread declines in arthropods while pointing towards weather anomalies and climate change as an important driver.

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Permits – All carabid beetles are protected under German law (§45 Abs. 7 Satz 1 Nr. 3 BNatSchG / §4 Abs. 3 BArtSchV). Eberswalde Univ. for Sustainable Development holds a special permit for sampling insects for educational and scientific purposes, which was issued by the Brandenburg State Office for the Environment (LfU, permit: LFU-N4-730/11+16 no. 125696/2021).

Author contributions

Fabio Weiss: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Henrik von Wehrden:** Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (supporting). **Andreas Linde:** Conceptualization (equal); Data curation (equal); Investigation (lead); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from PubData: https://doi.org/10.48548/pubdata-46 (Weiss et al. 2023b). The R code is available at https://github.com/fabioweiss/forest_carabid_declines.

Supporting information

The Supporting information associated with this article is available with the online version.

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