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Long-term trends in carabid communities of old lowland beech forests in the context of severe drought

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Preface

This dissertation is presented as a framework paper and a series of manuscripts (Appendices I-IV). These manuscripts are designed to be stand-alone articles and have as such been published in international peer-reviewed scientific journals (see list of publications). The respective content is the same as the published article, and they are included in their original format as they appeared in the journals or have been submitted. Due to the requirements of the individual journals, formatting styles (also with regard to the references and Supporting Information) may very among the different parts of this dissertation.

I, Fabio Weiss, am the sole author of the framework paper. I use the pronoun "we" in the following, as this work is based on my own work and on the work of my co-authors (Appendices I-IV). The framework paper uses the APA reference formatting style (American Psycological Association 7th edition).

This is the revised version of this dissertation (as of 19.9.2024). The submitted dissertation featured an unpublished manuscript as Appendix IV. This version features the published article as Appendix IV. Empty pages were removed for digital publication and page numbers vary from the printed version. All other parts of this dissertation remain unchanged.

List of publications

The following list includes the four manuscripts that contribute to this dissertation. The full manuscripts and information as required by the dissertation guidelines including publication status, journal details, individual author contributions (CRediT taxonmony) and author status/weighing factor are provided in Appendices I-IV, respectively.

Appendix I

Weiss, F., & Linde, A. (2022). How to estimate carabid biomass? - An evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement. *Journal of Insect Conservation*, *26*, 537–548. https://doi.org/10.1007/s10841-022-00391-6

Appendix II

Weiss, F., von Wehrden, H., & Linde, A. (2023). Random year intercepts in mixed models help to assess uncertainties in insect population trends. *Insect Conservation and Diversity, 16*(4), 531–537. https://doi.org/10.1111/icad.12644

Appendix III

Weiss, F., von Wehrden, H., & Linde, A. (2024). Long-term drought triggers severe declines in carabid beetles in a temperate forest. *Ecography*, *2024*(4), e07020. https://doi.org/10.1111/ecog.07020

Appendix IV

Weiss, F., Winter, S., Pflugmacher, D., Kolling, T. & Linde, A. (2024). Evidence for regional-scale declines in carabid beetles in old lowland beech forests following a period of severe drought. *Landscape Ecology, 39,* article 123, (2024). https://doi.org/10.1007/s10980-024-01920-1

List of abbreviations

AIC	Akaike's Information Criterion (Akaike, 1998)
CI	Confidence interval
CM	Community mean
CWM	Community weighted mean (weighted by abundance)
CWB	Climatic water balance
GAMM	Generalized additive mixed model
GLMM	Generalized linear mixed model
LM	Linear model
SPEI	Standardized Precipitation Evapotranspiration Index (Vicente-Serrano et al., 2010)

Abstract

Evidence for widespread declines in insect populations is growing, and the search for the responsible drivers continues. Forests are generally underrepresented in long-term studies of insect populations, which indicates a crucial research gap. In Europe, an unprecedented period of drought that began in 2018 severely affected forests, with as yet unknown consequences for forest insects. With the aim of shedding light on recent trends in forest insects and their influencing factors, this dissertation analyzed long-term trends in ground beetles in lowland beech forests and the role of drought effects.

For this purpose, we relied on two complementary datasets: 1. a continuous time series of carabid samples from a small forest area near Eberswalde, Germany, covering the period 1999-2022. 2. a three-year (1999-2001) survey of carabid beetles at 11 old beech forest sites in northeastern Germany, which we resampled from 2020-2022 using identical methods. These study sites included several old-growth beech forests of high conservation value such as two UNESCO World Heritage Sites.

In preparation for the main data analysis, we evaluated and expanded size-weight equations for carabid beetles, which allowed us to calculate the biomass of carabid samples more accurately. Additionally, we tested a statistical method to account for insect fluctuations and year effects in insect trend analysis, which enabled us to assess uncertainties in estimated trends more reliably. Both contributions served as crucial methodological groundwork for our further analyses but also provide valuable insights for future research on insect trends and applied environmental monitoring.

We then analyzed the Eberswalde time series data modeling linear and nonlinear trends in carabid abundance, biomass, taxonomic diversity and selected species traits via GLMMs and GAMMs. We tested drought, represented by the Standardized Precipitation Evapotranspiration Index, as an additional predictor in trend models. Subsequently, we used the repeated sampling data from 1999-2001 (reference) and 2020-2020 (during/after drought) to test the previous findings at the regional scale and explore how local changes were mediated by the local context.

We found consistent evidence for declines in both datasets. Within the study period, the man carabid abundance and biomass declined by 51% and 65%, respectively, at the regional scale. Nonlinear trends at the local study site revealed that the most severe declines occurred in recent years and were closely correlated with the drought index. Larger and less mobile species representing typical forest specialists showed overproportionate declines. Taxonomic diversity declined in the Eberswalde study area, but showed neither clear effects of drought nor consistent trends at the regional scale. Declines occurred independently of the local conservation status, and the decline in biomass was strongly linked to the local landscape composition (i.e., forest cover).

These findings are worrying because they highlight the decline of a pivotal insect family in forests that plays a crucial role in conserving natural biodiversity. Furthermore, they support recent studies suggesting that weather anomalies and climate change as major drivers of insect populations and point to possible future declines and changes. Future conservation planning needs to recognize the limitations of local conservation and the importance of the spatial context in mitigating the effects of climate change on (insect) biodiversity. This requires further research on the fine-scale dynamics and underlying ecological processes of extreme weather impacts on forest insects.

Zusammenfassung

Es gibt immer mehr Hinweise auf einen weit verbreiteten Rückgang von Insektenpopulationen. Jedoch sind die Ursachen für diese Rückgänge weiterhin nicht eindeutig geklärt. Wälder sind unter den relevanten Langzeitstudien von Insektenpopulationen insgesamt unterrepräsentiert, was eine wichtige Wissenslücke darstellt. In Europa hat eine beispiellose Dürreperiode seit 2018 die Wälder stark in Mitleidenschaft gezogen, mit noch unbekannten Folgen für Waldinsekten. Mit dem Ziel, die jüngsten Trends bei Waldinsekten und ihre Einflussfaktoren zu beleuchten, untersucht diese Dissertation die langfristigen Trends bei Laufkäfern (Coleoptera: Carabidae) in Tiefland-Buchenwäldern und die diesbezügliche Rolle von Dürreeffekten.

Zu diesem Zweck nutzten wir zwei komplementäre Datensätze: 1. eine kontinuierliche Zeitreihe von Laufkäferfängen von einem kleinräumigen Waldgebiet in der Nähe von Eberswalde, Deutschland, die den Zeitraum 1999-2022 abdeckt. 2. eine dreijährige (1999-2001) Erhebung von Laufkäfern an 11 Buchenwaldstandorten in Nordostdeutschland, die wir 2020-2022 mit identischen Methoden wiederholten. Zu diesen Untersuchungsgebieten gehörten auch mehrere alte Buchenwälder mit hohem Naturschutzwert, darunter zwei UNESCO-Welterbestätten.

Im Zuge dessen evaluierten und erweiterten wir außerdem Größen-Gewichts-Gleichungen für Laufkäfer, wodurch wir die Laufkäferbiomasse für unsere eigenen Daten genauer berechnen konnten. Außerdem testeten wir eine statistische Methode zur Berücksichtigung von jährlichen Populationsschwankungen bei der Analyse von Insektentrends, die es uns ermöglichte, Unsicherheiten in den geschätzten Trends zuverlässiger zu bewerten. Beide Studien dienten als wichtige methodische Grundlage für unsere weiteren Analysen, lieferten aber auch wertvolle Erkenntnisse für die künftige Forschung zu Insektentrends und das angewandte Insektenmonitoring.

Anschließend analysierten wir die lokalen Zeitreihendaten und modellierten mit Hilfe von GLMMs und GAMMs lineare und nichtlineare Trends hinsichtlich Laufkäferabundanz, -biomasse, taxonomischer Vielfalt und ausgewählter Artenmerkmale. Wir testeten Trockenheit, repräsentiert durch den Standardized Precipitation Evapotranspiration Index, als zusätzlichen Prädiktor in Trendmodellen. Anschließend nutzten wir die Daten der Wiederholungsaufnahme aus den Jahren 1999-2001 (Referenz) und 2020-2020 (während/nach der Dürre), um die vorherigen Ergebnisse auf regionaler Ebene zu validieren und zu untersuchen, wie kleinräumige Trends durch den lokalen Kontext beeinflusst wurden.

In beiden Datensätzen fanden wir übereinstimmende Hinweise auf Rückgänge. Innerhalb des Untersuchungszeitraums ging auf regionaler Ebene die Laufkäferabundanz um durchschnittlich 51 % und die Biomasse um 65 % zurück. Nichtlineare Trends in dem Eberswalder Untersuchungsgebiet zeigten, dass die stärksten Rückgänge in den letzten Jahren auftraten und eng mit dem Trockenheitsindex korrelierten. Größere und weniger mobile Arten, die typische Waldarten darstellen, verzeichneten überproportionale Rückgänge. Die taxonomische Vielfalt nahm lokal im Eberswalder Untersuchungsgebiet ab, zeigte aber weder eindeutige Zusammenhänge mit der Trockenheit noch beständige Trends auf regionaler Ebene. Generell traten Rückgänge unabhängig vom lokalen Schutzgebietsstatus auf. Allerdings korellierte der Rückgang der Laufkäferbiomasse stark mit der lokalen Landschaftszusammensetzung (d. h. der Waldbedeckung).

Diese Ergebnisse sind besorgniserregend, da sie den Rückgang einer wichtigen Insektenfamilie in Wäldern aufzeigen, die eine entscheidende Rolle bei der Erhaltung der natürlichen Biodiversität spielen. Darüber hinaus stützen sie neuere Studien, die Wetteranomalien und den Klimawandel als wichtige Faktoren für Rückgänge in Insektenpopulationen identifizieren, und weisen auf wahrscheinliche künftige Rückgänge und Veränderungen hin. Die begrenzte Wirksamkeit lokaler Naturschutzansätze und die Bedeutung des räumlichen Kontexts sollten in der zukünftigen Naturschutzplanung größere Beachtung finden, um die Auswirkungen des Klimawandels auf die (Insekten) Biodiversität abzuschwächen. Dies erfordert jedoch weitere Forschungen zu den von Extremwetterereignissen hervorgerufenen Auswirkungen auf Waldinsekten, unter Beachtung kleinräumigerer Dynamiken und den zugrundeliegenden ökologischen Prozessen.

1. Background and research aim

The following section provides an introduction to the topic. It describes the current scientific discourse, illustrates knowledge gaps and sets the scope for this research.

1.1 Declining insect populations have become a topical issue

Insects are responsible for providing diverse ecosystem services and thus essentially contribute to the functioning of ecosystems (Eisenhauer et al., 2023; Noriega et al., 2018; Yang & Gratton, 2014). Concerns about declining insect populations have been growing for decades (e.g. Conrad et al., 2004; Goulson et al., 2008; Kotze & O'Hara, 2003) and have been recognized as part of the ongoing global biodiversity crisis (Dirzo et al., 2014; Hochkirch, 2016; Potts et al., 2010). However, it was not until 2017 that the topic gained the attention of a wider scientific audience and the general public, triggered by reports of severe declines in flying insect biomass (Hallmann et al., 2017). This has sparked calls for action (Cardoso et al., 2020; Forister et al., 2019; Harvey et al., 2020), statements of caution (Cardoso et al., 2019; Saunders et al., 2020; Thomas et al., 2019) and contrasting reports (Crossley et al., 2020; Willig et al., 2019). Consequently, the number of studies on trends in insect populations has been rapidly increasing since then - especially in Europe and North America (Blüthgen et al., 2023; Didham, Barbero, et al., 2020; Weisser et al., 2023).

To date, the wealth of available data and research has led to a more nuanced picture: several studies (Hallmann et al., 2020; Harris et al., 2019; Staab et al., 2023), including larger meta-studies (van Klink et al., 2020, 2023), found further alarming declines, while others have reported stable or even increasing insect populations (Crossley et al., 2020; Fürst et al., 2023; Macgregor et al., 2019). Trends may vary spatially (Crossley et al., 2021; Wagner, Fox, et al., 2021) and for different insect taxa (Didham, Barbero, et al., 2020; Hallmann et al., 2020; van Klink et al., 2020). Moreover, declines are not always of a direct quantitative nature, as they may not only affect overall insect abundance (and biomass). They may also be related to taxonomic and functional insect diversity (Atmore & Buss, 2023; Harris et al., 2019; Homburg et al., 2019; Krehenwinkel et al., 2022) or shifts in spatial (Engelhardt et al., 2022; Neff et al., 2022; Rödder et al., 2021) or temporal distributions (Irmler, 2022; Pozsgai & Littlewood, 2014), potentially leading to local declines in abundance and/or diversity. Some of the influential studies were followed by substantial criticism (Daskalova et al., 2021; Desquilbet et al., 2020, 2021; Mupepele et al., 2019) as the analysis of insect trends offers many potential pitfalls (Didham, Basset, et al., 2020; Duchenne et al., 2022; Welti et al., 2021). However, despite the heterogeneity in trends and the controversy surrounding some reports, there seems to be a consensus that insect populations are generally under increasing pressure globally (Blüthgen et al., 2023; Montgomery et al., 2020; Weisser et al., 2023).

1.2 Consistent insights into the drivers of declines are still missing

There is 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. As trends derived from different insect time series can be expected to be heterogeneous due to their varying contexts (Duchenne et al., 2022), inference about the driving factors is crucially needed to make findings more generalizable and transferrable (Habel & Schmitt, 2018; Weisser et al., 2023). The debate about the underlying causes has been the subject of numerous studies (Cardoso et al., 2020; Rumohr et al., 2023; Sánchez-Bayo & Wyckhuys, 2021; Wagner, Grames, et al., 2021). Likely candidates include intensive agri- or silviculture (Crossley et al., 2022; Fox, 2013; Neff et al., 2022; Outhwaite et al., 2022; Raven & Wagner, 2021), habitat loss (Forister et al., 2023; M. S. Warren et al., 2021), -fragmentation (Nagy et al., 2019) and –degradation (Fox, 2013; Habel et al., 2022), urbanization (Ellis et al., 2023; Piano et al., 2019; Vaz et al., 2023), including light pollution (Stewart, 2021; Vaz et al., 2021), pollution and pesticides (Brittain et al., 2010; Egan et al., 2014; Nocera et al., 2012; Roth et al., 2021) and climate change (Engelhardt et al., 2022; Halsch et al., 2021; Harris et al., 2019; Harvey et al., 2022). Recent studies indicate that weather anomalies in particular drive flying insect biomass (Müller et al., 2023; Welti et al., 2022). Often, different drivers interact (e.g. Neff et al., 2022; Rashid et al., 2023). However, investigating the potential drivers of insect population trends is challenging because standardized insect data are required at considerable temporal and spatial scales (Engelhardt et al., 2022; Montgomery et al., 2020; Rumohr et al., 2023). Due to a lack of such data, scientists often rely on imperfect substitutes such as opportunistic data (Boyd et al., 2023), experiments (Weisser et al., 2023), space-for-time approaches (Blüthgen et al., 2022) or a combination thereof (Montgomery et al., 2020).

1.3 Temperate forests and recent drought events

In light of the recent surge in long-term studies of European insect populations, temperate forests still represent a relatively understudied habitat (Blüthgen et al., 2023; Staab et al., 2023). This might be because some of the suspected drivers of insect decline (such as intensive agriculture with the use of pesticides and fertilizers, habitat loss, urbanization or light pollution) are more strongly associated with open landscapes. However, some of the few available studies in European forests have reported declines (Barendregt et al., 2022; Seibold et al., 2019; Staab et al., 2023). Moreover, temperate forests are doubtlessly exposed to the effects of climate change, such as increasing overall temperature and weather anomalies (Oakes et al., 2014; Seidl et al., 2017; Senf et al., 2018). This also affects forest insects (Cours et al., 2023; Jaworski & Hilszczański, 2013), as supported by long-term studies from other continents support this (Evans et al., 2022; Harris et al., 2019). On the other hand, forests have the capacity to offset temperature and retain moisture (Davis et al., 2019; De Frenne et al., 2021; Haesen et al., 2021), and some researchers have proposed that forests – specifically deciduous forests with high structural diversity – could act as important refuges under climate change (Braunisch et al., 2014; Frey et al., 2016). In general, there remains an important gap in the knowledge of how climate change and extreme weather events will affect the microclimatic conditions of forests and what consequences this will have for (insect) biodiversity (De Frenne et al., 2021).

In 2018/2019, Europe was hit by an unprecedented drought (Büntgen et al., 2021; Rakovec et al., 2022; Treydte et al., 2023), which affected hydrological conditions at least until 2022 (Schumacher et al., 2023). This had significant negative impacts on European forests (Rukh et al., 2023; Schnabel et al., 2022; Senf et al., 2020) with persistent legacy effects (Knutzen et al., 2023) and most likely also affected forest insects (Blüthgen et al., 2023; Cours et al., 2023). To date, the effects of this recent drought period on forest insects (except for those considered pests, Thonfeld et al., 2022) have not been investigated.

1.4 Carabid beetles

Large proportions of the invertebrate biodiversity and biomass of temperate forests can be found in the litter and upper soil layers (Rosenberg et al., 2023; Schowalter, 2017). This ecological importance of the forest floor is often overlooked (Decaëns, 2010), and most long-term studies (Seibold et al., 2019; Staab et al., 2023) and studies regarding climate change- and drought effects (Cours et al., 2022; Gely et al., 2020; Sallé et al., 2021) have focused on flying forest insects. Some herbivorous insect groups, especially saproxylic ones, might actually benefit from drought conditions (Gely et al., 2020; Johnson & Haynes, 2023; Vitasse et al., 2024). Carabid beetles (Coleoptera: Carabidae), on the other hand, could be particularly negatively affected. This diverse family of mostly predatory beetle species makes up a considerable proportion of the epigeic fauna in temperate forests (Magura, 2002). Most typical forest carabid species depend on a relatively stable, cool and moist microclimate throughout their lifecycle (Fitzgerald et al., 2021; Koivula et al., 1999; Müller-Motzfeld, 2001). Due to their sensitivity to environmental conditions, they have a history of being used as bioindicators (Koivula, 2011; Rainio & Niemelä, 2003). They play a variety of roles in the biocenosis of the forest floor and can therefore serve as indicator of changes in the forest food web. Carabids often prey on invertebrates of lower trophic levels, such as springtails (Collembola) and other smaller insects, slugs and snails (Gastropoda) and worms (Annelida and Nematoda) (Holopainen & Helenius, 1992; Renkema et al., 2014; Thiele, 1977). As scavengers, they contribute to the decomposition of organic matter (Benbow et al., 2013; Kočárek, 2003), and many species have been found to interact with fungal communities (Heitmann et al., 2021; Pozsgai et al., 2021).

Previous long-term population studies of forest carabids have mostly investigated local trends (Brooks et al., 2012; Hallmann et al., 2020; Homburg et al., 2019; Irmler, 2007) and drawn an overall inconsistent picture. Other studies indicate that carabid communities respond to weather anomalies (Evans et al., 2022; Fitzgerald et al., 2021; Zajicek et al., 2021) and may be sensitive to climate change (Brandmayr & Pizzolotto, 2016; Müller-Kroehling et al., 2014; Williams et al., 2014). The effects of droughts on forest carabid beetles have been the subject of several small-scale observational studies of limited duration (Kirichenko-Babko et al., 2020; Šiška et al., 2020; Šustek et al., 2017) and experiments (Jouveau et al., 2019; Williams et al., 2014). However, to the best of our knowledge, no long-term studies have investigated the response of forest carabids to drought.

Carabid beetles have a long history in ecological research (Kotze et al., 2011), with sampling methods that have changed little for almost a century (Barber, 1931), useful resources for species identification (Müller-Motzfeld, 2004) and extensive knowledge of their ecology (Thiele, 1977). Although sampling methods vary to some extent (Brown & Matthews, 2016), they are usually cost-effective and easy to reproduce (Montgomery et al., 2021) and collect quantitative data (i.e. probability samples, Boyd et al., 2023). From a practical point of view, this makes carabid beetles a likely insect group for finding suitable long-term data or historical data that might be used as a quantitative baseline for resampling to investigate trends and drought responses.

1.5 Research scope and aims

This dissertation set out with the goal of expanding the evidence on local (and regional) insect population trends. We particularly investigated trends in forest insects, as this realm has received comparatively little attention to date. In addition, we wanted not only to describe the population trends but also to investigate possible drivers of the trends, as this increases the generalizability of the findings. In 2019, the consequences of the prolonged drought in 2018/2019 were noticeable throughout Germany. This immediate and large-scale relevance prompted us to analyze drought conditions as a potential driver of insect trends.

We set our scope for extensively managed and protected old lowland beech (*Fagus sylvatica*) forests in northeastern Germany for several reasons:

a) These forests represent the dominant form of potential natural forest vegetation (Bohn et al., 2000; Bohn & Gollup, 2007). The region holds a special responsibility for its conservation, contributing to the preservation of natural biodiversity (P. Meyer et al., 2023; Springer et al., 2024; Winter, 2005). It is therefore of general interest how insect biodiversity has changed there over time.

b) It is still under debate how resilient old deciduous (beech) forests can be expected to respond to climate change and weather anomalies (Braunisch et al., 2014; Frey et al., 2016, but see P. Meyer et al., 2023). Regional beech forests have clearly been affected by recent drought periods (B. F. Meyer et al., 2020; Weigel et al., 2023), but the consequences for insect biodiversity remain unclear.

c) Old deciduous forests are highly important for a specialized carabid communities (Fuller et al., 2008; Müller-Motzfeld, 2001; Winter et al., 2005), which might also be very vulnerable to potential changes in the microclimate.

d) The low management intensity and perpetuality of these forest sites largely exclude other potential influencing factors and allowed us to study in relative isolation the effects of drought (see Evans et al., 2022, and Jambrošić Vladić & Šerić Jelaska, 2020, for similar approaches and reasoning).

e) Finally, in terms of practical benefits, the regional proximity allowed us to maintain close contact with the managing authorities, which provided crucial access to the data and (informal) metadata.

Specifically, this dissertation aims to answer the following questions:

1. What were the general trends (abundance, biomass, taxonomic diversity, functional composition) in carabid communities of old lowland beech forests in northeastern Germany over the past 24 years?
2. How do these trends relate to drought conditions, particularly during recent periods of severe drought?
3. Does the local context, for instance the protection status, mediate trends and potential drought effects?

2. Research approach

This section describes which data we used and how to answer the research questions. Furthermore, we describe the methodological challenges and how we addressed them. Detailed descriptions of the data selection, -data processing and statistical methods used are provided in Appendices I-IV.

2.1 Data

The temporal scope of doctoral research is usually limited to a few years. Investigating trends in insect populations, however, requires standardized long-term data (Didham, Basset, et al., 2020; Thomas et al., 2019), which would therefore normally lie beyond the temporal scope of doctoral research. In addition, long-term data on insects covering larger spatial scales are rare, as their collection is labor intensive, and funding is usually available only for a limited period of time (Didham, Barbero, et al., 2020). We navigated this challenge by drawing on and expanding different complimentary datasets and combining insights from their analysis.

In 1995, Eberswalde University for Sustainable Development started sampling carabid beetles in a small forest area close to Eberswalde, Germany, for educational purposes. Since 1999, this has been done annually with highly standardized methods, which meant sampling at the same locations at the same time of the year (May to July) using consistent methods. The data were collected from 13 different forest plots with four pitfall traps per plot in a forest area of approximately 1 km² (Figure 1). The area was extensively managed with few small-scale interventions. Large areas feature old beech forest and there have been no major management interventions since 1999. Drawing on data from 1999 to 2022 provided us with a 24-year time series of highly standardized data consisting of 1,866 insect samples containing records of more than 24,000 carabid beetles (Linde et al., 2023). Having access to approximately 200 archived student reports from 1995 to 2022 added valuable information about the sampling history of the data.

Additionally, we had access to a second dataset from the same region (Figure 1): from 1999 to 2001, the ‘Research and Development Project’ ‘Naturschutzstandards für die Bewirtschaftung von Buchenwäldern im nordostdeutschen Tiefland‘ investigated the ecological properties of managed and unmanaged old beech forests in northeastern Germany (Winter, 2005; Winter et al., 2003, 2005). As part of this project, carabid beetles were sampled from 1999 to 2001 at different forest sites. All of these forest sites featured old beech forests that were either extensively managed (Winter et al., 2020) or strictly protected. From 2020 to 2022, we resampled 79 of the original trap locations distributed across 11 forest sites. For that purpose, we located the exact sampling location using GPS coordinates and detailed tree survey maps from Begehold et al. (2016). The resampling was conducted with methods identical to those used for 1999-2001. The full dataset (1999-2001 and 2020-2022) consisted of approximately 2,400 samples containing close to 11,000 carabid beetles (Weiss et al., 2024).

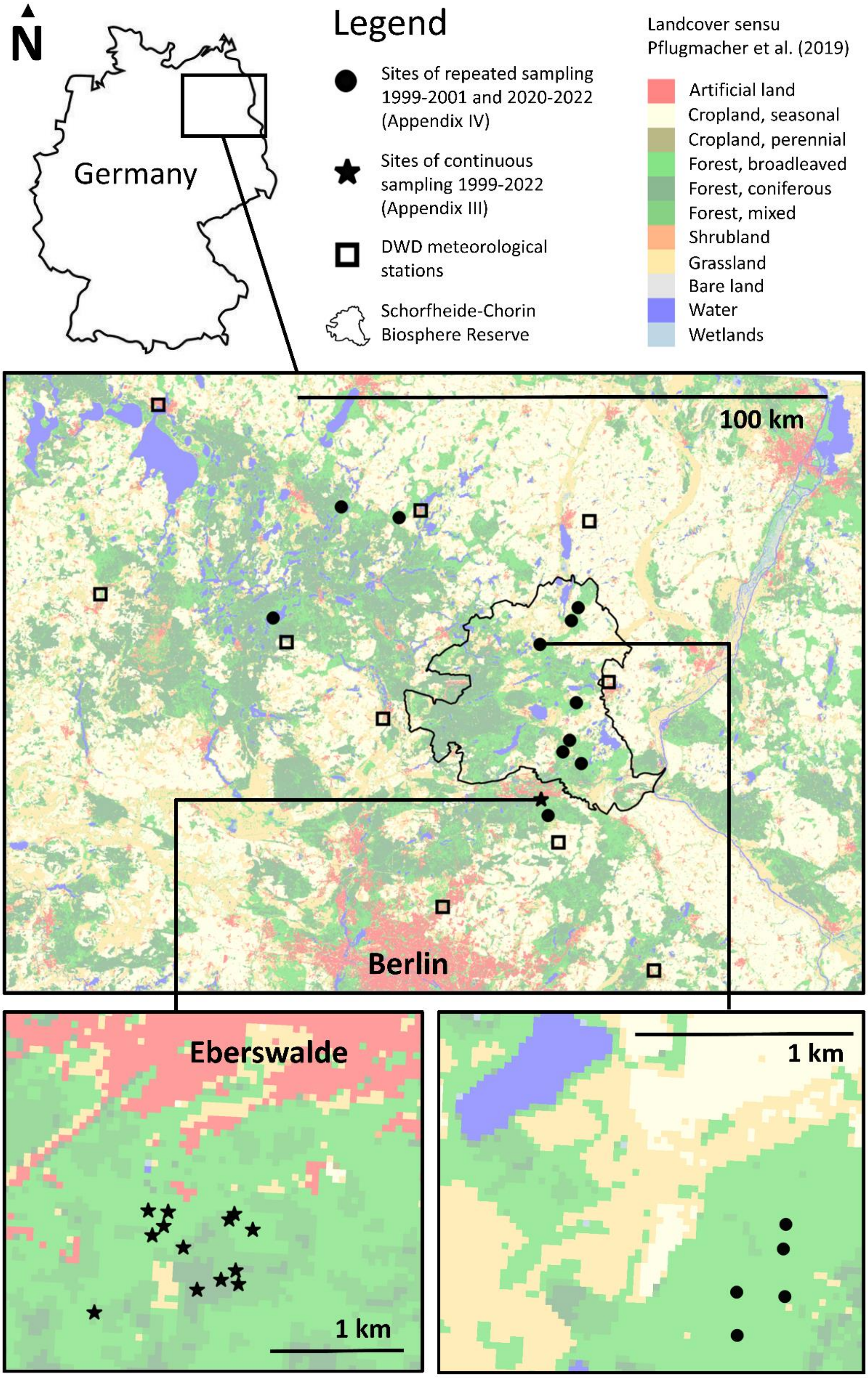

Figure 1. Map of the study region (center), of the continuous sampling site near Eberswalde/Appendix III (bottom-left) and one of the sampling site of the repeated sampling/Appendix IV (bottom-right).

Due to the very similar context of both datasets, it was possible to relate the findings from their analysis. Both originated from the same region (Figure 1). Both fall within the same period. Both were collected using almost identical sampling methods (i.e., same type of pitfall traps), avoiding potential biases (Boetzl et al., 2018; Brown & Matthews, 2016). In both cases, carabid beetles were identified by the same people (Thomas Kolling, Fabio Weiss) using the same method (Müller-Motzfeld, 2004, and previous edition). Finally, both datasets were sampled from old beech forests with very similar management regimes. The absence of any serious management interventions such as larger-scale timber harvests or the use of pesticides/fertilizers, allowed us to consider in relative isolation from other potential (local) drivers the effect of climatic conditions such as drought.

2.2 Considering trends and changes using different metrics

We explored trends and changes using the same metrics for both datasets. We considered overall carabid abundance (number of individuals belonging to species of the Carabidae family), carabid biomass, taxonomic diversity and species traits.

Although abundance is a central metric commonly used for investigating population dynamics in carabid beetles, biomass has become an important alternative metric (Evans et al., 2022; Hallmann et al., 2020; Skarbek et al., 2021), especially after Hallmann et al. (2017) reported severe declines in flying insect biomass. Studying insect biomass can provide additional insights and often reveals contrasting patterns to insect abundance (Montgomery et al., 2020; Saint-Germain et al., 2007). Insects play an important role in food webs (Yang & Gratton, 2014), and insect biomass is a particularly meaningful metric when considering trophic energy fluxes (van Klink et al., 2022). Depending on the sampling methods used and the available data, different methods are available for measuring or calculating insect biomass. We used the size-weight equations of Szyszko (1983) and Booij et al. (1994) to calculate carabid biomass based on species sizes provided by Müller-Motzfeld (2004) (see Box: Methodological challenge I: Carabid biomass).

Methodological challenge I: Carabid biomass

Challenge: There exist a variety of methods to measure carabid biomass. Some studies dry the sampled beetles before weighing them (e.g. Evans et al., 2022) others weigh wet beetles after draining the samples as currently still recommended by in the framework for nationwide insect monitoring by the BfN (Federal Agency for Nature Conservation Germany, 2023). However, these methods are work-intensive and have been demonstrated to introduce considerable bias (Braun et al., 2009; Knapp, 2012). Moreover, they require the original insect samples, which are often not available for digitally archived data. In these cases, size-weight equations, which utilize the correlation of body length and body weight, can be a solution. There exist different versions of such equations for carabid beetles. They originate from different geographic areas, are based on varying number of measured beetles and use either fresh weights or dry weights (Booij et al., 1994; Gruner, 2003; Hódar, 1996; Jarosik, 1989; Sabo et al., 2002; Szyszko, 1983). Although, these equations are assumed to be context specific and only valid for certain taxonomic groups, habitats and geographic areas (de los Santos Gómez, 2013; Sabo et al., 2002; Versluijs et al., 2023) they are more often than not applied outside their original context (e.g. Hallmann et al., 2020; Homburg et al., 2019;

Skarbek et al., 2021). Moreover, none of these equations has ever been evaluated with independent data. The data used for this research was archived digitally and the original samples were not preserved. For investigating trends in carabid biomass we therefore relied on methods that permitted the calculation of carabid biomass from digital data.

Approach: We explored different options of size-weight equations by evaluating two existing equations of Szyszko (1983) and Booij et al. (1994). Previous research showed that the accuracy of size-weight equations generally improves with increasing taxonomic specificity (Sabo et al., 2002). Therefore, we also developed alternative size-weight equations with additional taxonomic parameters of different complexity: Following the approach of Szyszko (1983) and Booij et al. (1994) we fit LMs with log-transformed sizes and weights based on published data of Booij et al. (1994). We added a) a random intercept for subfamily to account for uneven representation in training data, b) a fixed effect for subfamily allowing taxonomically specific predictions and c) an interaction of ln(weight) and subfamily allowing taxonomically specific predictions based on varying correlation slopes. Finally, we used relative deviation graphs (Mitchell, 1997) and observed versus predicted regression (OP regression, Piñeiro et al., 2008) to compare prediction of all models to independent data of carabid fresh weights published by Schultz (1996).

In addition to potential changes in abundance (and biomass), we were also interested in how taxonomic diversity changed during the study period. A considerable number of long-term studies did not find declines in the abundance or biomass of European carabid beetles (Fürst et al., 2023; Homburg et al., 2019; Zajicek et al., 2021). However, potential drivers of declines might affect the abundance of different carabid species positively or negatively. This could lead to changes in species composition but balance out any trends in overall abundance (Morecroft et al., 2002). For instance, Homburg et al. (2019) found neither significant declines in overall abundance nor in biomass but in species richness. Species richness alone, however, is insufficient to reliably detect changes in taxonomic diversity and community assemblage (Edmonds et al., 2024; Hillebrand et al., 2018; Pozsgai et al., 2016). Temporal trends in taxonomic diversity are therefore at best analyzed using multimetric approaches (Blowes et al., 2022). We used the framework of hill numbers (Hill, 1973) and explored taxonomic diversity by deriving ${}^{0}D$ (equivalent to species richness), ${}^{2}D$ (equivalent to the inverse Simpson index) and ${}^{2}D/{}^{0}D$ (evenness, Jost, 2010). ${}^{0}D$ and ${}^{2}D$ vary in their sensitivity to rare species, while evenness describes how abundance is distributed among species. These diversity metrics are highly influenced by sample size (abundance), as smaller samples often leave rarer species undetected (Chao & Jost, 2012; Gotelli & Colwell, 2001; Roswell et al., 2021). We therefore standardized all diversity metrics by coverage (i.e., estimated sample completeness) using the framework of Chao et al. (2014).

Table 1. Overview of the species traits considered, indications of why these traits are of interest for the study and the source of the trait data.

Trait	References	Source
Local abundance	Habel & Schmitt (2018), van Klink et al. (2023): Large-scale insect decline appears to be driven by declines of formerly abundant species. Staab et al. (2023): Greater declines in relatively abundant forest insect species in the same area.	Own data
Body size	Nolte et al. (2019): Larger species have a higher extinction risk. Staab et al. (2023): Greater declines in larger forest insect species in the same area.	Homburg et al. (2014) complemented by Müller-Motzfeld (2004)
Wing-morphology	Homburg et al. (2013), Nolte et al. (2017): Flightless (brachypterous) species are typically associated with stable habitats. Qiu et al. (2023): Flightless forest carabids are forecasted to decline under climate change.	Homburg et al. (2014) complemented by Müller-Motzfeld (2004)
Trophic role	Jouveau et al. (2019), Kirichenko-Babko et al. (2020): Predatory forest insects/carabids are especially drought sensitive. Staab et al. (2023): Greater declines in predatory forest insect species in the same area.	Homburg et al. (2014) complemented by Müller-Motzfeld (2004)
Humidity preference	Morecroft et al. (2002), Šustek et al. (2017): Species that prefer humid conditions are more sensitive to drought.	Šustek (2004)
Latitudinal center of distribution	Chen et al. (2011), Jaworski & Hilszczański (2013), McCarty (2001): Climate change leads to shifts in species' distribution ranges. Species might more under pressure toward the southern limits of their distribution range	Homburg et al. (2014)

Finally, we considered community assemblages from a functional perspective. Carabid species can be characterized based on their traits, which describe species-specific properties, such as physiology, life history, geographic distribution or habitat preferences. These traits can be used as indicators of how species interact with their environment, and they may help to draw conclusions about ecological processes (Kotiaho et al., 2005). Staab et al. (2023) reported that among the flying forest insects in the region, species with certain traits (large, abundant predators), in particular, have declined. In carabids, species traits, particularly body size and wing morphology, were found to be meaningful predictors of extinction risk (Nolte et al., 2019) and the ability of species to cope with fluctuating environmental conditions (Homburg et al., 2013; Nolte et al., 2017; Qiu et al., 2023). We were therefore interested in whether the carabid community changed in terms of body size, wing morphology, feeding guild, humidity preference, latitudinal center of distribution range and local abundance (Table 1). We obtained data on species traits mostly from Homburg et al. (2014, carabids.org). We specifically decided against including traits representing habitat preferences and the reproductive cycle. Both are highly variable and strongly depend on the local context (Matalin, 2007; Müller-Motzfeld, 2001), making it difficult to obtain reliable data for all species.

2.3 Trends and drought effects at the Eberswalde site

The population trends in insects are most likely not linear (Didham, Basset, et al., 2020). Continuous time series data with high (i.e., annual) temporal resolution enabled us to investigate both linear and nonlinear trends in carabid abundance, biomass and diversity metrics using GLMMs as well as GAMMs. Modeling nonlinear trends in abundance or diversity is useful for detecting turning points of trends (Dornelas et al., 2013; Habel et al., 2022; Knape, 2016). Both linear and nonlinear trend estimates can be crucially affected by population fluctuations (Didham, Basset, et al., 2020; Knape, 2022). We addressed this challenge in a separate study (see Box: Methodological challenge II: Fluctuations in insect populations), which helped us to determine a suitable random effect structure and led us to conduct sensitivity analyses for all trend models.

Methodological challenge II: Fluctuations in insect populations

Challenge: Early on in the debate about reported declines in insect population calls for a more careful and rigorous approach to trend analysis grew louder (Thomas et al., 2019). Many of the influential studies that reported declines were followed by criticisms from the science community concerning their methodology (e.g. Daskalova et al., 2021; Desquilbet et al., 2020, 2021; Mupepele et al., 2019). One of the issues is that the abundance of insects – particularly in carabids - are known to fluctuate considerably between years (Dallas et al., 2023; Günther & Assmann, 2004; Schwerk et al., 2006). There different reason for these fluctuations and they can be caused extrinsically by annually varying environmental conditions or availability of prey but also intrinsically through variations in species’ life cycles (Daskalova et al., 2021; Irmler, 2007). Such year effects, which are known from other ecological studies (Werner et al., 2020), can introduce relevant bias when simply dismissed as noise. Moreover, all insect time series - even the longer ones (Bell et al., 2020; Macgregor et al., 2019; Neff et al., 2022) - only represent a limited window in time with the initial year acting as a baseline for trend analyses. Therefore it has a disproportionately large effect on estimated trends (Bahlai et al., 2021; Didham, Basset, et al., 2020; Duchenne et al., 2022; Knape, 2022) with this effect increasing in shorter time series (Daskalova et al., 2021; Duchenne et al., 2022). However, year effects may considerably reduce the reliability of initial years as baselines for trend analyses (Werner et al., 2020).

Daskalova et al. (2021) argued that the significant declines found by Seibold et al. (2019) during a period of ten years were mostly driven by data from the initial year which featured unusually high insect abundances. Daskalova et al. (2021) proposed the use of random intercepts for individual sampling years in GLMMs, in addition to using them as a fixed effect variable. According to them, this accounts for temporal pseudoreplication (meaning annually varying conditions) and therefore limits influence of interannual fluctuations and exceptional years. However, this approach remains controversial. Seibold et al. (2021) argue that potential temporal autocorrelation in insect abundance and overlapping effects with included environmental predictors may cause issues. Thus far, random year intercepts are only rarely used in insect trend analyses (see Bell et al., 2020, for a rare example).

Approach: When preparing the analysis of the continuous time series data we were interested in how the inclusion of year effects as random intercepts would affect trend estimates for our carabid data. We used carabid abundance data to fit different GLMMs with different combinations of random year intercepts and environmental predictors (temperature and precipitation, as fixed effects). We then tested their sensitivity toward single years by iteratively excluding data of single years from the time series. We compared trend coefficients, confidence intervals and p values of the different models using pairwise tests (parametric and nonparametric).

Independent of diversity metrics such as richness, carabid communities can be expected to exhibit considerable species turnover between single years (Morecroft et al., 2002; Schwerk et al., 2006). The continuous nature of the data allowed us to investigate potential directional trends in turnover in addition to the previously described diversity metrics. Moreover, we fitted linear abundance trend models (GLMMs) for the 27 most abundant species and explored associations between classified trends (increasing, stable/uncertain, declining) and species traits (Table 1).

Continuous data on both the carabid community and the environment are crucial for investigating potential environmental drivers such as drought (Rumohr et al., 2023). Forests are able to buffer heat and maintain moisture (De Frenne et al., 2021; Gohr et al., 2021). However, it is highly context dependent at which point this capacity is exceeded (Davis et al., 2019), and it is therefore unclear at which temporal scale drought affects forest insects in the study area. Moreover, the life cycles of different carabid species vary (Matalin, 2007), leading to potentially delayed responses to drought (Šiška et al., 2020; Šustek et al., 2017). Continuous long-term data enabled us to investigate drought responses at different temporal scales. We chose the Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010) to represent drought. The SPEI is a relative drought index based on monthly precipitation and temperature and can be calculated for different time spans. Moreover, it is known to be sensitive to climate change (Vicente-Serrano et al., 2010) and is widely used in drought research (Slette et al., 2019). It is a proven proxy for investigating drought effects on forest ecosystems (Buras et al., 2018; B. F. Meyer et al., 2020) as well as forest carabids (Šiška et al., 2020; Šustek et al., 2017). We calculated the SPEI based on meteorological data from the German Weather Service (DWD, 2023) for different time scales (12-72 months), each with different delays (same season, one year previous, two years previous). The procedure we used to calculate and aggregate different SPEI variables is illustrated in Figure 2.

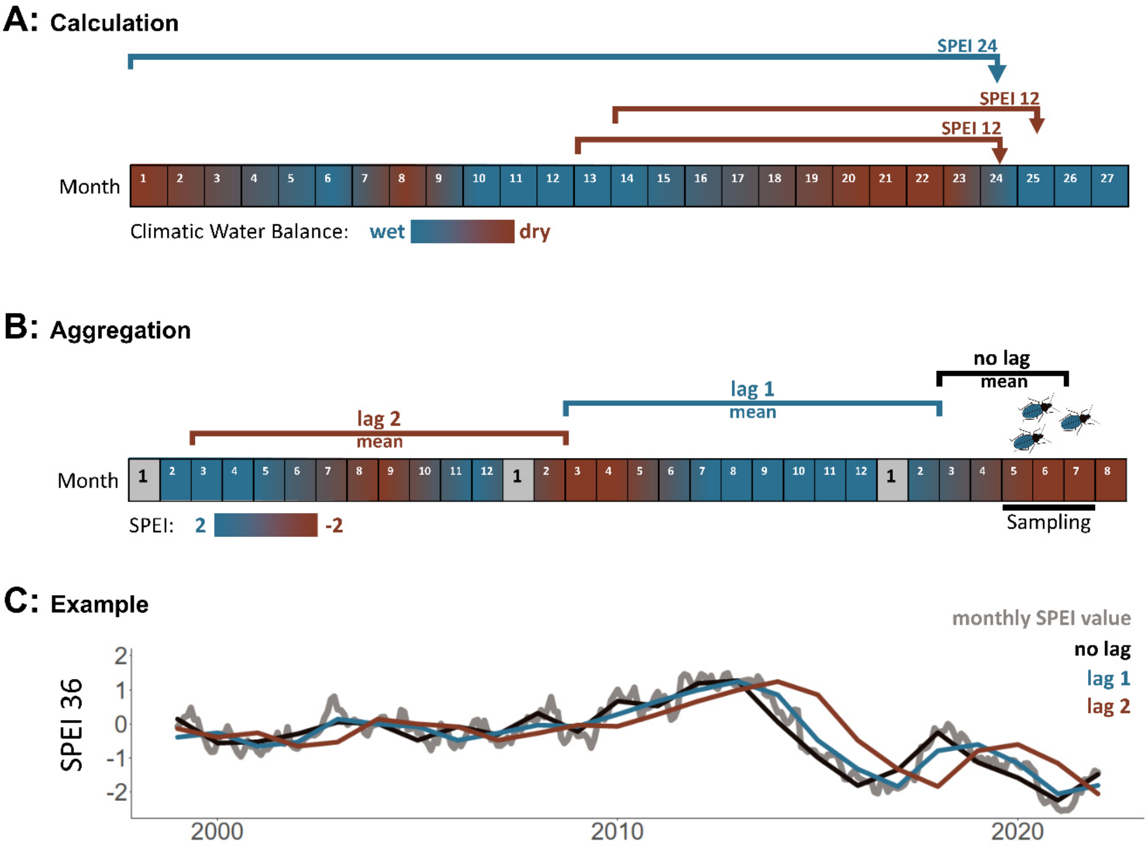

Figure 2 (unchanged figure from Appendix III)**.** The methodological scheme which was used to calculate and aggregate SPEI-variables: (A) monthly SPEI values were calculated at different temporal scales (e.g. 12 and 24 months) taking into account the climatic water balance of the previous months. (B) 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 (temporal scale: 36 months).

We tested the effect of drought by individually adding SPEI variables of different temporal scales and delays as predictors to the GLMMs for abundance, biomass and diversity metrics and comparing the AIC values of the original model and those with different SPEI predictors (Burnham & Anderson, 2004). If the inclusion of a certain SPEI variable as a predictor led to a better model fit (i.e., lower AIC), we considered this to support a drought effect at this particular temporal scale and delay. Additionally, we ran a similar AIC-based model selection for the individual species GLMMs. This time, however, we used the SPEI variable at the temporal scale, which was previously found to be most relevant for overall abundance and only tested different delays, which might vary with the different species' ecology.

2.4 Testing previous findings at the regional scale

Although the analysis of the local dataset provided detailed insights into trends and drought effects, these insights were limited to a relatively small spatial area. We first used data from stations of the German Meteorological Service (DWD, 2023) and calculated time series of the SPEI for different locations throughout the study region to ensure that climatic patterns were consistent with those found at the local site. We then used the second dataset to compare the carabid communities of eleven old beech forest sites for 1999-2001 (reference) and 2020-2022 (during/after drought) and tested the previous findings at larger spatial scale. We were interested in whether the changes in the carabid community at the regional scale corresponded to the trends we had previously observed at the local scale.

When investigating changes in insect populations by comparing data from two periods, findings are prone to bias due to false-baseline or snapshot effects (Didham, Basset, et al., 2020). This is especially an issue when comparing single years (see Lister & Garcia, 2018, for a prominent example). Carabid species in particular are known to fluctuate strongly between single years (Dallas et al., 2023; Irmler, 2007; Rainio & Niemelä, 2003). We compared periods of multiple years across different species and locations (Knape, 2022) in addition to using an appropriate random effect structure (Chaves, 2010; Daskalova et al., 2021), which provided some safeguarding. There are several good examples of insect population studies that use this approach to investigate changes over time (Harris et al., 2019; Schuch et al., 2012). In this case, nonlinear trends found in the previous analysis provided an additional important context that facilitated interpretation.

Table 2 (modified table from Appendix IV)**.** Overview of the different site variables that were used in an explorative correlation analysis investigating potential causes of heterogeneity in site-specific changes.

Site variable	**Reference**
Latitude Longitude	Duchenne et al. (2022): Insect population trends can be expected to show spatial variations.
Protection status	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 microclimate during extreme weather.
Initial community size	Cours et al. (2023): Larger species might be affected more severely by droughts.
Mean precipitation	Davis et al. (2019): Local water availability affects the microclimatic buffering capacity of forests. We use mean precipitation as a very simple proxy for water availability.
Landscape composition	Gohr et al. (2021): Forests and wetlands mitigate extremes in land surface temperature. Tammaru et al. (2023): Forest cover plays an essential role for other insect groups (butterflies) on the landscape scale, likely due to microclimatic effects.
Canopy	Davis et al. (2019), De Frenne et al. (2021), Blumröder et al., (2021): Canopy cover affects the microclimatic buffering capacity of forests.

We used GLMMs to compare abundance, biomass and diversity metrics between the two periods. We also investigated selected species traits that were associated with classified trends during the previous analysis. As we were not examining changes in individual species at this time, we compared the community means (CMs) and community weighted means (CWMs) for these traits between the two time periods. Furthermore, we were interested in whether these changes were consistent among the different resampling sites. Although all the study sites were relatively similar in terms of forest vegetation and management, we expected some spatial heterogeneity (Duchenne et al., 2022). The pressure of drought on the carabid community might vary based on local water availability (Davis et al., 2019), landscape composition in the surrounding area (Gohr et al., 2021; Mann et al., 2023), vegetation structure (Davis et al., 2019), or the initial composition of the carabid community (Kotiaho et al., 2005). We therefore investigated the associations of different site variables (Table 2) with changes at the site level using t tests and correlation tests (Pearson).

2.5 Robust evidence from a combined approach

Figure 3 illustrates how the separate contributions of this dissertation fall into the overarching framework: Appendices I and II contributed to optimizing the methodology for the following trend analyses at the local (Appendix III) and regional (Appendix IV) scales. By utilizing a similar context, the trend analysis with small-scale time series data (Appendix III) provided an important context for analyzing the repeated sampling data at the regional level (Appendix IV). Drawing on the findings of all contributions allowed for robust regional-scale evidence on long-term trends and drought effects in carabid communities.

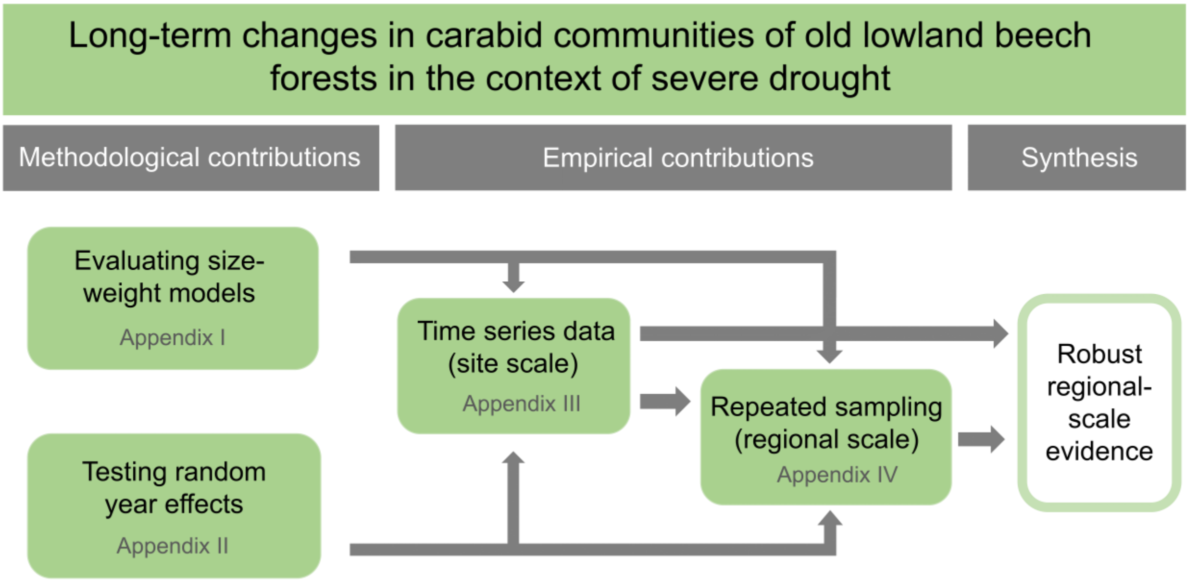

Figure 3. Conceptual framework of this dissertation with its individual contributions.

3. Key findings

The following section provides a summary of the key findings of each contribution. Detailed descriptions and figures of the respective findings are provided in Appendices I-IV.

3.1 How to estimate carabid biomass? - an evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement (Appendix I)

We evaluated two widely used size-weight models for carabid beetles. Moreover, we explored additional taxonomic parameters of different complexities. When using independent data from Schultz (1996) for validation, we found that the model of Szyszko (1983) was more accurate for larger carabid species, while the model of Booij et al. (1994) was more accurate for smaller carabid species. Adding additional taxonomic predictors gradually improved the prediction accuracy with increasing model complexity. Overall, the most complex model allowing for varying slopes of the size-weight relationship for different carabid subfamilies provided the most balanced and most accurate biomass predictions.

The data of Schultz (1996), which we used for validation, originated from a different region and habitat than those used by Szyszko (1983) and Booij et al. (1994) for training their respective models. Furthermore, it represented a more balanced distribution of carabid sizes, while Booij et al. (1994) featured smaller species, and Szyszko (1983) most likely featured larger species. Independent of region and habitat, the models of Szyszko (1983) and Booij et al. (1994) were most accurate for the size range that was represented in their respective training data. We therefore propose that the accuracy (and validity) of such size-weight equations is mostly governed by the size range of the carabid beetles represented in the training data. None of the existing models account for such imbalances in the training data. We assume that size-weight models with additional taxonomic parameters provide greater model flexibility and therefore perform best in accounting for imbalances and reflecting this size-specificity.

Although taxonomically more specific size-weight equations have proven promising, their applicability remains limited by the available data on carabid fresh weights, which can be used for training. We therefore recommend the combined use of the models of Szyszko (1983) and Booij et al. (1994) for carabids ≥ 11.8 mm and < 11.8 mm, respectively, as a practical interim solution. Consequently, we used this approach for calculating carabid biomass for both datasets (Appendices III and IV).

3.2 Random year intercepts in mixed models help to assess uncertainties in insect population trends (Appendix II)

We were interested in whether the addition of random year intercepts in GLMMs can help to better account for interannual fluctuations and year effects in insect time series, as proposed earlier by Daskalova et al. (2021). We tested the outcomes of including random year intercepts for analyzing abundance trends using a 24-year time series of carabid abundances while ensuring that carabid abundances were not temporally autocorrelated. We found that including random year intercepts had a significant effect on the estimated trend coefficients, independent of whether we also included additional environmental predictors. In our case, and in contrast to the findings of Daskalova et al. (2021), trends were estimated to be more negative when we included random year intercepts. In accordance with other studies, trend coefficient CIs became wider, and p values increased with the inclusion of random year intercepts. In the sensitivity analysis (iterative exclusion of individual years), the trend coefficients showed similar fluctuation patterns, regardless of whether random year intercepts, environmental predictors or both were included. P values, however, showed significantly different patterns between model structures. They were completely unaffected by the exclusions of individual years when random year intercepts were not included but showed strong fluctuations when they were. This effect was partly mitigated when both random year intercepts and environmental predictors were included. Both random year intercepts and environmental predictors individually increased the relative overlap of trend CIs in the sensitivity analysis and the respective full model. The best results were obtained when random year intercepts and environmental predictors were included simultaneously, leading to almost complete overlap of CIs.

We concluded that the inclusion of random year intercepts in GLMMs does not reduce the susceptibility of trend coefficients to year effects, which is a strong case for sensitivity tests in insect trend analyses (see Appendix III). Random year intercepts, however, increase the sensitivity of p values with regard to influential years, which can be helpful in sensitivity tests. Most importantly, random year intercepts in combination with additional environmental predictors lead to more reliable CIs that incorporate uncertainties due to fluctuations and year effects. These findings, together with the additional work of Knape (2016), convinced us to include random year intercepts in the GLMMs and GAMMs used for trend analyses in Appendices III and IV.

3.3. Long-term drought triggers severe declines in carabid beetles in a temperate forest (Appendix III)

We analyzed the continuous time series data from 1999 to 2022 using GLMMs and GAMMs to investigate trends in carabid abundance, biomass and taxonomic diversity. We examined the trends of the 27 most abundant species and how these trends were linked to a set of species traits. Finally, we were interested in how the investigated trends were related to a drought index (SPEI) by testing this relationship at different temporal scales and with potential delays via model selection.

We found significant negative linear trends in biomass, abundance and different standardized metrics of taxonomic diversity (except for standardized richness). We observed mean annual decline rates of -3.1% (0.95 CI [-5.3, -1]) in overall abundance and –4.9% (0.95 CI [-9.4, -1.6]) in biomass. The observed species turnover revealed a significant shift in species composition. Nonlinear trends of abundance and biomass showed fluctuations with (local) maxima in 2015 and 2016, which were followed by sudden steep declines until 2022 of -71% in abundance (0.95 CI [-84, -61]) and -89% in biomass (0.95 CI [-97, -59]). These patterns showed a strong correlation with the SPEI when calculated for the previous 72 months and with a delay of 2 years (Figure 4). When this particular SPEI was included as an additional predictor in the GLMMs for abundance and biomass, the predictions closely resembled the estimated nonlinear trends of the GAMMs. Taxonomic diversity metrics only partly showed nonlinear trends, and if so, these trends were less strongly related to drought conditions. Drought had a weak positive effect on standardized richness, while the effect on standardized evenness was negative. Turnover showed a nonlinear trend with accelerated shifts in recent years. However, as this metric was not standardized, this pattern was most likely a statistical artifact caused by declines in abundance.

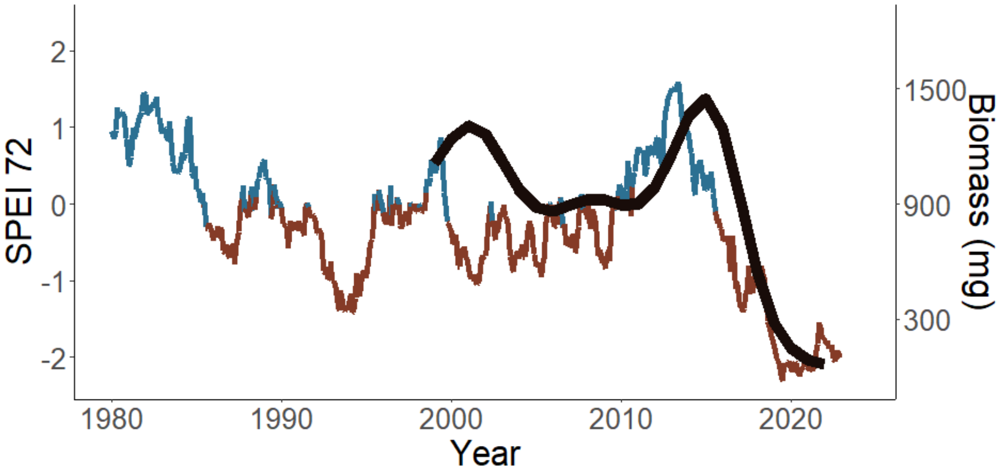

Figure 4 (modified figure from Appendix III)**.** Time series of the drought index (SPEI 72) with periods of dry conditions highlighted in red and wet conditions highlighted in blue and biomass prediction from the GAMM in black (separate scale, right side).

Of the 27 most abundant species, eight declined during the study period, while two species increased. Declines tended to affect the more locally abundant species. Furthermore, declining species were generally larger, predatory and either short-winged or dimorphic. In contrast, the two increasing species were relatively small and winged. Interestingly, the trends in species did not appear to be related to either humidity preference or the latitudinal center of distribution. Ten species responded negatively to drought conditions (with varying delays), while one increased with drought. The distribution of traits of drought-sensitive species were generally very similar to those of declining species.

3.4 Evidence for regional-scale declines in carabid beetles in old lowland beech forests following a period of severe drought (Appendix IV)

After finding a close relationship between long-term drought conditions and carabid abundance and biomass in Appendix III, we tested these findings at a larger spatial scale with the data from the eleven repeatedly sampled beech forest sites. Meteorological data revealed that temporal patterns of the SPEI were relatively consistent among different sites throughout the region and corresponded with those observed at the continuous sampling site (Figure 6 top). The SPEI indicated relatively wet conditions in 1998 and 1999, followed by moderate values (>-1) in 2000 and 2001. In contrast, the SPEI values were consistently low (<-1) after 2018/2019 throughout the region indicating unprecedentedly dry conditions. Based on the previous findings, we expected to see significant differences between the two periods regarding the carabid community.

We found significant changes from 1999-2001 to 2020-2022 of -51% (0.95 CI [-73%,-9%]) and -65% (0.95 CI [-81%,-36%]) across all sites. When estimating changes for individual sites, these changes were consistently negative (Figure 5). Changes in standardized taxonomic diversity metrics did not significantly change between the periods, while site-specific changes were highly variable. We found a significant decrease in the mean individual size (CWM) of -1.7 mm or -9.8% (0.95 CI [-18.2%,-0.7%]). The probability of sampling a winged individual increased slightly but significantly by 0.02. In contrast, there was no significant change in the probability of sampling a predatory individual. None of the traits showed significant changes when considered at the species-level (CM).

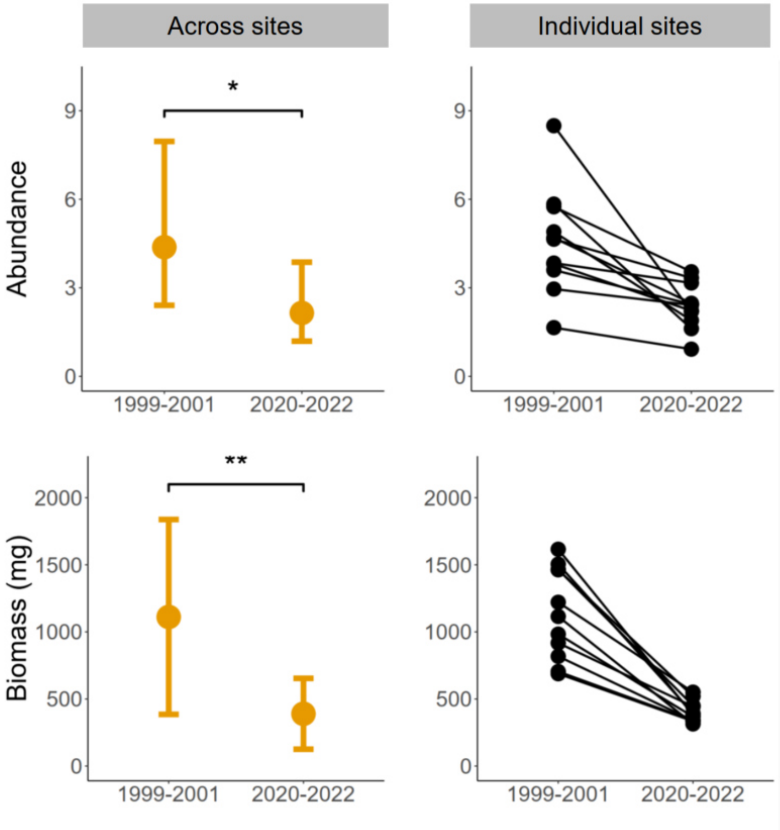

Figure 5 (unchanged figure from Appendix IV). Predictions for carabid abundance (top) and biomass (bottom). Estimates across all sites (left) and site specific estimates (right). Dots represent estimated means, errorbars (left plots) represent 0.95 confidence intervals. Significance codes: ** p=0.001-0.01, * p=0.01-0.05, n.s. p>0.05.

We explored possible associations of site-specific changes and site context and found the strongest association between local relative changes in biomass and landscape composition with greater declines ocurring at sites that had less forest (and wetlands) in their vicinity. This was supported by the bootstrapped p value and CIs (r=0.839, CI [0.601, 0.954], p=0.0011). Furthermore, declines in CWM size were greater toward the north, at protected sites and at sites that had a greater initial CWM size in 1999-2001. The latter also showed stronger declines in biomass. We found no significant differences in abundance or biomass changes between the extensively managed and the protected sites. Protected old-growth forest sites were among those with the greatest relative declines in biomass, including the two UNESCO World Heritage sites, with biomass declines of -72% and -55%, respectively.

4. Synthesis

The following section reviews and discusses the findings of this dissertation. It briefly addresses the two methodological contributions and explains how they have facilitated the following work. It extensively discusses further findings with regard to the initial research questions and relevant scientific work of others. While there are a large number of valuable long-term studies of carabid populations, we mostly relate our work to studies from forests in Europe. Finally, this section expands on the aspect of uncertainty and the different implications of our findings.

4.1 Methodological groundwork

The first two contributions (Appendices I and II) served as crucial methodological groundwork for our further analyses but also provide valuable insights for future research on insect trends and applied environmental monitoring.

Biomass proved to be a key metric when we investigated trends and drought effects in the carabid community. Previously, we evaluated and expanded size-weight equations for carabid beetles, which allowed us to calculate the biomass of carabid samples more accurately (Appendix I). While life sampling and direct weighing provide the most accurate biomass measurements, this method is often not feasible (see Knapp, 2012). Weighing samples from common (kill) traps will most likely lead to biased results (ibid.). Generally, size-weight equations provide a simple and quick method for calculating carabid biomass that facilitates the use of carabid biomass as an additional metric. The sizes of sampled individuals can be measured (representatively) to increase accuracy. If samples are no longer available, as in the case of digital-only data, they can be obtained from the literature or from trait databases. Our findings and recommendations will help to calculate carabid biomass more accurately in future research or insect monitoring. We would like to encourage trait databases to also include species (mean) biomass under the condition that the method of calculation or source is made transparent. The ultimate goal should be the development of a global size-weight model based on taxonomically complete data for carabids. With the advent of AI-assisted camera traps for insects, size-weight models hold a great potential for future insect monitoring (van Klink et al., 2022).

Furthermore, we thoroughly tested random year intercepts as a method to account for insect fluctuations and year effects in GLMMs using our own data, which enabled us to assess uncertainties in estimated trends more reliably (Appendix II). To date, only a few studies have used temporally explicit random effects for insect trend analyses so far. If applied more consistently, this approach could help to bring more emphasis to trend uncertainties, which receive relatively little attention in the discourse to date (Boyd et al., 2022; Daskalova et al., 2021; Simmonds et al., 2022). Additionally, this would increase the reliability of uncertainty measures and enhance the scientific debate on declining insect populations.

4.2 Research questions

Which were the general trends (abundance, taxonomic diversity, functional composition) in carabid communities of old lowland beech forests in northeast ern Germany over the past 24 years?

The Eberswalde time series data (Appendix III) indicated significant linear declines in the abundance and biomass of carabid beetles of -3.1% and -4.9% (annual means), respectively. GAMMs revealed that abundance and biomass fluctuated at a relatively high level and only sharply declined in recent years. The regional data (Appendix IV) support these declines at a larger scale and correspond with the local GAMM predictions (Figure 6, bottom). The overall declines in abundance and biomass are not only notable in the predicted means. For carabid beetles, it can generally be expected that samples exhibit considerable fluctuations between years as well as great dispersion within the same year (Irmler, 2007; Kotze & Niemelä, 2002). This is illustrated by wide confidence intervals for abundance and biomass up to approximately 2018 in the GAMMs (Appendix III and Figure 6 bottom). After that, not only do the estimated means decline, but the confidence intervals also become much narrower. This is the case in both analyses, providing further consistent evidence for declines. We observed significant declines in different metrics for taxonomic diversity at the Eberswalde site. At the regional scale, however, changes in taxonomic diversity were not consistent and assumingly reflected local ecological processes. Moreover, the results from both analyses agree that larger and less mobile (i.e., short-winged or dimorphic) species decline disproportionally. Overall, stronger declines in biomass than in abundance, which were observed for both datasets, support this finding. At the regional scale, this trend shows some variability, which could be caused by initial differences in species relative abundance.

Our results roughly correspond with annual declines in carabid abundance of -4.3% found by Hallmann et al. 2020 in a partly forested landscape in the Netherlands. Conversely, Brooks et al. (2012) reported increasing abundances at forest sites in the UK. Our findings also contrast those of Homburg et al. (2019) from a German forest site, who found no declines in abundance or in biomass but in (rarified) species richness and particularly in smaller, more mobile species. However, a large-scale study by Staab et al. (2023), which investigated trends in flying forest insects, partly in the same region, revealed corresponding trends in species traits. This heterogeneity in findings does not come surprising - even for similar habitats and the same group of insects - as the different studies vary in time series length and use different baseline years (Bahlai et al., 2021; Duchenne et al., 2022). None of these studies analyzed data recorded after 2017, the period in which we found the greatest declines. Most of the abovementioned studies were conducted at relatively small spatial scales, each in a slightly different context. It is known that diversity trends in carabid communities can vary locally and do not always reflect large-scale processes (Valdez et al., 2023; Zajicek et al., 2021). This is also illustrated by our findings regarding taxonomic diversity. In this context, it is all the more important to emphasize that we found consistent declines in abundance, biomass and certain traits at the regional scale. Standardized long-term studies of carabid beetles at this spatial scale are rare (Evans et al., 2022; Zajicek et al., 2021), and to our knowledge, ours is the only such example for forest carabids in Europe.

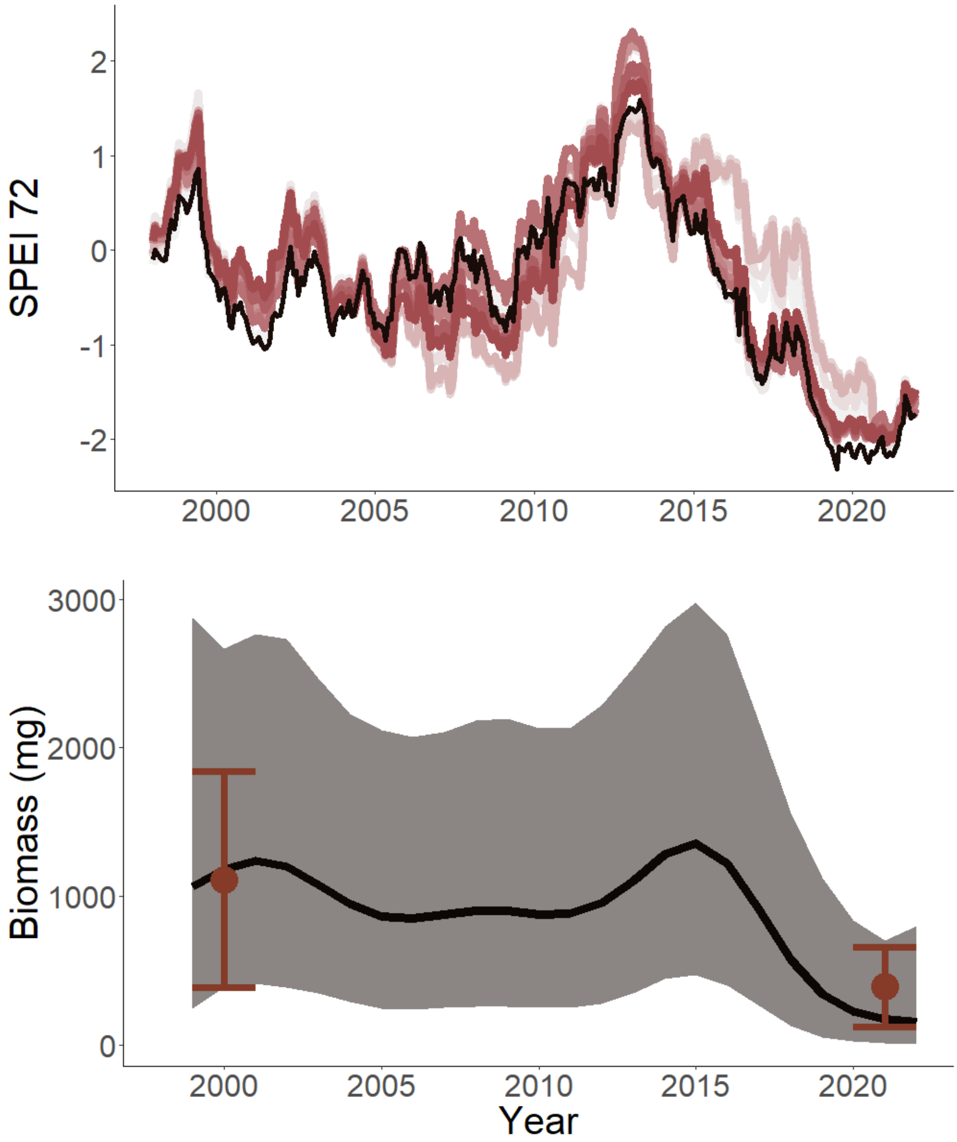

Figure 6. Top: Time series of the drought index (SPEI 72) for the site of continuous sampling (black) and the eleven sites of repeated sampling (reds). **Bottom:** Biomass predictions from the GAMM for the continuous data (black, 0.95 CIs in grey) and the GLMM for the repeated sampling data (red, 0.95 CIs as error bars).

How do these trends relate to drought conditions, particularly during recent periods of severe drought?

We found strong evidence for negative effects of drought on carabid abundance, biomass and the relative abundance of larger, less mobile species. Drought (i.e., SPEI) had the strongest effect when it considered the CWB of the previous six years and affected carabid beetles with a delay of up to two years. Correspondingly, we observed similar changes (in comparison to the reference period) at the regional scale when we resampled carabids two years after the onset of a longer drought period. Metrics for taxonomic diversity showed no or weaker correlations with drought conditions. On the regional scale, changes in (standardized) taxonomic diversity were not consistent, despite consistent drought conditions, indicating no systematic drought effects.

Weather anomalies as potential drivers of carabid trends have been the subject of previous studies. While Hallmann et al. (2020) did not find annual precipitation and temperature to be meaningful predictors for carabid beetles in open land, Skarbek et al. (2021) and Zajicek et al. (2021) found significant effects of annual precipitation on species composition. Evans et al. (2022) investigated trends of carabid beetles in Japanese forests and reported that a general increase in precipitation and temperature led to increased species richness, abundance and biomass in deciduous broadleaved forests. In this research, we included short-term precipitation and temperature anomalies as predictors, mostly to account for short-term weather-induced effects on sampling efficiency (Saska et al., 2013). In contrast to the abovementioned studies, we specifically focused on drought (the interplay of temperature and precipitation) as a potential driver and considered its effects on a larger temporal scale.

In line with our findings, two observational studies from European forests by Šiška et al. (2020) and Šustek et al. (2017) reported that drought (also represented by the SPEI) negatively affected the abundance of forest carabid beetles. Additionally, both studies also highlighted a 1- to 2-year delay in carabid responses to drought conditions. Two experimental studies by Jouveau et al. (2022) and Williams et al. (2014) also supported drought-induced abundance declines. These studies also reported – together with Šustek et al. (2017) – declines in species richness in response to (simulated) droughts. The different responses of species richness compared to our findings may be due to different reasons. On the one hand, none of the abovementioned studies standardized species richness, and the respective declines might be artifacts of simultaneous declines in abundance (Chao et al., 2014). On the other hand, the carabid communities of the old European beech forests typically feature relatively few species with relatively high abundances (Müller-Motzfeld, 2001). Therefore, diversity metrics might be more robust to changes in the communities in our case. Although the effect of drought on the relative abundance of carabid traits has not been directly tested thus far, our findings resonate with those of other studies. Distributional studies of carabid traits highlight that large, flightless species are usually associated with relatively stable habitats (Homburg et al., 2013; Nolte et al., 2017). Conversely, these species typically decrease with disturbance, which generally favors small generalist species with good dispersal abilities (Rainio & Niemelä, 2003). Generally, large, flightless carabid species are expected to experience relative declines due to climate change in the future (Brandmayr & Pizzolotto, 2016; Qiu et al., 2023), which is in line with our findings with regard to the predicted increase in the intensity and frequency of droughts (Carretta et al., 2022).

In open landscapes, the effects of precipitation (or a lack thereof) on the carabid community seem to be more immediate (Skarbek et al., 2021; Zajicek et al., 2021). Our findings and those of other studies suggest that drought effects act on a larger temporal scale in forests (Šiška et al., 2020; Šustek et al., 2017). Structurally rich, old deciduous forests are often attributed with a high capacity for buffering extreme events such as heat and drought (Frey et al., 2016). This might explain why drought had the most apparent effects when we considered it for a relatively long period (i.e., 72-month SPEI). Multiyear drought events such as this from 2018 on "… could push [beech trees] beyond their hydraulic safety margins" (direct citation, Rukh et al., 2023), affecting tree vitality and ultimately reducing canopy cover as well as transpiration. We assume that this in turn triggers positive feedback loops of reduced humidity and increasing temperatures (Allen et al., 2015; Buras et al., 2020). Consequently, longer water deficiency leads to increased exposure to extreme conditions even in forests with greater microclimatic buffering capacities.

Based on our findings, it remains difficult to precisely attribute drought-induced declines and changes to single ecological processes. Reduced soil moisture might have direct effects and lead to desiccation of carabids, especially larvae, which are most sensitive to microclimatic conditions (Magura et al., 2021). Different types of life cycles can explain delayed effects of up to two years (Irmler, 2007; Matalin, 2007). Such delays could, however, also be caused by drought affecting organisms at lower trophic levels, leading to a lower prey abundance for mostly predatory carabid beetles in the following season(s) (Irmler, 2007; Šiška et al., 2020; Šustek et al., 2017). Another factor could be potential top-down processes, for example, the increased foraging of vertebrate predators in the relatively softer soils of deciduous forests during drought (Baubet et al., 2003).

Does the local context, for instance the protection status, mediate trends and potential drought effects?

When we explored site-specific changes in carabid communities (Appendix IV), we found associations with several of the tested site variables (Table 2). Most strikingly, sites with less forest (incl. waterbodies and wetlands) in their vicinity showed stronger declines in biomass. Gohr et al. (2021) showed that these types of land cover significantly offset temperature extremes. Mann et al. (2023) found that this offset was smaller in fragmented forest areas, most likely due to edge effects. We assume, that in our study the sites with less surrounding forest area also represented more fragmented forest areas or areas along the edges of larger forest areas. Stronger edge effects probably led to greater exposure to extreme conditions and, in turn, to greater declines in carabid biomass. It is important to note that the amount of forest cover was independent of all other site variables that showed any association with trends.

Moreover, stronger declines in biomass as well as in CWM size were also associated with a greater initial CWM size of carabid beetles. This corresponds with relatively stronger declines in larger species found in this research and predicted by other studies (Brandmayr & Pizzolotto, 2016; Nolte et al., 2019; Qiu et al., 2023) and highlights that community responses to disturbances such as drought may vary with the respective community’s trait composition (Kotiaho et al., 2005). Protected forest sites did not show any significant difference in abundance or biomass trends from those of managed sites, but stronger declines in CWM size. This association may hint at more sensitive carabid communities with forest specialists at these sites but could also be confounded by the spatial distribution of protected sites, as latitude was associated with both protection status and declines in CWM size.

4.3 Critical reflection on the confidence of results and model uncertainties

To some extent, uncertainty and limited confidence are unavoidable in insect trend analysis. Important aspects in this regard are time-series length (Cusser et al., 2021), biased baselines (Bahlai et al., 2021; Duchenne et al., 2022) or the local context (Duchenne et al., 2022). When analyzing the local time series data (Appendix III), we used rigorous sensitivity tests to validate our results against the potential effects of single years and plots. Statistical models with appropriate random effect structures provided reliable confidence intervals (Appendix II). Additionally, modeling nonlinear trends provided additional insights and safeguarded against overconfidence in linear estimates. A second independent dataset consistently supported these declines at a larger scale (Appendix IV). Nevertheless, the estimated decline rates for both datasets were accompanied by relatively broad CIs and should be understood as a general order of magnitude for declines rather than an exact rate. However, the trend estimates for biomass and abundance showed consistently negative confidence intervals in all analyses, which should generally be taken as clear evidence of a decline. As the local time series consisted of data that were collected mainly from May to July, it seemed possible that changes were caused by phenological shifts (Irmler, 2022; Pozsgai & Littlewood, 2014). The repeated sampling data, however, were collected throughout the whole period of the main carabid activity (April-November). As the results from both datasets showed consistent patterns, we consider phenological shifts to be unlikely confounding factors.

Moreover, there is reason to assume that estimated declines in biomass are conservative estimates. This is especially relevant considering the observed link between declines and drought conditions. The sizes of adult carabid beetles strongly depend on conditions during larval development (Huk & Kühne, 1999; Magura et al., 2021; Tseng et al., 2018). Extreme conditions such as drought and heat might not only lead to direct desiccation but also reduce the size of adult beetles. In this study, however, we used size-weight equations to calculate biomass based on average beetle sizes from the literature. We argue that unfavorable environmental conditions after 2018 most likely led to smaller adult beetles, which we did not account for, probably leading to stronger declines in biomass than we described.

It is important to note that our analysis of site variables that might affect local trends was *post hoc* (Appendix IV). Due to the original context (Winter, 2005), the study sites were not specifically distributed or stratified to investigate these variables. Moreover, the variables were coarsely aggregated and the number of independent samples (n=11) was relatively low. Therefore, the findings might lack empirical robustness and allow only limited causal inference. The heterogeneity of site-specific trends might not only be caused by mediated drought effects, but could also potentially result from varying background trends independent of droughts. However, we are convinced that the striking results regarding the landscape context (i.e., forest area in the surrounding area) are especially relevant findings. In the context of other research (Gohr et al., 2021; Mann et al., 2023), these findings provide valuable information for further research and important management implications.

4.4 Implications and outlook

Old beech forests constitute an essential component of natural biodiversity in Europe (Brunet et al., 2010; Springer et al., 2024). Germany bears a great responsibility for their protection and conservation due to the current distribution of these forests (P. Meyer et al., 2023; Springer et al., 2024; Winter, 2005). This dissertation revealed significant declines in the overall abundance, biomass and relative abundance of certain traits in the carabid beetle community of these forests in northeastern Germany over the last 24 years. Worryingly, these declines also affected old-growth beech forests of high conservation interest, such as UNESCO World Heritage Sites, which are situated in the core zones of a national park and a UNESCO Biosphere Reserve. Due to the pivotal role of carabid beetles in the food webs of the forest floor, we assume that their decline indicates and/or results in further changes throughout the ecosystem.

A predominant portion of these declines was found to be related to recent periods of severe drought starting in 2018. Previous studies have indicated that beech forests are already under pressure due to climate change (Dulamsuren et al., 2017; Martinez del Castillo et al., 2022) and have been severely impacted by recent droughts (B. F. Meyer et al., 2020; Rukh et al., 2023; Weigel et al., 2023). Our findings represent the first evidence that this was also the case for insects. On the one hand, insect populations are known to recover from disturbances such as drought (Ewald et al., 2015). On the other hand, extreme weather events such as droughts are expected to increase in severity and frequency in the course of climate change (Carretta et al., 2022). In particular, the recent drought periods have been described as unprecedented and have been attributed to climate change (Hari et al., 2020; Schumacher et al., 2022, 2023). Therefore, the resulting declines in the carabid community might also be unprecedented. Although precisely forecasting trends in insect populations in this context is extremely difficult (Bahlai, 2023), we assume that climate change will result in recurring periods of declines and changes in the carabid communities of beech forests. At the ecosystem level, this might lead to modifications in food webs.

We found that it was not the local protection status but the landscape structure that was associated with the severity of biomass declines. This indicates the potential limitations of strict local protection under climate change (R. Warren et al., 2018). Future conservation efforts and strategies should more often consider the greater spatial context and exposure to climate change effects into account to protect (insect) biodiversity effectively.

Although we present strong evidence for drought effects on forest carabid communities, the underlying processes and mechanisms remain largely unclear. Currently, we still lack a spatially and temporally detailed understanding of how extreme weather events affect microclimatic conditions in different forest ecosystems (De Frenne et al., 2021). Moreover, relatively little is known about how relationships and interdependencies in food webs are affected by changes in microclimate, especially in soils. Gaining such insights will be of paramount importance for predicting climate change impacts on biodiversity and adapting conservation planning.

5. Conclusions

This dissertation investigated temporal trends in carabid communities in old lowland beech forests and tested drought as a potential driver. We found that

a) carabid abundance and biomass consistently declined throughout the study region, which especially affected larger species with lower dispersal abilities, while the trends in taxonomic diversity varied.

b) the declines occurred mainly in recent years and were related to long-term drought conditions.

c) the declines were independent of the local conservation status, and the decline in biomass was strongly linked to the local landscape composition.

These findings are worrying because they highlight the decline of a pivotal insect family in forests that play a crucial role in conserving natural biodiversity. Furthermore, they support recent studies pointing to weather anomalies and climate change as major drivers of insect populations and point to possible future declines and changes. Future conservation planning needs to recognize the limitations of local conservation and the importance of spatial context in mitigating the effects of climate change on (insect) biodiversity. This requires further research on the fine-scale dynamics and underlying ecological processes of extreme weather impacts on forest insects.

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Appendix I

Title	How to estimate carabid biomass?—an evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement
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Data	Data available in cited literature
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ORIGINAL PAPER

How to estimate carabid biomass?—an evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement

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Abstract

Biomass is an important metric for monitoring carabid populations and serves as an ecological indicator. Models that predict carabid weight based on body size represent a simple and straightforward method to estimate biomass and are therefore commonly used. However, such models are rarely evaluated against independent validation data. In this study, we evaluated the two widely used size-weight models by Szyszko (1983) and Booij et al. (1994) drawing on previously published independent data. Additionally, we developed and tested four new models to also evaluate the potential effect of taxonomic parameters; and compared model predictions with actual measurements of biomass using relative deviation graphs and observed versus predicted from regression. We show that the two models by Szyszko (1983) and Booij et al. (1994) contain systematic bias towards larger and smaller carabids, respectively, suggesting restricted applicability of such models. Additional taxonomic parameters improved weight predictions, indicating one possible solution to the issue of restricted applicability. We discuss further relevant limitations of size-weight models and their application and recommend a combined use of the models of Szyszko (1983) and Booij et al. (1994) for carabids ≥ 11.8 mm and < 11.8 mm, respectively.

Implications for insect conservation: Size-weight models are a suitable and simple method to estimate the biomass of carabids and have great potential to be used in monitoring schemes, the investigation of long-term trends and ecological studies. It is, however, essential that researchers pay special attention to potential restrictions in their applicability and methodological limitations.

Keywords Insect monitoring · Size weight equation · Insect biomass · Insect decline · Ecological modelling · Model validation

Introduction

Since the first reports on a global decline in the insect population started to emerge, insect biomass has become an increasingly studied and discussed subject. At first glance, abundance or diversity seem to be the more obvious ways of describing an insect population or community. However, insect biomass might be of similar or even greater importance when it comes to reflecting insects as components of the ecosystem. It reflects the role of insects as trophic component in food webs (Yang and Gratton, 2014; Shaftel et al., 2021), while a study by Barnes et al. (2016) observed that invertebrate biomass can predict ecosystem functioning on larger spatial scales. Insect biomass has been also proposed as an indicator of insect diversity (Hallmann et al., 2021a, b), yet evidence exists highlighting the contrasting patterns in this regard (Homburg et al., 2019; Uhler et al., 2021; Vereecken et al., 2021). When studying insect populations,

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investigating biomass can consequently yield additional insights and lead to very different results and interpretations (Saint-Germain et al., 2007). In the context of the reported global decline of insects, measuring the biomass of insects becomes increasingly relevant. Numerous studies have already reported declines in this regard (e.g. Hallmann et al., 2017; Harris et al., 2019; Seibold et al., 2019), Researchers use a variety of methods: Some studies use fixed protocols to weigh their insect catches manually (Sorg et al., 2013; Hallmann et al., 2017), while others employed size-weight models for the estimation of biomass (Seibold et al., 2019; Hallmann et al., 2020). Predictive models, which are based on the correlation of the body length of an insect and its weight, were developed as early as 1976 (Rogers et al., 1976), but since then there have been various additions, improvements and taxon-specific approaches (e.g. Sample et al., 1993; Sabo et al., 2002; García-Barros, 2015).

Studying biomass has a longer tradition in carabid research (Grüm, 1975; Thiele, 1977; Szyszko, 1983), but recently it has been used increasingly as a tool to monitor long-term population trends. It therefore plays a key role in the investigation of population declines, which have also been reported for ground beetles (Brooks et al., 2012; Hallmann et al., 2020; Liu et al., 2022). Hence, measuring carabid biomass has been included in the recently developed framework for nationwide insect monitoring by the German Federal Agency for Nature Conservation (Federal Agency for Nature Conservation Germany, 2021). Furthermore, carabid biomass has proven to be a valuable indicator of forest naturalness (Winter, 2005; Schreiner, 2011) or habitat succession (Schwerk, 2014), often used in connection with the concept of mean individual biomass (MIB; Schwerk and Szyszko, 2007, 2011).

Table 1 Overview of existing carabid-specific size-weight models (in the order of their publication), their region of origin, the type of modelled weight and examples of use in carabid research

Model/Author(s)	Region	Type of weight	Examples of use
Szyszko (1983)	Poland	fresh	Cárdenas and Hidalgo (2007) Šerić Jelaska et al. (2011) Gobbi (2014) Schreiner (2015) Jambrošić Vladić and Šerić Jelaska (2020)
Jarosik (1989)	Czech Republic	fresh	Saint-Germain et al. (2007)
Booij et al. (1994)	Netherlands	fresh	Homburg et al. (2019) Hülsmann et al. (2019)
Sabo et al. (2002)	California	dry	Hallmann et al. (2020) Skarbek et al. (2021)
Gruner (2003)	Hawaii	dry	

As with insects in general, there exists a variety of methods to determine carabid biomass. Most commonly, ground beetles are sampled with pitfall traps (Barber, 1931), into which individuals fall and are then killed and preserved by a trapping fluid until the trap is collected. Some studies weigh the whole catch or single beetles after letting them drain on a sieve or filtering paper (e.g. Cvetkovska-Gjorgjievska et al., 2017), or they determine dry weights (e.g. de los Santos Gómez, 2013). However, methodological research shows that these methods tend to introduce a certain bias. A study by Knapp (2012), for example, found that different trapping fluids, such as ethylene glycol or propylene glycol or Bryne (saturated sodium chloride solution), and storage fluids, such as ethyl acetate, propylene glycol or ethanol, can change the drained weights and/or dry weights of carabids to a varying extent. Only formaldehyde, which is unfortunately highly toxic, not only to carabids, but also to other animals and humans (Teichmann, 1994), seemed to produce reliable results for both drained and dry weights (but see Wetzel et al., 2005). Moreover, research by Braun et al. (2009) showed that the retention time of carabids in trapping and storage fluids can alter the measured drained and dry weights and even differences in the chemical grades of trapping fluids can affect weights (Braun et al., 2012). Thoroughly cleaning the carabids of adherent dirt or other particles before weighing represents an additional challenge. Few studies use additional non-fatal pitfall traps or hand-collecting to sample live beetles for the determination of actual fresh weight (Knapp, 2012; Heitmann et al., 2021; Yarwood et al., 2021). However, this procedure is very labour-intensive and therefore is often not feasible. Another problem in this regard relates to historic or archived data, in that original beetles often no longer exist and therefore cannot be weighed if biomass needs to be compared with this of more recent data.

The application of size-weight models is one solution to this problem. The abovementioned model by Rogers (1976) has also been used for carabids (Woodcock et al., 2010), but several carabid-specific size-weight models are also regularly used in carabid research (Table 1). There has been some discussion on whether they are restricted in their applicability to certain regions, habitats or taxa (Sabo et al., 2002; Gruner, 2003; de los Santos Gómez, 2013). Despite this they are often used outside their region or habitat of origin (e.g. Cárdenas and Hidalgo, 2007; Hülsmann et al., 2019; Hallmann et al., 2020). Sabo et al. (2002) observed that the accuracy of size-weight models improves with increasing taxonomic specificity. Nevertheless, to date, no taxonomically informed size-weight model for carabids has been proposed. Moreover, none of these models has ever been validated using either original data (e.g. with cross-validation) or independent data. An evaluation of size-weight models for carabids with independent data would provide important insights in how accurate these models predict carabid weights and shed light on possible restrictions in applicability.

In this study, we evaluate the two commonly used models devised by Szyszko (1983) and Booij et al. (1994) (in the following referred to as $m_{Szyszko}$ and m_{Booij}), as well as four newly developed models, three of which feature taxonomic parameters. This is achieved by using two previously published datasets of measured carabid fresh weights, one of which was used to train our own model candidates and the other one to validate $m_{Szyszko}$, m_{Booij} and our own models. To our knowledge, this is the first time size-weight models for carabids have been validated against independent data.

Materials and methods

Data

We compiled the data for this study from material published by two other studies. Booij et al. (1994) caught ground beetles in May and June of 1987 at "various locations" in the Netherlands. Schultz's (1996) data originated from different habitats (pastures, carrs, red beds, salt marshes, open soil) near the German coast (Baltic Sea) and were collected over a non-specified period in 1995. Both studies caught live ground beetles by hand. Booij et al. (1994) additionally used dry pitfall traps, which were emptied daily. In both cases, the weights represent the mean fresh weights of a varying number of measured carabids of respective species. While Booij et al. (1994) also provided mean size measures for all collected species, Schultz (1996) only stated size classes. Therefore, we supplemented size values for the Schultz (1996) data, according to Müller-Motzfeld (2004), by taking the mid-point of the stated size range for each species. If this information was not available in Müller-Motzfeld (2004), we obtained it from Homburg et al. (2014). In all cases, body length represents the distance of the most forward tip of the mandibles and the rear tip of the elytra (hereinafter simply referred to as "size"). It is important to note that because these weight-size data pairs consist of mean values of a varying number of measurements, they do not represent true data pairs. This adds some level of imprecision to the data, as one may expect a non-linear relationship between size and weight - not only between species (Fig. 1a), but also among differently sized individuals of the same species (but see *Poecilus cupreus*, Booij et al., 1994). Where we complemented sizes from Müller-Motzfeld (2004), this imprecision is likely to be even greater, since midpoints do not necessarily resemble the mean size of the populations actually sampled by Schultz (1996). On the other hand, this aggregation of the data omits the issue of the unequal representation of different species potentially introducing bias into the fitted models. After all, this choice of data is a trade-off. Collecting live ground beetles and recording their fresh weight is extremely work-intensive, which would not have been feasible in our case. Despite the described imprecision, we believe that the data used herein illustrate the general size-weight relationship in carabids and contain valuable information that can be used to develop and evaluate size-weight models.

We used the dataset of Booij et al. (1994), which was originally also used to fit their model, to also fit our own model candidates. The dataset of Schultz (1996) represents truly independent data for all of the six tested models and therefore served as a validation dataset. In order that both datasets featured the same subfamilies with at least two

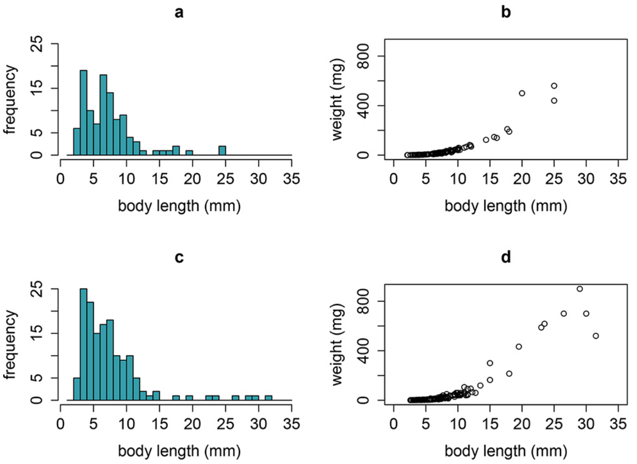

Fig. 2 Size histograms and fresh weights plotted against size for the dataset of Booij et al. (1994) (a, b) andthe dataset of Schultz (1996) (c, d)

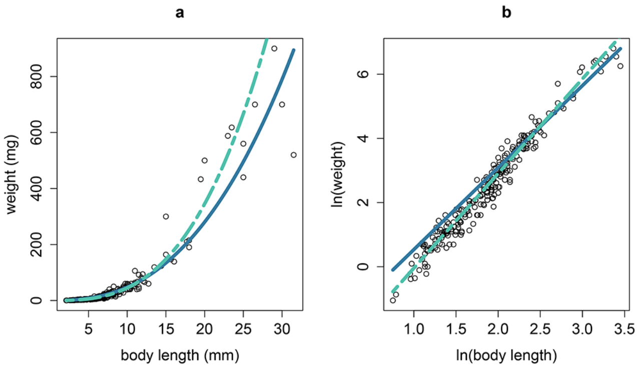

Fig. 1 Fresh weights (y-axis) of different carabid species from both datasets (training and validation) plotted against the respective size (body length)(x-axis) on the original scale (a) and log-transformed (b); added lines display predicted weights calculated with the models of Booij et al. (1994) (dashed) and Szyszko (1983) (solid) on both scales

representing species, we removed three species from the training dataset and five from the validation dataset (Table S1, Supplementary Material). This was done in order to fit and validate model terms with taxonomic predictors. Finally, training and validation data consisted of 107 and 149 species, respectively, belonging to six different subfamilies: Carabinae (n = 4/8), Elaphrinae (n = 2/4), Harpalinae (n = 57/90), Nebriinae (n = 8/8), Scaritinae (n = 6/10) and Trechinae (n = 30/29). In both datasets, smaller carabid species were considerably overrepresented. Histograms and graphs illustrating both datasets can be found in Fig. 2.

Development of taxonomical models

We used the R-statistical language and environment version 4.1.2 (R Core Development Team, 2021) for the development of statistical models and the analyses.

Following the approach of other size-weight models (e.g. Rogers et al., 1976; Sample et al., 1993; Gruner, 2003), we developed power functions by transforming size and weight values, using the natural logarithm and fitting a linear regression model. Overall, we fitted four different models, three of which were fitted using linear models ('lm' function from the 'stats' package, R Core Development Team 2021): the base model without any taxonomic parameters (in the following referred to as $\mathrm{m}_{\mathrm{base}}$), a model with an added effect for the subfamily (in the following referred to as $\mathrm{m}_{\mathrm{fixed}}$) and a model with an interaction term for the subfamily (in the following referred to as $\mathrm{m}_{\mathrm{inter}}$) (Eq. 1).

$$\ln\left(weight\left[mg\right]\right)=a+x+b*z*\ln\left(bodylength\left[mm\right]\right)\ (1)$$

where a represents the intercept with the y-axis and b the effect of size (slope), x represents the added effect of the subfamily and z represents the interaction coefficient of the subfamily. The simple added effect ($\mathrm{m}_{\mathrm{fixed}}$) allows the y-intercept of the size-weight relationship to shift upwards or downwards for the respective subfamily, without changing the slope of the general relationship. The interaction term ($\mathrm{m}_{\mathrm{inter}}$) also allows for changed regression slopes for the subfamilies. We assume that the different taxonomic groups in carabids (here subfamilies) have certain shape characteristics, that result in modifications to the general size-weight relationship. Accounting for these characteristics by including taxonomic effects and interactions in the model could therefore increase the accuracy of weight estimates. Our base model $\mathrm{m}_{\mathrm{base}}$ is very similar to the approach taken by Booij et al. (1994) and is fitted with almost the same dataset. However, validation results can be expected to differ slightly, as we removed three species from the original dataset (see previous section) and use $\mathrm{m}_{\mathrm{Booij}}$ with the rounded coefficients as provided by its original source (Booij et al. 1994). $\mathrm{M}_{\mathrm{base}}$ therefore serves as a reference model for the other model candidates. As a fourth model, we fitted a linear mixed-effect model ('lmer' function from the 'lme4' package, Bates et al., 2021) with a random effect for the subfamily (in the following referred to as $\mathrm{m}_{\mathrm{mixed}}$). This model accounts for taxonomic effects in the data but allows for estimating the size-weight relationship on the population level. It also considers the unequal representation of the different subfamilies in the data and makes it possible to predict at a later stage the weights of carabids belonging to subfamilies that were not represented in our training data. We checked model assumptions for all models performing post-hoc model diagnostics using the 'DHARMa' package (Hartig, 2021). Diagnostic qq-plots are provided in the Supplementary Material (Fig. S5-S8, Supplementary Material).

Model evaluation

To evaluate the two size-weight models $\mathrm{m}_{\mathrm{Booij}}$ and $\mathrm{m}_{\mathrm{Szyszko}}$, as well as our model candidates ($\mathrm{m}_{\mathrm{base}}$, $\mathrm{m}_{\mathrm{fixed}}$, $\mathrm{m}_{\mathrm{mixed}}$, $\mathrm{m}_{\mathrm{inter}}$), we calculated fresh weights for all species in the validation dataset, using the equations as originally stated by the authors (Eqs. 2 and 3) or by predicting with the estimated model coefficients from the models previously fitted to the training dataset. Predictions with $\mathrm{m}_{\mathrm{mixed}}$ were made based on the population level, not applying the random effect.

$$\boldsymbol{m_{Szyszko}}:\ln\left(weight[\,g\,]\right)=-8.92804283+2.5554921*\ln\left(size[\,mm\,]\right)\ (\mathrm{Szyszko},1983)\ (2)$$

$$\boldsymbol{m_{Booij}}:\log\left(weight\left[mg\right]\right)=-1.3+2.95*\log\left(size\left[mm\right]\right)\ (\mathrm{Booijetal.},1994)\ (3)$$

We could have refitted $\mathrm{m}_{\mathrm{Booij}}$ with its original dataset to acquire the unrounded coefficients (Booij et al. (1994) present their model with rounded coefficients, see Eq. 3). However, we decided to use the rounded coefficients as this is how potential users will most likely apply the model.

To evaluate each model's predictions we visualised predicted weights in deviation graphs similar to those proposed by Mitchell (1997). Here, we calculated the deviation of each predicted weight from the respective observed weight. To remove the scale effect of size, we then converted absolute deviation to relative deviation by expressing it as a percentage of the observed weight. The relative deviation of each size-weight model was then plotted against size. Although these relative deviation graphs do not provide any statistic validation, they allow detailed examination of the models' predictions.

In a next step, we regressed observed vs. predicted weights (OP-regression), following the approach presented by Piñeiro et al. (2008). We fitted a linear model ('lm' function from the 'stats' package, R Core Development Team 2021) in which predicted weights were used to predict the respective observed weights. We added an interaction term for the predicting size-weight model, also adding a reference category in which the "predicted" equalled the observed weights. This was done to check which of the six tested models showed significant differences in intercept and slope in relation to the reference. A significantly altered intercept without a significant change in slope identifies a general over- or under-prediction of the respective size-weight model, while a significantly changed slope (potentially accompanied by a significantly changed intercept) indicates a varying over- or under-prediction along the gradient of weight. Additionally, we calculated the coefficient of determination (R^2) of observed vs. predicted weights, which indicates how much of the linear variation in the observed weights is explained by the variation in the predicted weights (Piñeiro et al., 2008). In this case, R^2 was calculated (sensu Nagelkerke, 1991) by fitting separate linear models with observed vs. predicted weights for each size-weight model. When the OP-regression is fitted with untransformed data (actual weights in milligram), the predicted weights of the few large carabid species will introduce most of the variance and have increased leverage. Model estimates and R^2 values will therefore be mainly driven by these larger species. On the other hand, when the OP-regression is fitted with log-transformed data (as it is used to fit the size-weight equations), the weight and size scales are distorted in favour of the smaller species. In this case, they have an over-proportionate effect on model estimates and R^2 values. To solve this issue, we fitted two OP-regression models with both log-transformed and untransformed data, and used both to draw conclusions about the six models' predictions.

Results

Ln(size) had a significant positive effect on ln(weight) in all four models fitted to the training data. In m_{fixed}, three subfamilies (Nebriinae, Scaritinae and Trechinae) had a significantly changed intercept compared to the reference subfamily (Harpalinae). M_{inter} featured no significant effects except that of ln(size). We provide the full model summaries in Table 2 and plotted prediction curves in the Supplementary Material (Figures S1 – S4).

The deviation graphs for the six evaluated models are shown in Fig. 3. $M_{Szyszko}$ tended to overestimate the majority of smaller carabid species, while all other models over- and underestimated smaller species to a similar extent. Towards the middle of the size range, all models slightly underestimated weights, and especially m_{Booij} and m_{base} had a tendency to overestimate the larger species. For m_{fixed} and m_{mixed} this tendency was less pronounced, and $m_{Szyszko}$ and m_{inter} were most the balanced in their predictions for larger species.

During the OP-regression with log-transformed weights, only $m_{Szyszko}$ showed significant changes in intercept and slope from the reference. Changes in R^2 values between the six models were not detectable or only marginal, with m_{fixed} and m_{inter} having a slightly larger R^2 than the other models (0.9516 and 0.9520 vs. 0.9515). As mentioned in the previous section, these results are primarily of concern for predictions of smaller species. The results of the OP-regression with untransformed weights, which emphasises predictions for larger species, conveyed a different image. Here, m_{base} was the worst-performing model with both significantly altered intercept and slope, and it yielded the lowest R^2 value (0.8516). M_{Booij}, m_{fixed} as well as m_{mixed} displayed a significant change in slope. The R^2 values were 0.8539, 0.8584 and 0.8558, respectively. $M_{Szyszko}$ and m_{inter} were the only two models showing no significant changes in slope or intercept compared to the reference, and they also had the two highest R^2 values of 0.8823 and 0.9052. The main results of the two observed vs. predicted regression approaches are highlighted in Fig. 4. Full model summaries are provided in Table 3. Both regression models display non-normality for residuals (Figure S9, Supplementary Material) and should therefore be interpreted with caution. This is especially the case for the OP-regression of untransformed weights, which is most likely caused by the abovementioned introduced variance and increased leverage of certain data points. Nevertheless, we are convinced that, when considered carefully, both OP-regression models are appropriate for our evaluation of size-weight models. We assume that the results presented above are reliable, as they correspond with the patterns highlighted in the relative deviation graphs.

Discussion

Using an independent dataset, this study set out to evaluate two widely used size-weight models for carabids and to investigate whether the inclusion of taxonomic parameters can help to improve such models.

Based on our validation dataset (Schultz, 1996), our findings reveal general differences in the weight predictions of the two models provided by Szyszko (1983) and Booij et al. (1994). $M_{Szyszko}$ generally overpredicted carabid weights of smaller species. It correspondingly displayed significant changes in prediction compared to the reference during the OP-regression with log-transformed weights (Fig. 4), but it was more accurate for larger carabids and therefore showed no significant changes in intercept and slope and yielded a relatively high R^2 value of 0.882 during OP-regression with

Table 2 Estimated model coefficients of the four developed models. Harpalinae served as reference level for the effect of subfamily. R² values are adjusted pseudo-R² values (Nagelkerke, 1991) for models m_{base}, m_{fixed} and m_{inter} and marginal / conditional R² (sensu Nakagawa et al., 2017) for model m_{mixed}

	m_{base}			m_{fixed}			m_{mixed}			m_{inter}		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
(Intercept)	-3.0848	-3.2290 – -2.9406	**< 0.001**	-2.8707	-3.0966 – -2.6448	**< 0.001**	-3.0309	-3.2354 – -2.8264	**< 0.001**	-2.8287	-3.1108 – -2.5465	**< 0.001**
ln size	2.9783	2.9036–3.0530	**< 0.001**	2.8983	2.7907–3.0059	**< 0.001**	2.9250	2.8322–3.0177	**< 0.001**	2.8778	2.7424–3.0133	**< 0.001**
[Carabinae]				-0.0898	-0.3047–0.1251	0.409				1.9128	-1.9753–5.8010	0.331
[Elaphrinae]				0.1094	-0.1469–0.3656	0.399				1.2201	-2.5670–5.0071	0.524
[Nebriinae]				-0.1377	-0.2723 – -0.0030	**0.045**				-0.4022	-1.2543–0.4499	0.351
[Scaritinae]				-0.3676	-0.5364 – -0.1988	**< 0.001**				-0.0369	-0.8849–0.8111	0.931
[Trechinae]				-0.1175	-0.2246 – -0.0104	**0.032**				-0.2870	-0.7123–0.1383	0.184
ln size * [Carabinae]										-0.6432	-1.9078–0.6214	0.315
ln size * [Elaphrinae]										-0.5538	-2.4360–1.3283	0.560
ln size * [Nebriinae]										0.1324	-0.2894–0.5542	0.535
ln size * [Scaritinae]										-0.2482	-0.8307–0.3343	0.400
ln size * [Trechinae]										0.1118	-0.1493–0.3730	0.397
Random effect							$6_{subfamily}$					
Observations	107			107			107			107		
Degrees of freedom	105			100			103			95		
R^2	0.983			0.986			0.981 / 0.986			0.986		
F statistic (p)	6249 (< 0.001)			1244 (< 0.001)			3910.4 (< 0.001)			668.2 (< 0.001)		

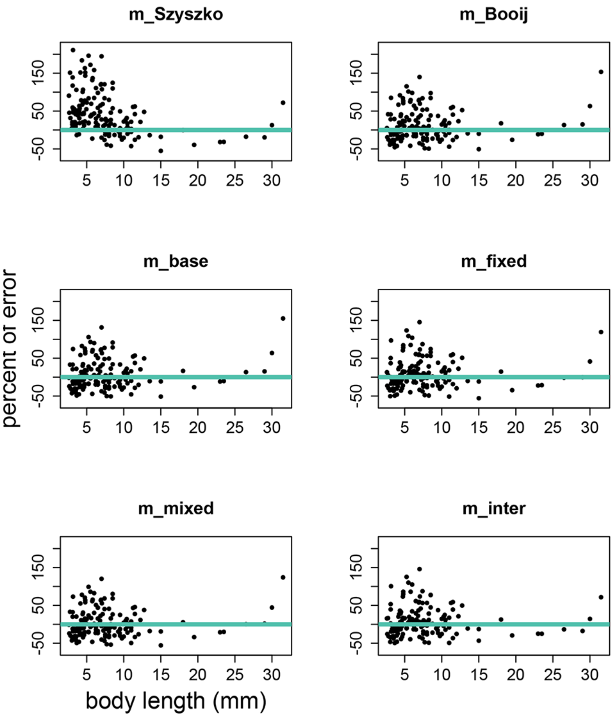

Fig. 3 Deviation graphs of all six models showing the relative deviation as percentage of observed weight on the y-axis against size (body length) on the x-axis. The line (y = 0) represents the observed weights for reference

untransformed weights. In contrast, m_{Booij}, predicted more accurately for smaller carabid species, with no significant changes in intercept and slope during OP-regression with log-transformed weights. It tended to overestimate larger species. Consequently, its predictions significantly differed from the reference during the OP-regression with untransformed weights. It also yielded a lower R^2 value compared to $m_{Szyszko}$. Despite the mentioned imprecision and the limited representation of larger carabid species in our validation dataset, we are confident that our results reveal systematic patterns in the two models' weight predictions, which likely originate from the two models' varying methodological background. Several studies emphasise the specific applicability of size-weight equations in terms of certain regions or habitats (Sabo et al., 2002; Gruner, 2003; de los Santos Gómez, 2013). Our validation data featured some of the same species as the data used by Booij et al. (1994) and was possibly recorded in similar habitats but originated from a different geographical region ("various locations" in the Netherlands vs. the German Baltic Sea coast). $M_{Szyszko}$ was developed using carabids caught with pitfall traps in Polish forests (Szyszko, 1983), while, in contrast, Booij et al. (1994) collected carabids by hand also at "various locations" in the Netherlands. One likely contributing aspect is the varying assemblages of carabids across climatic zones or between different habitats (Thiele, 1977); for example, larger species tend to be more abundant in forests (Schreiner, 2011; Schwerk and Szyszko, 2011; Šerić Jelaska et al., 2011). Yet another important aspect are the different sampling methods. It is known that smaller species are well represented in hand catches, while pitfall traps tend to predominantly capture larger species (Boetzl et al., 2018; Knapp et al., 2020). We see that smaller carabid species were over-represented in the data of Booij et al. (1994) (Fig. 2), and although we did not have access to the original data from Szyszko (1983), we can assume that it featured comparatively larger carabid species. The different regions and habitats, as well as different catching methods, therefore led to different representations of sizes and taxa in the two models' training data.

We found that taxonomic parameters are capable of improving weight predictions of size-weight models for carabids. Our model candidates m_{fixed}, m_{mixed} and mjnter featured 'subfamily' as fixed effect, random effect or interaction term, while m_{base} featured no taxonomic parameters and served as a reference model fitted to the exact same training dataset. Relative deviation graphs and OP-regression indicated that the inclusion of taxonomic parameters can increase the accuracy of predicted weights for independent data. Just as with m_{Booij}, the four models showed no significant changes in intercept and slope during OP-regression with log-transformed weights. During OP-regression with untransformed weights, both m_{fixed} and m_{mixed} showed significantly different slopes compared to the reference. However, changes in slope were less pronounced than with m_{base}. M_{fixed} and m_{mixed} also yielded larger R^2 values, thereby indicating improved predictions for larger carabid species. Overall, m_{mixed} performed marginally worse than m_{fixed} in terms of R^2 values, which is due to the fact the predictions of m_{mixed} were made on the population level only (excluding the estimated random effect). Although subfamily had no significant effects in the fitted model (Table 2), m_{inter} was the most accurate model for both smaller and larger species, showing no significant changes in intercept or slope and yielding the largest R^2 values in both OP-regression approaches. Sabo et al. (2002) observed that the accuracy of size-weight models for insects improves with increasing taxonomic specificity, while Gruner (2003) found that the inclusion of an additional width-parameter can enhance (dry) weight predictions for carabids. Mroczyński and Daliga (2016) used the differentiation of morphological types to improve size-weight models for beetle larvae. Consequently, different taxonomic groups in carabids (here subfamilies) could also have certain shape characteristics, which result in modifications to the general size-weight relationship. Our findings support this hypothesis, as additional taxonomic parameters were capable of improving model

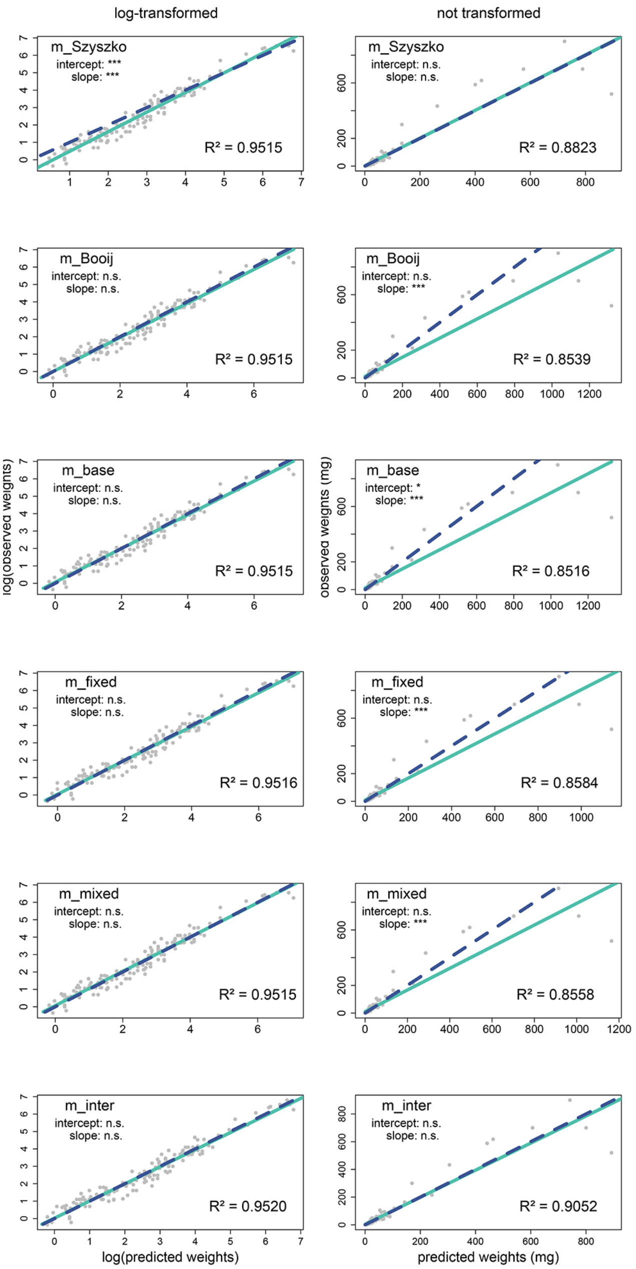

Fig. 4 Observed weights plotted against predicted weights for all six models on the log-scale (left) and the original scale (right), showing the reference line 1:1 (dashed) and the individual regression line (solid). Take note of the different scales on the x-axis. Significance codes for intercept and slope are: *** (<0.001), ** (<0.01), * (<0.05)

accuracy in our study. Another possible explanation in this regard could be that the different subfamilies represent specific size ranges. For example, species belonging to Carabinae are typically relatively large, while Trechinae species are usually comparatively small. Figure 1b indicates that the relationship between log-transformed body length and log-transformed fresh weight may not be perfectly linear. In this case, an additional taxonomic parameter would improve the model by adding flexibility. Owing to the limitations of the two datasets used in our study, we estimated model coefficients for only six subfamilies, which considerably limits the practical applicability of the models described herein. Nevertheless, we believe that the inclusion of a taxonomic parameter as a random effect could be a promising approach to formulating size-weight models that are less biased by their training data - and therefore less restricted in their applicability. Such models would not require specific taxonomic predictors when applied to independent data.

It needs to be mentioned that size-weight models for carabids have disadvantages and limitations. M_{Booij} and our approach are based on training data that contain certain inaccuracies. This might also be the case for $m_{Szyszko}$, as the original reference does not provide detailed information in this regard (Szyszko, 1983). Furthermore, size-weight models are usually fitted on the logarithmic scale; therefore, prediction errors for larger species translate exponentially into relatively large absolute errors. This general problem was described by Koch and Smillie (1986) for hydrological models, but it also applies to size-weight models for insects (e.g. Rogers et al., 1976). Another sensitive aspect is determining which sizes are used when applying size-weight models. There are intraspecific differences in size between different regions and habitats (Szyszko et al., 1996; Baranovská and Knapp, 2014; Baranovská et al., 2019). Individual size usually also varies between females and males of the same species (Riecken and Raths, 1996; Knapp, 2012; Baranovská and Knapp, 2014), while both the magnitude of this sexual dimorphism and the abundance ratio of male and female beetles can vary spatially - within the same species and population (Yarwood et al., 2021). Additionally, the size of carabid imagos is affected by conditions during larval development and can therefore vary considerably (Szyszko et al., 1996; Baranovská and Knapp, 2014; Tseng et al., 2018). Moreover, size-weight models cannot account for phenological variations in biomass within the same species at different times of the year: carabids are usually lighter after overwintering or as teneral imagos, but they increase in weight towards reproduction (Grüm, 1975; Booij et al., 1994; Szyszko et al., 1996). In the context of the described limitations and the imprecision of the aggregated data in this study, the predicted weights and calculated relative deviations (Fig. 3) should not be taken literally; instead, they should be considered as a whole, in order to reveal systematic patterns in the weight predictions of the different models.

After all, size-weight equations are models and therefore only approximations of reality. We thus recommend directly measuring carabid fresh weights, whenever feasible. This represents a considerable amount of work and requires very specific methods (Booij et al., 1994; Knapp, 2012), as

Table 3 Estimated model coefficients of the observed vs. predicted regression models (sensu Pineiro et al. 2008) for log-transformed predictions (left) and not transformed predictions (right). R^2 was calculated as adjusted pseudo-R^2 (Nagelkerke, 1991)

	Observed vs. predicted regression					
	log-transformed			**not transformed**		
	Estimate	CI	p	Estimate	CI	p
(Intercept)	0.00	-0.10–0.10	1.000	0.00	-8.06–8.06	1.000
predicted weight	1.00	0.97–1.03	**<0.001**	1.00	0.95–1.05	**<0.001**
[m_szyszko]	-0.64	-0.80 – -0.49	**<0.001**	1.49	-9.93–12.91	0.798
[m_booij]	0.00	-0.14–0.14	0.975	10.91	-0.38–22.21	0.058
[m_base]	0.06	-0.07–0.20	0.367	11.45	0.16–22.74	**0.047**
[m_fixed]	0.04	-0.09–0.18	0.531	8.72	-2.60–20.04	0.131
[m_inter]	0.02	-0.11–0.16	0.727	3.39	-7.99–14.76	0.560
[m_mixed]	0.06	-0.07–0.20	0.358	10.43	-0.88–21.73	0.071
pred. weight * [m_szyszko]	0.13	0.08–0.18	**<0.001**	0.00	-0.08–0.08	0.974
pred. weight * [m_booij]	-0.02	-0.07–0.02	0.333	-0.31	-0.38 – -0.24	**<0.001**
pred. weight * [m_base]	-0.03	-0.08–0.01	0.173	-0.31	-0.38 – -0.24	**<0.001**
pred. weight * [m_fixed]	-0.03	-0.07–0.20	0.249	-0.20	-0.27 – -0.13	**<0.001**
pred weight * [m_inter]	-0.02	-0.06–0.03	0.461	-0.02	-0.10–0.06	0.571
pred weight * [m_mixed]	-0.01	-0.06–0.03	0.540	-0.22	-0.29 – -0.15	**<0.001**
Observations	1043			1043		
Degrees of freedom	1029			1029		
R^2	0.958			0.885		
F statistic (p)	1828 (<0.001)			619.7 (<0.001)		

commonly used catching and storing fluids can introduce some bias (Braun et al., 2009, 2012; Knapp, 2012). However, if this is neither feasible nor possible (e.g. for historic or archived data), size-weight models are a suitable solution. We explicitly advise against obtaining the weights of certain species directly from the literature because they can underlie substantial variations. Carabid (mean) sizes should be measured directly (see Šerić Jelaska et al., 2011) and only be substituted from the literature when this is also neither feasible nor possible. Researchers should preferably use size-weight functions from the same region and habitat, if available. However, special attention should be paid to the methodological background of both the size-weight model and one's own data. Generally, we recommend the combined application of the models of Szyszko (1983) and Booij et al. (1994), with the former used for larger and the latter for smaller carabid species. The two models intersect at approximately x = 2.4655, y = 4.2801 on the log-scale, which converts to 11.77 mm and 72.25 mg, respectively. We therefore recommend the use of m_{Booij} for carabids < 11.8 mm and $m_{Szyszko}$ for carabids ≥ 11.8 mm. Furthermore, it should be noted that biomass data from different studies should only be compared when they were derived with the same method, which also means that they should have been predicted with the same model (or a combination of models).

Conclusions

We found the size-weight model provided by Booij et al. (1994) is more accurate for smaller carabids, while the model of Szyszko (1983) is more accurate for larger carabids when tested against independent data. Additional taxonomic parameters have the potential to improve the weight predictions of size-weight models and may lessen restrictions in terms of applicability. Although it is preferable to measure the biomass of carabids directly, estimating weights with size-weight models is generally less work-intensive, and sometimes it is the only available method. For further application, we recommend a combined use of the models of Booij et al. (1994) and Szyszko (1983), with the former used to predict the weights of smaller carabids (< 11.8 mm) and the latter to predict the weights of larger carabids (≥ 11.8 mm).

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Data availability We declare that the data used in this research is not our own. It has been previously published by Booij et al. (1994) and Schultz (1996) and can be found in these publications. Carabid species included in this research, their respective source publication and the modelling results of this research are provided in the Supplementary Material (Table S1).

Code availability The R code is available at https://github.com/fabio-weiss/carabid_biomass.

Declarations

Conflict of Interest/Competing interests All involved authors declare that they have no conflicts of interest.

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Appendix II

Title	Random year intercepts in mixed models help to assess uncertainties in insect population trends
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SHORT COMMUNICATION

Insect Conservation and Diversity

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Random year intercepts in mixed models help to assess uncertainties in insect population trends

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Abstract

1. An increasing number of studies is investigating insect population trends based on time series data. However, the available data is often subject to temporal pseudoreplication. Inter-annual variability of environmental conditions and strong fluctuations in insect abundances can impede reliable trend estimation. Temporal random effect structures in regression models have been proposed as solution for this issue, but remain controversial.
2. We investigated trends in ground beetle abundance across 24 years using generalised linear mixed models. We fitted four models: A base model, a model featuring a random year intercept, a model featuring basic weather parameters, and a model featuring both random year intercept and weather parameters. We then performed a simple sensitivity analysis to assess the robustness of the four models with respect to influential years, also testing for possible spurious baseline and snapshot effects.
3. The model structure had a significant impact on the overall magnitude of the estimated trends. However, we found almost no difference among the models in how the removal of single years (sensitivity analysis) relatively affected trend coefficients. The two models with a random year intercept yielded significantly larger confidence intervals and their *p*-values were more sensitive during sensitivity analysis. Significant differences of the model with random year intercept and weather parameters to all other models suggest that the random year effects and specific weather effects are rather additive than interchangeable.
4. We conclude that random year intercepts help to produce more reliable and cautious uncertainty measures for insect population trends. Moreover, they might help to identify influential years in sensitivity analyses more easily. We recommend random year intercepts in addition to any variables representing temporally variable environmental conditions, such as weather variables.

KEYWORDS
arthropod decline, false baseline effect, insect decline, mixed models, robustness, sensitivity analysis, snapshot effect, temporal pseudoreplication, time series, uncertainty, year effects

INTRODUCTION

The number of annually published studies that examine temporal changes in insect populations has more than doubled in the last decade (with 79 studies in 2012 and 180 in 2022, based on a search in Web of Science using the search string 'insect* AND population AND trend' performed on March 13th 2023). Some of these studies reported dramatic declines in insect abundance, biomass or diversity (e.g., Hallmann et al., 2017; Lister & Garcia, 2018; Seibold et al., 2019) triggering public interest in this topic and causing widespread concern. Although more and more long-term data sets are becoming available (e.g., Van Klink et al., 2020) there yet remains the need for longitudinal long-term data to better understand the spatial and temporal patterns of insect trends and gain insights about their drivers (Montgomery et al., 2021; Mupepele et al., 2019; Thomas et al., 2019). Most long-term monitoring schemes started well after 1980 (Brooks et al., 2012; Hallmann et al., 2020; Homburg et al., 2019) and data sets exceeding 40 years are still rare (Bell et al., 2020; Macgregor et al., 2019; Martins et al., 2013). This represents a considerable challenge for deriving reliable trends, because many insect populations show a strong inter-annual variability (e.g., Aldercotte et al., 2022; Günther & Assmann, 2004; Pollard, 1991), penalising trend estimations. Daskalova et al. (2021) recently observed that studies investigating shorter time series tended to find the strongest trends—both, positive and negative. They attributed this heterogeneity to the increased impact of exceptional years in terms of environmental conditions and insect occurrences. Didham et al. (2020) also addressed this issue and emphasised the strong leverage of years close to the start or the end of a time series causing so-called false baseline effects or snapshot effects. Daskalova et al. (2021) therefore advocated the use of random year effects in generalised linear mixed models (GLMMs) to gain more reliable trend estimates as they help to account for inter-annual variability and temporal pseudoreplication. The issue of pseudoreplication in ecological studies working with experimental or observational data has been known and discussed for almost four decades (Hurlbert, 1984). Modern implementations of mixed model frameworks allow addressing this problem by including random effect structures (Chaves, 2010). Previously, Werner et al. (2020) had used random year intercepts in GLMMs to account for temporal pseudoreplication in vegetation data, and similar approaches to investigate trends have been utilised for bird or insect population data using generalised additive mixed models (GAMMs) (Bell et al., 2020; Knape, 2016). In a reply to Daskalova et al. (2021), Seibold et al. (2021) questioned the use of random year intercepts due to a lack of independence between single years and propose that specific environmental parameters (e.g., weather variables) are more suitable to account for varying environmental conditions and annual fluctuations in insect occurrences.

We used a 24-year data set of ground beetle (Coleoptera: Carabidae) abundances from Eberswalde, Germany, to explore trends estimated with GLMMs featuring different combinations of random year intercepts and weather variables. We tested the different model structures for their robustness towards influential years by performing a simple sensitivity analysis.

METHODS

We used data on ground beetle sampling abundances (in the following simply referred to as abundances) from a previously unpublished data set. Ground beetles were caught from 1999 to 2022, between the beginning of May and the end of July each year, on 13 forest plots within one forest site (with an extension of approximately 1×1 km) close to Eberswalde, Germany (52.820000, 13.790000). Not all plots were sampled each year and we only included data from plots, which were sampled in 3 years or more. We used pitfall traps consisting of 400 mL glass jars positioned in a piece of PVC pipe (see Boetzl et al., 2018), formaldehyde as trapping fluid and metal roofs. There were four pitfall traps at each plot, organised as either square or transect with approximately 20 m between the traps. The layout of traps (square or transect) remained consistent for each plot throughout all sampled years. During the sampling period, the traps were emptied 3 times, usually after 4 weeks (28 days), however, the exact sampling length occasionally varied. Prior to data analysis, we excluded all data from traps that had been disturbed by factors such as rain, wild animals or vandalism. Abundances represent the sum of all individuals of species belonging to the Carabidae family that were caught in one pitfall trap during one sampling interval. We excluded data of one species (*Nebria brevicollis*, Fabricius 1792), which is known to display extreme fluctuations in numbers between years (Nelemans et al., 1989). We modelled ground beetle abundance using GLMMs of the negative-binomial family (link = log) fitted with the glmmTMB R package (glmmTMB function, Brooks et al., 2022). The simplest model (base model) featured linear terms for year (continuous) and sampling interval (factor) as well as a quadratic term for days of sampling (continuous) (see Schirmel et al., 2010) as fixed effects. Furthermore, the base model included a random intercept specific for each trap and year, as the trap numbering and their exact locations varied among years, nested within the plot. We tested for temporal auto-correlation among years with the testTemporalAutocorrelation function of the DHARMa package (Hartig, 2021), which showed no indication for any relevant temporal autocorrelation between years (Durbin–Watson test: 1.63, *p*-value = 0.3499). Based on this base model, we then performed a stepwise forward model selection with additional weather variables. We derived all weather variables from publicly available data (daily mean temperature and daily sum of precipitation) recorded at a meteorological station located approximately 27 km from the study site (DWD, 2023). The mean daily temperature during sampling (as interaction with sampling interval), sum of precipitation during sampling and mean early spring temperature (March) were tested as additional variables. All of these parameters have been observed to affect ground beetle sampling abundances in earlier studies (Honěk, 1997; Irmler, 2022; Tsafack et al., 2019; Wang et al., 2014). We added each variable to the model as either linear or quadratic fixed effect resulting in different model candidates, which were then compared via AIC (note: cAIC is not available for glmmTMB, models were fitted with maximum likelihood (REML = FALSE) with all random effects remaining constant). The variable yielding the lowest AIC was kept in the model formula, while all remaining variables were again added in the next step creating new model candidates. Finally, the base model as well as the model resulting from the model selection were each expanded by a random intercept for year (factor), which was crossed with all other random effects. This resulted in the following four model structures (we report the model formulas as R-syntax here and additionally provide mathematical equations in the Supporting Information S1):

$$\textbf{Base model}: abundance \\ \sim year + sampling\ length + I\left(sampling\ length^2\right) \\ + sampling\ interval + (1|plot/trap)$$

$$\textbf{Random year model}: abundance \\ \sim year + sampling\ length + I\left(sampling\ length^2\right) \\ + sampling\ interval + (1|year\_factor) \\ + (1|plot/trap)$$

$$\textbf{Weather model}: abundance \\ \sim year + sampling\ length + I\left(sampling\ length^2\right) \\ + sampling\ interval * temperature + precipitation \\ + I(precipitation^2) + spring\ temperature \\ + I(spring\ temperature^2) + (1|plot/trap)$$

$$\textbf{Combined model}: abundance \\ \sim year + sampling\ length + I\left(sampling\ length^2\right) \\ + sampling\ interval * temperature + precipitation \\ + I(precipitation^2) + spring\ temperature \\ + I(spring\ temperature^2) + (1|year\_factor) \\ + (1|plot/trap)$$

We performed a simple sensitivity test by running each model 24 times, while iteratively excluding the data of individual years during each run. We then used visualisation to compare the resulting model estimates to those of the respective full model. In addition, we used pairwise tests to compare effect coefficients, their respective confidence intervals (CIs) and p-values as well as deviation of effect coefficients and p-values from the respective full model. Moreover, we compared the percentage of CI overlap, where a value of 100% meant that the CI lies entirely within the respective full model's CI. All the above-mentioned metrics where tested for normality at their different levels (model structures). We then used either *t*-test (parametric) or Wilcoxon signed rank test (non-parametric) for pairwise comparisons (both with Holm-adjusted *p*-values).

We used bootstrapping to compute 0.95 CIs: Full model CIs were bootstrapped using the ggpredict function of the ggeffects package (Lüdecke et al., 2022) within the bootMer function of the lme4 package (Bates et al., 2022) based on 1000 simulations. We used the bootstrap_model function of the parameters package (Lüdecke et al., 2023) with 120 simulations to calculate CIs for trend coefficients during the sensitivity analysis.

All analyses were performed with R (version 4.2.2, R Core Development Team, 2022). Further methodological details and the full R code can be found in the Supporting Information of this article (S1).

RESULTS AND DISCUSSION

Trend estimates for ground beetle abundance significantly differed among the four model structures (base model, random year model, weather model and combined model): The random year and the combined models, which both included a random year intercept, generally estimated trends over time to be significantly more negative than both models without random year intercepts (Figures 1, 2a–d and 3a). In contrast, Daskalova et al. (2021) observed negative trends becoming shallower when re-analysing the Seibold et al. (2019) data with random year intercepts. However, they found trend estimates to become less extreme with the inclusion of random year intercepts mostly in shorter time series (<25 years). Generally, there should be no expectation in which direction trend estimates change when random year intercepts are included as the underlying data are usually unique in their study design and sampling history, leading to different patterns of temporal pseudoreplication. We observed slightly different patterns among the four tested model structures in how trend coefficients fluctuated during sensitivity analysis (Figure 2a–d). However, contrary to assumptions, there was no significant difference in how strongly trend estimates changed during sensitivity analysis between any two of the four models (Figure 3d). We do not have a clear explanation for this observation. We would have expected to see significantly different patterns as the random year model and the combined model accounted for temporal pseudoreplication, while the other two models did so only partly (weather model) or not at all (base model). We can only speculate that in this case, the time series length of 24 years might be long enough so that data from a single year contribute relatively little to the overall temporal pseudoreplication. Of course, this also depends on the individual sample history of the data, and we would expect shorter time series to show stronger differences in trend fluctuations.

We observed that model estimates the random year and the combined models had significantly larger CIs (Figures 1, 2a–e and 3b) and *p*-values (Figure 2f–h, Figure 3c), which is in line with the findings of Daskalova et al. (2021) and Knape (2016).

The sensitivity analysis revealed that several influential years considerably contributed to negative trends (2002 and 2020–2022) with all 4 model structures indicating similar snapshot effects for the last 3 years of the time series (sensu Didham et al., 2020). Trends estimated with random year intercepts displayed significantly stronger fluctuations in *p*-values during the sensitivity analysis (Figure 2e–h, Figure 3f). The impact of influential years on trend coefficients was present for all model structures during sensitivity analysis, but was more clearly indicated by higher *p*-values in the random year model and the combined model (Figure 2e–h).

During the sensitivity analysis, CI overlap slightly increased with the addition of random year intercepts or weather variables, but was significantly larger in the combined model than in the other three models (Figure 3e). We consider this an indication that random year intercepts as well as appropriate weather variables help to estimate trend uncertainties (CIs) that are more robust towards the impact of single years, especially when time series feature strong inter-annual

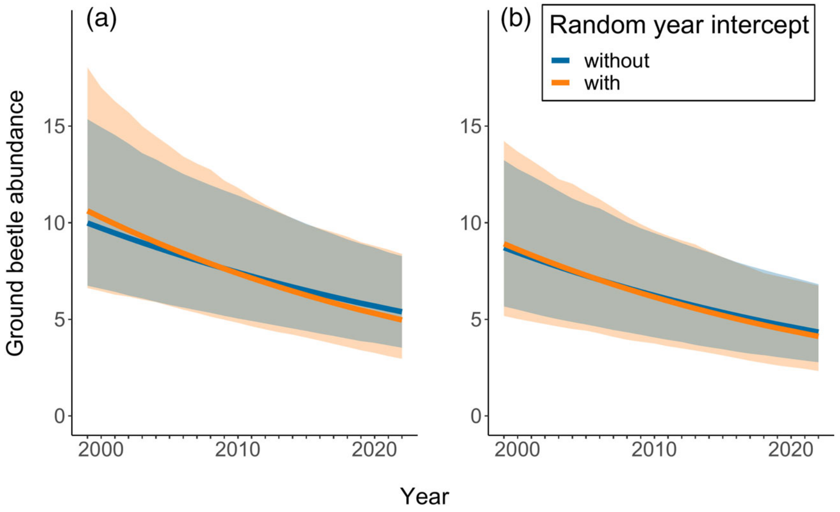

FIGURE 1 Estimated trends over time in ground beetle abundance for the respective full models. Ribbons represent 0.95 confidence intervals (CIs). (a) Base model (blue) and random year model (orange). (b) Weather model (blue) and combined model (orange). Predictions and CIs refer fixed effects only and were made for the third sampling interval (July) and a sampling length of 28 days. All weather-related variables were set to the respective mean value. A coloured version of this figure can be found online.

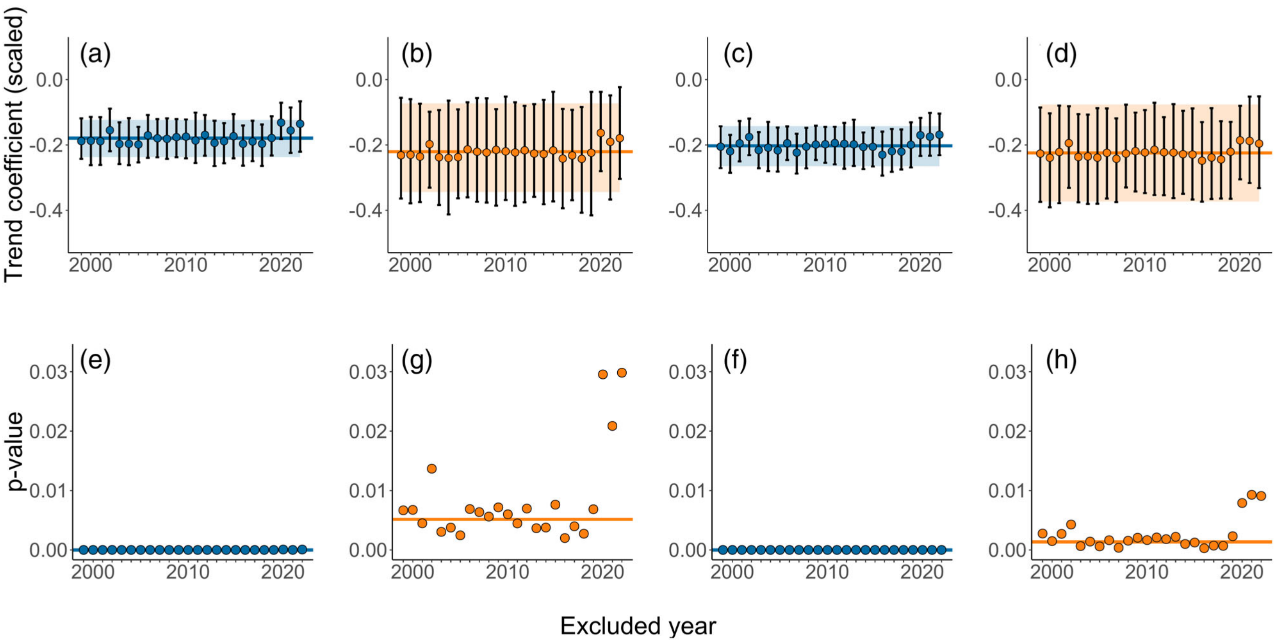

FIGURE 2 Results of the sensitivity analysis with the iterative removal of single years from the time series. Top: The estimated coefficient for fixed effects of 'year' (scaled) with their respective 0.95 confidence intervals (CIs) (whiskers). Horizontal lines and shadings indicate the estimated coefficient and CI of the respective full model. Bottom: p-values for fixed effects of 'year'. Horizontal solid lines indicate the p-value of the respective full model, horizontal dashed lines mark $p = 0.05$ for reference. Letters refer to the following models **a** and **e**: Base model; **b** and **g**: Random year model; **c** and **f**: Weather model; **d** and **h**: Combined model. A coloured version of this figure can be found online.

fluctuations or include outlier years. In addition, random year intercepts lead to more sensitive *p*-values, which could help to reduce type I errors and, at the same time, be advantageous in sensitivity analyses such as the one presented here. Trend uncertainties are currently often neglected but should play a more prominent role in population trend analyses (Wauchope et al., 2019).

Nevertheless, the use of random year intercepts is controversial: Seibold et al. (2021) caution that for insect time series, consecutive years may lack the statistical independence required to include random year intercepts. On the other hand, temporal autocorrelation can be tested (e.g., Bell et al., 2020; this study) and, if present, accounted for (Knape, 2016). Seibold et al. (2021) further argue that the inclusion

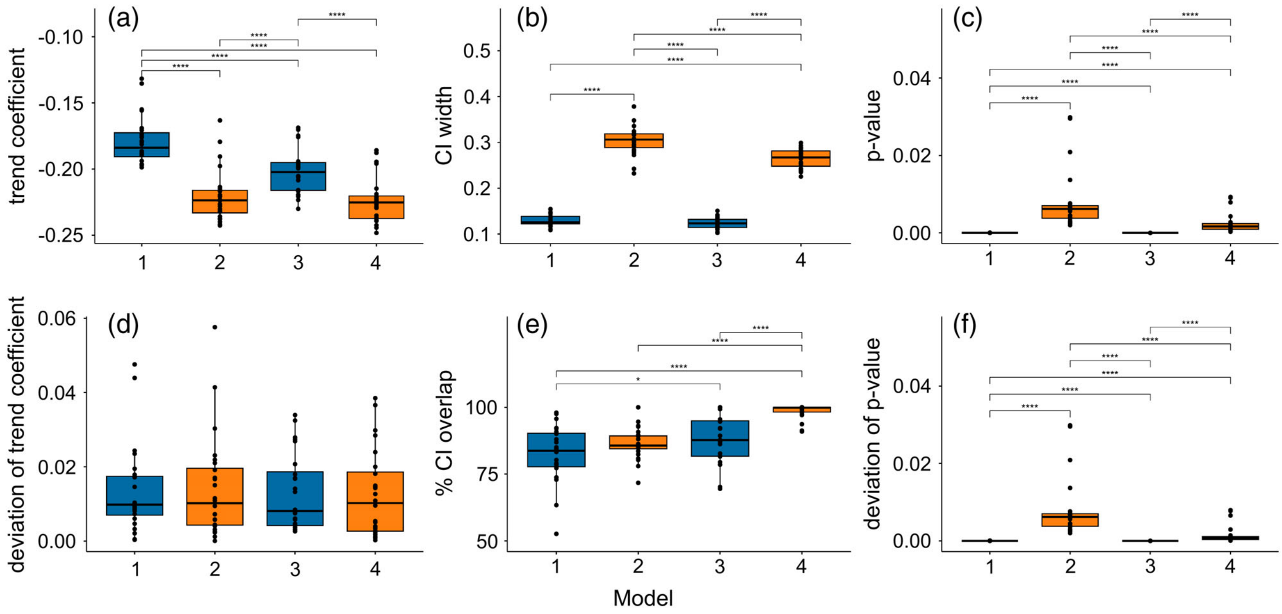

FIGURE 3 Results of the sensitivity analysis for the base model (**1**), random year model (**2**), weather model (**3**) and combined model (**4**) with pairwise comparisons of trend coefficients (**a**), confidence intervals (CI) width (**b**), and p-values (**c**). Deviation of trend coefficient (**d**), CI overlap (**e**), and deviation of *p*-value (**f**) refer to the respective full model. Significance codes: <0.0001****, <0.001***, <0.01**, <0.05*. A coloured version of this figure can be found online.

of weather variables such as site-specific temperature and precipitation might be more suitable to account for inter-annual variation in environmental conditions and should therefore be used. However, ecosystems are complex and even well-chosen parameters might be insufficient to fully adjust for year-to-year variance in environmental conditions that affect insect communities (Daskalova et al., 2021).

We found that random year intercepts and weather variables both similarly modified trend coefficients, but patterns in CIs and *p*-values significantly differed between the two approaches. Moreover, significant differences of the combined model to the two previously mentioned models in trend coefficients, CIs, CI-overlap, *p*-values and deviation of *p*-values suggest that these effects are rather additive than interchangeable. We assume that random year intercepts and weather variables at least partly account for different sources of variance. Our results therefore suggest that environmental parameters such as weather variables and random year intercepts could be included simultaneously, ultimately leading to potentially different model estimates than if only one of them was included. We propose that meaningful environmental variables should be used, when available, while random year intercepts could be added as a precautious standard to adjust for any additional unaccounted year-to-year variance. Consequently, this will lead to more robust CIs and more cautious *p*-values, reducing the likelihood of type I errors. Contrariwise, failing to account for year-to-year variation and temporal pseudoreplication in insect time series with random year intercepts might result in false confidence in trend estimates and inflated type I errors. These problems are likely to be even more severe when time series are shorter (Daskalova et al., 2021).

Our findings also demonstrate that even in longer time series, a single year can substantially affect trend coefficients, and false baseline and snapshot effects might be present—with or without random year intercepts. This highlights the importance of rigorous and appropriate sensitivity analyses. Regarding the length of time series there exists no reliable threshold from which trend estimates become reliable and their sensitivity should always be tested. This can be done, for instance, by excluding single years (Seibold et al., 2019; this study) or multiple years from the start (left censoring) or the end of the time series (right censoring) (e.g., Roth et al., 2021) to uncover potential false baseline effects or snapshot effects (Didham et al., 2020; Fournier et al., 2019). Other options include the permutation of years (Aldercotte et al., 2022; Crossley et al., 2020) or the exclusion of trends of single species (Dennis et al., 2019), certain plots or whole study areas (Van Klink et al., 2020).

We conclude that random year intercepts help to account for inter-annual variation of environmental conditions, random population fluctuations and inherent temporal pseudoreplication in insect time series. Models with random year intercepts yield trend estimates with wider but more robust confidence intervals and more sensitive *p*-values and thereby lead to more cautious measures of uncertainty and decrease chances of type I error. We therefore advocate for the use of random year intercepts in mixed models investigating insect population trends, in addition to specific variables that account for year-to-year variation in environmental conditions.

AUTHOR CONTRIBUTIONS

Fabio Weiss: Conceptualization; methodology; visualization; writing – original draft; writing – review and editing; investigation; formal analysis. **Henrik von Wehrden:** Supervision; methodology; writing – review and editing; formal analysis. **Andreas Linde:** Data curation; supervision; resources; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in PubData at https://doi.org/10.48548/pubdata-23, reference number 20.500.14123/30.

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SUPPORTING INFORMATION

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

Data S1 Supporting Information: R version package.

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Appendix III

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

Research article

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 north-east 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

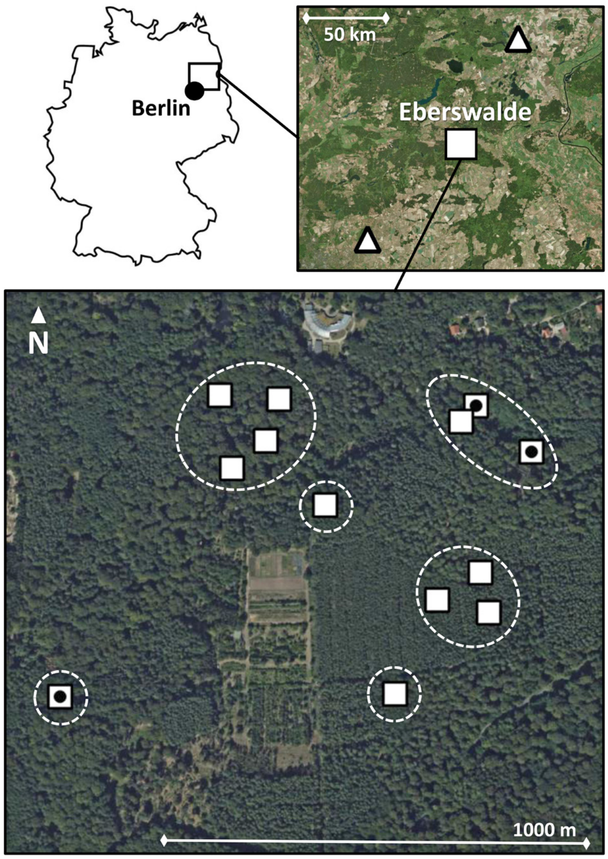

Figure 1. Location of the study area (top) and layout of the plots (bottom). Triangles (top right) mark the meteorological stations (DWD) of which data was used. Squares mark the 13 forest plots (with four pitfall traps each), arranged in either a square (blank) or a transect (dot). Dashed circles indicate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

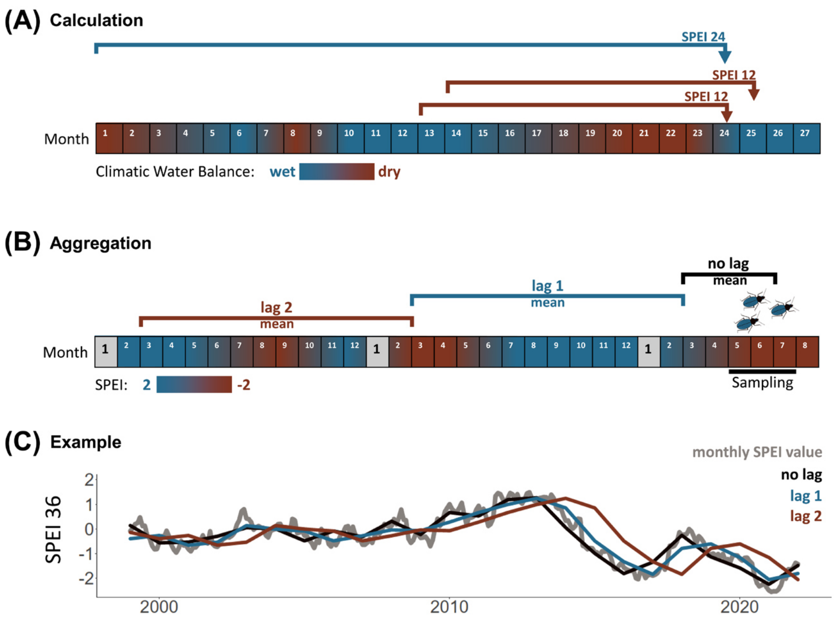

Figure 2. Methodological scheme which was used to calculate and aggregate SPEI-variables: (A) monthly SPEI values were calculated at different temporal scales (e.g. 12 and 24 months) taking into account the CWB of the previous months. (B) Monthly SPEI values were aggregated with different time lag in 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 ΔAIC > 2 compared to the initial GLMM, Burnham and Anderson 2004).

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

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

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.

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

$$\begin{aligned}&\text{Biomass GAMM: Biomass}^{1/3} \sim s\left(\text{year}, k = 8, \text{fx} = \text{TRUE}\right)\\ &\quad + \text{Sampling effort} + I(\text{Sampling effort}^2)\\ &\quad + \text{Sampling month} + \text{Temperature}\\ &\quad + \text{Precipitation} + \left(1|\text{year}\right) + \left(1|\text{Site/plot/trapID}\right),\\ &\quad \text{Family } = \text{Gaussian}\left(\text{link} = \text{identity}\right)\end{aligned}$$

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.

$$\begin{aligned}&\text{Diversity GLMM(s): Diversity metric}^* \sim \text{Year}\\ &\quad + \left(1|\text{year}\right) + \left(1|\text{Site/plot}\right),\\ &\quad \text{Family} = \text{Gamma}\left(\text{link} = \text{'log'}\right) \text{ or beta\_family}\left(\text{link} = \text{logit}\right)\\ &\text{Diversity GLMM(s): Diversity metric}^* \sim s\left(\text{year}, k =, \text{fx} = \text{TRUE}\right)\\ &\quad + \left(1|\text{year}\right) + \left(1|\text{Site/plot}\right),\\ &\quad \text{Family} = \text{Gaussian}\left(\text{link} = \text{'identity'}\right)\end{aligned}$$

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 $\Delta AIC > 2$ (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 ^0D) 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 ^2D) 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 (^2D / ^0D) 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.

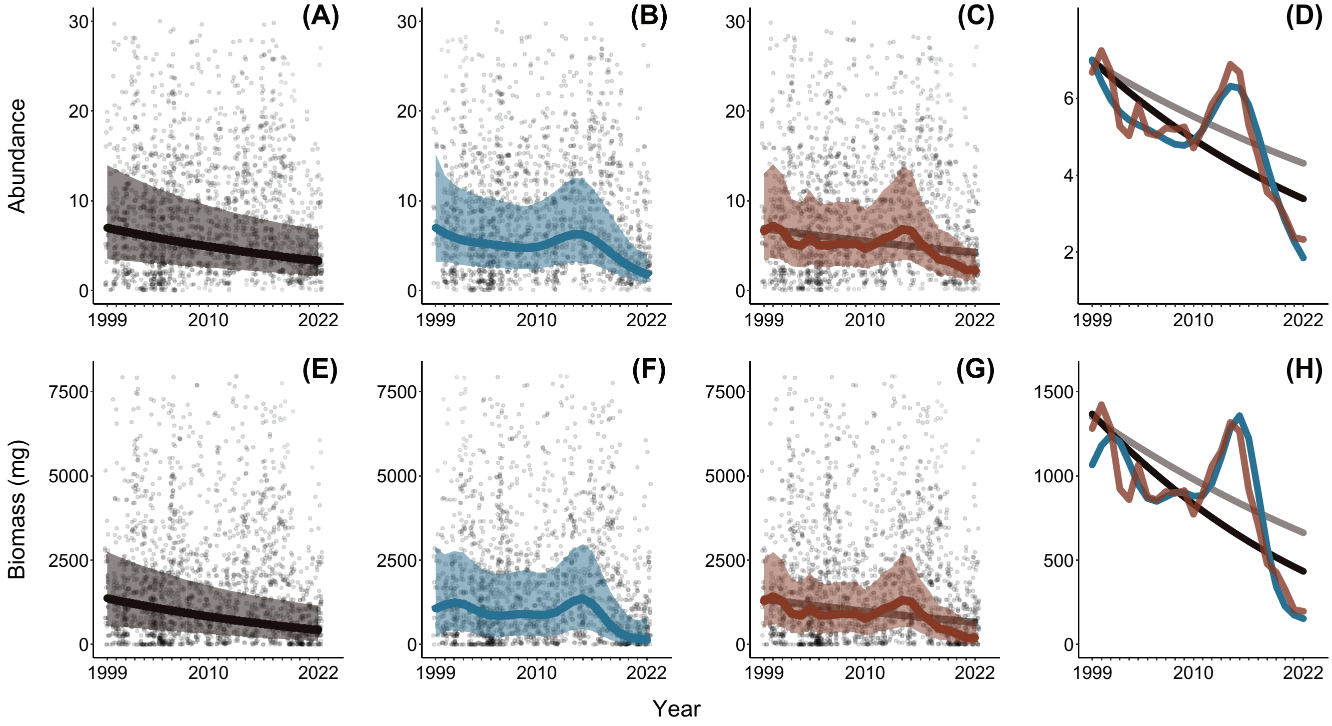

Figure 3. Trends in overall abundance (top) and biomass (bottom) of carabid beetles (excluding. *N. brevicollis*): linear trend (A), (E), non-linear trend (B), (F) and linear trend accounting for the effect of SPEI based on annual values (red) and estimated backround trends with fixed SPEI (grey) (C), (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

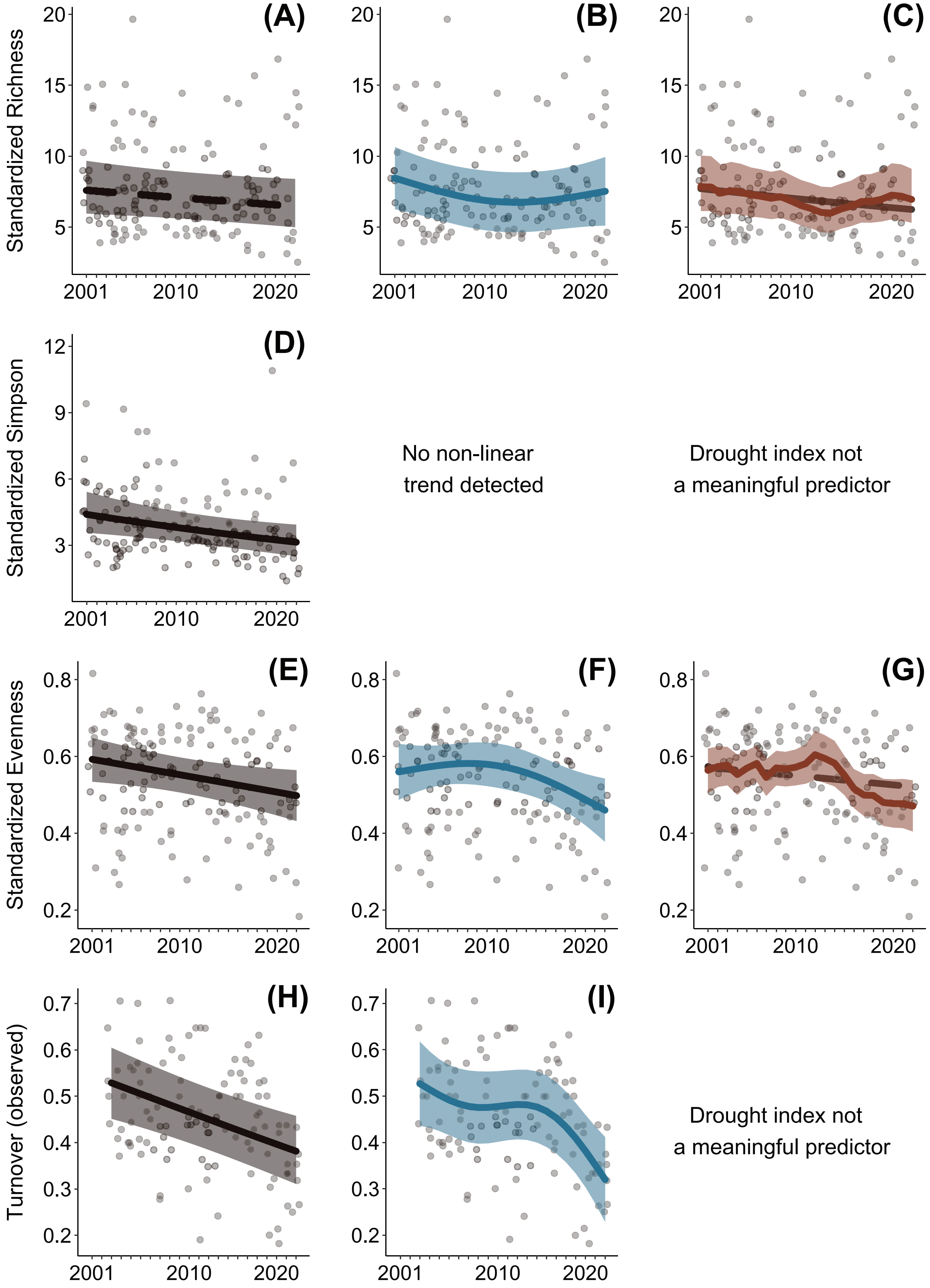

Figure 4. Predicted trends of standardized richness (A)–(C), standardized Simpson (D), standardized evenness (E)–(G) and observed species turnover expressed as Jaccard similarity (H)–(I). Different plots show linear trends (black), non-linear trends (blue) and linear trends accounting for the effect 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.

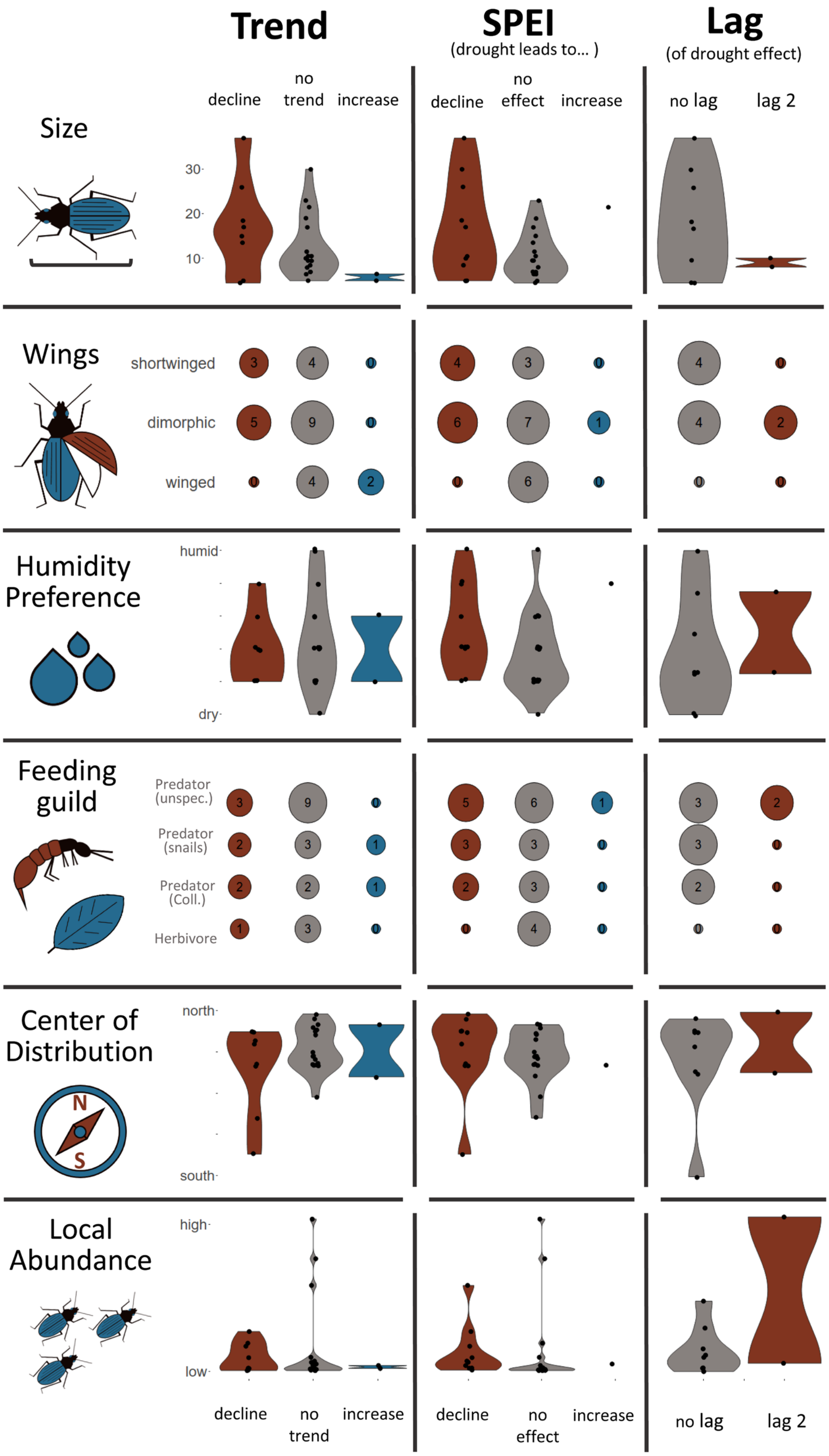

Figure 5. Classified trends (left column), drought effects (middle column) and delay (lag) of declines with droughts (right column) plotted against six species traits (rows). Distribution of trends, drought-effects and delays are visualized with violin plots for traits with continuous scale and with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

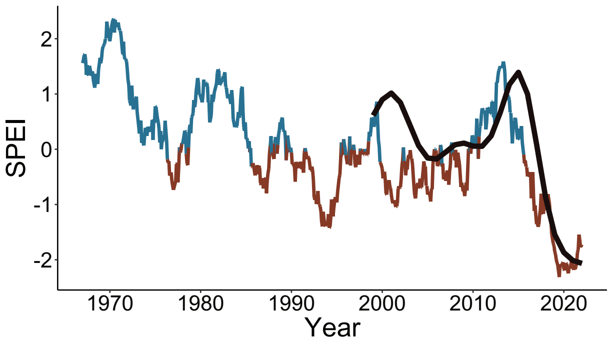

Figure 6. Relative monthly SPEI 72 values for the study area since 1967 with positive (wet) values in blue and negative (dry) values in red. The black line represents the overall biomass trend (GAMM) of carabid beetles found in this study since 1999. Biomass was scaled to match the scale of SPEI, refer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

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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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Appendix IV

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

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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

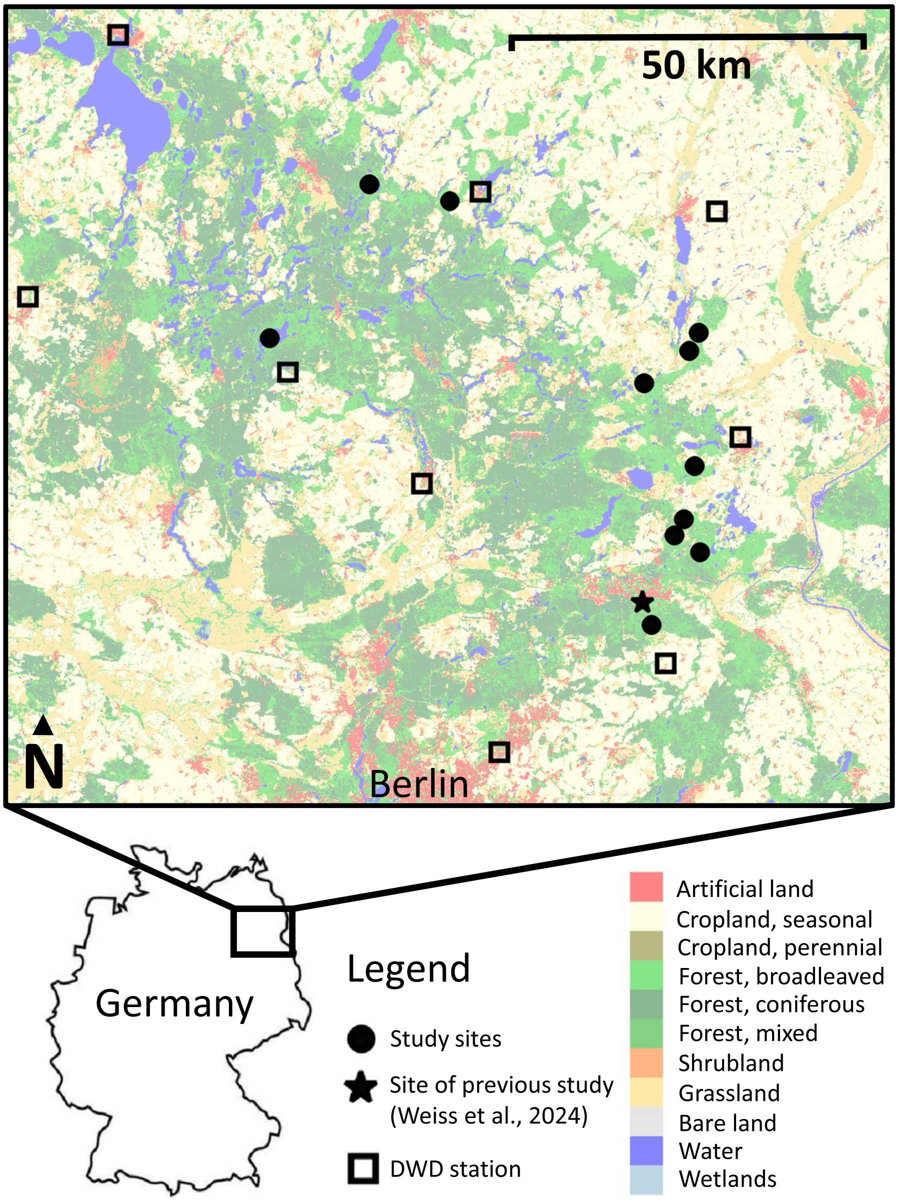

Fig. 1 Map of the study area. Study sites are shown as filled circles and DWD stations used to source meteorological data as squares (four stations outside the shown area). The study site of Weiss et al. (2024) is highlighted as star. Land cover classes are based on Pflugmacher et al. (2019). Only 9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

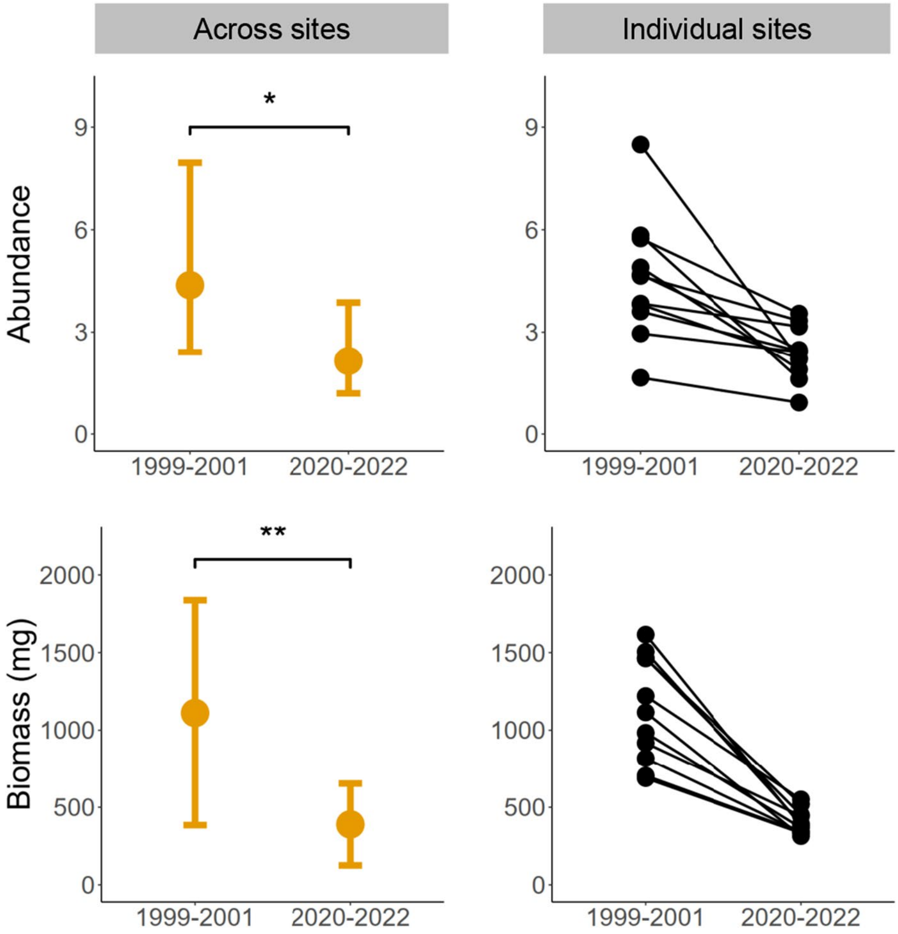

Fig. 2 Carabid abundance (top) and biomass (bottom): Estimated changes between 1999 and 2001 and 2020 and 2022 across all sites (left) and for specific study sites (right). Prediction were made with all other (scaled) fixed effects set to 0 and for marginal effects only. Dots represent estimated means, 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.

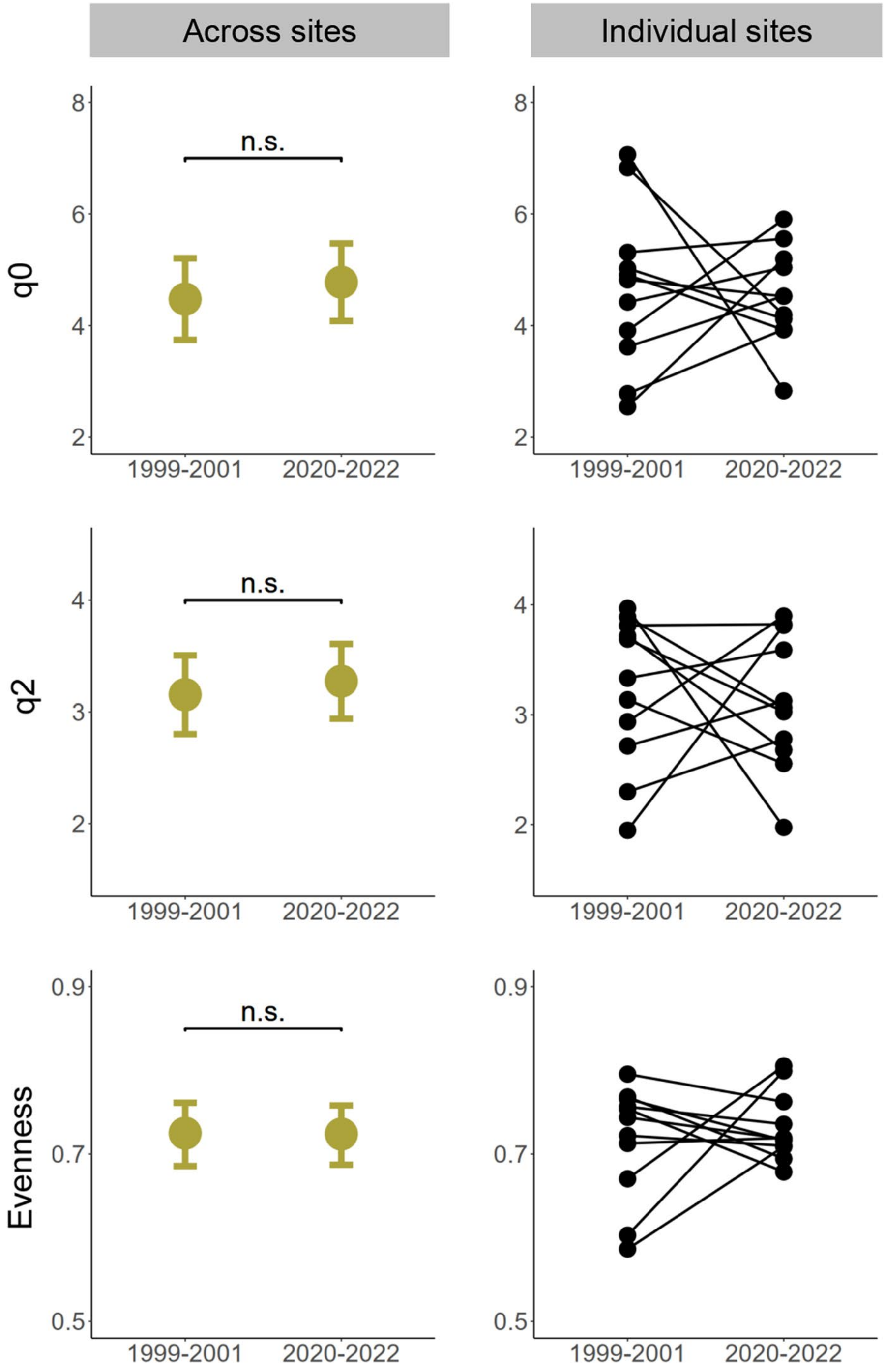

Fig. 3 Hill numbers: Estimated changes between 1999 and 2001 and 2020 and 2022 in q0 (top), q2 (middle) and evenness (bottom) across all sites (left) and for specific study sites (right). Dots represent estimated means, error bars (left plots) represent 0.95 confidence intervals. Significance codes: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

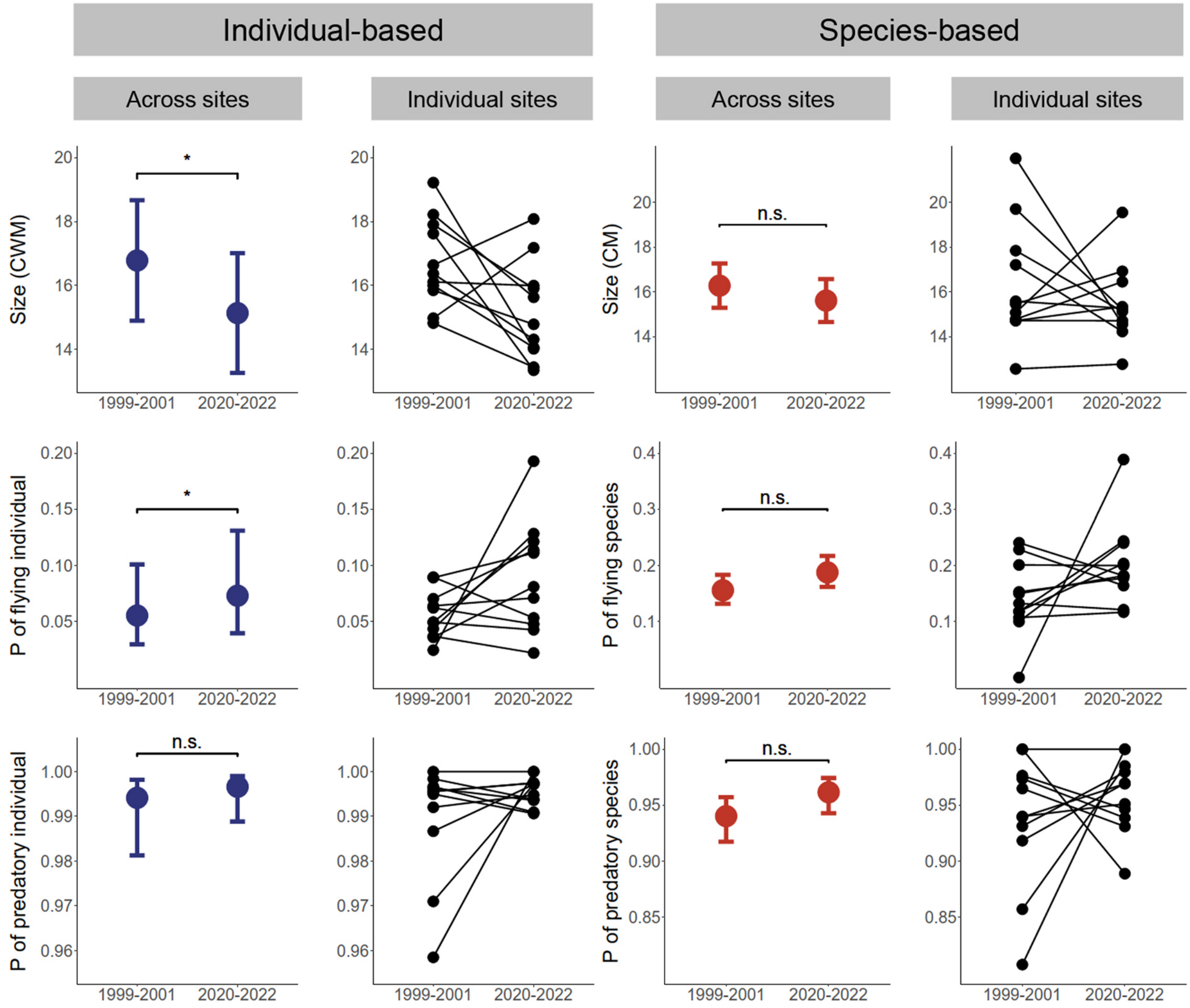

Fig. 4 Species traits: Estimated changes between 1999 and 2001 and 2020 and 2022 in Size (top), wing morphology/ability to fly (middle) and feeding guild/predators (bottom), each based on individuals and occurring species and across all sites and for specific study sites. Dots represent estimated means, 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

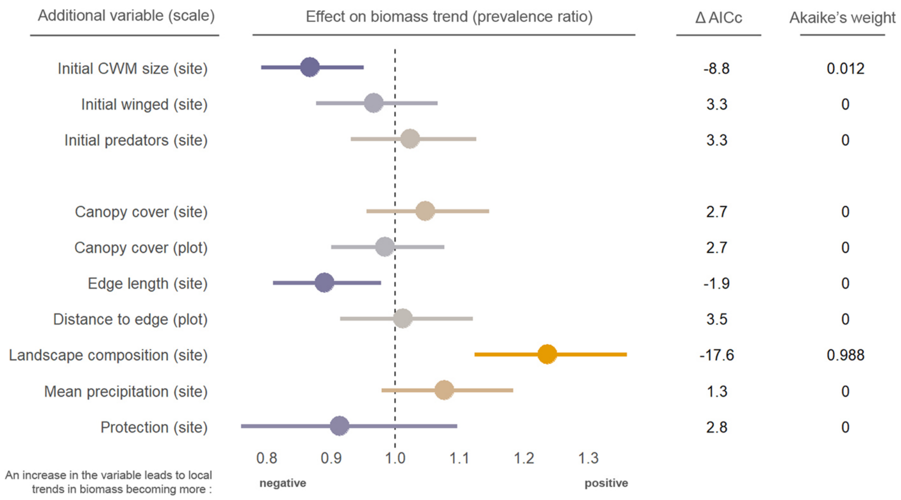

Fig. 5 Results from testing additional predictors and their effects on biomass trends. 'Scale' states the spatial resolution of the predictors. The points indicate the respective variable's effect on biomass trends expressed as prevalence ratio (i.e. 1 = no effect). Bars highlight the 0.95 confidence 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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