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Where have all the beetles gone? Long-term study reveals carabid species decline in a nature reserve in Northern Germany

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Abstract. 1. The drastic insect decline has received increasing attention in scientific as well as in public media. Long-term studies of insect diversity trends are still rare, even though such studies are highly important to assess extent, drivers and potential consequences of insect loss in ecosystems.

2. To gain insights into carabid diversity trends of ancient and sustainably managed woodlands, we analysed data of carabid beetles from a trapping study that has been run for 24 years in an old nature reserve of Northern Germany, the Lüneburg Heath. We examined temporal changes in several diversity measures (e.g. biomass, species richness, functional diversity and phylogenetic diversity) and tested diverse species traits as predictor variables for species occurrence.

3. In contrast to recently published long-term studies of insect diversity, we did not observe a decline in biomass, but in species richness and phylogenetic diversity in carabids at our study site. Additionally, hibernation stage predicted the occurrence probability of carabids: Species hibernating as imagines or both imagines and larvae and breeding in spring showed strongest declines.

4. We assume the detected trends to be the result of external effects such as climate change and the application of pesticides in the surrounding. Our results suggest that the drivers for the insect decline and the responses are multifaceted. This highlights the importance of long-term studies with identification of the catches to, at best, species level to support the understanding of mechanisms driving changes in insect diversity and abundance.

Key words. Biomass, functional diversity, ground beetle, insect decline, insect monitoring, phylogenetic diversity, species richness, traits.

Introduction

In recent years, a drastic decline of insects has been detected in diverse habitats and ecosystems (Dirzo *et al.*,

2014; Hallmann *et al.*, 2017). Since then the insect decline has received a lot of attention, both in ecological and conservation research and in public media as the phenomenon might occur globally at a high pace, with yet unknown ecological consequences (Leather, 2018). However, to entomologists this decline was not surprising news since early compilations (Didham *et al.*, 1996), older studies (e.g. Driscoll & Weir, 2005; Haskell, 2000) or analyses of red lists and large-scaled inventories (e.g. Desender *et al.*, 2010; Schmidt *et al.*, 2016) had already shown an

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increasing number of threatened and vulnerable insect species.

One meaningful approach to deliver a better evidence base to understand extent, significance and potential drivers of the fate of insect populations and species is to carry out long-term studies on specific sites. Only in such studies changes in assemblages or population sizes across time can be related to possible explanatory factors such as land use or climatic changes (e.g. Dieker *et al.*, 2011). Such studies can surely help to collect valuable information needed to develop effective conservation measures for insect populations, species and communities. Currently, long-term data on species' occurrences revealing insights into insect diversity and abundance trends are rare (see for exception: Brooks *et al.*, 2012; Hallmann *et al.*, 2018). This is in contrast to several well-organised monitoring programs on birds and mammals (cf. Battersby & Greenwood, 2003; Schmeller *et al.*, 2012) that have already generated solid data over large temporal and spatial scales.

Insects are the most diverse taxon on Earth in terms of species numbers, with beetles representing the largest proportion of this group of organisms. Insects are of considerable importance for ecosystem functioning (Samways, 2005). Especially carabids can be used as indicators for habitat quality, environmental changes as well as ecosystem resilience (Koivula, 2011) and are of high importance for the assessment of environmental impacts as well as for the evaluation of conservation measures (e.g. Kotze *et al.*, 2011; Thom *et al.*, 2017). Thus, the implementation of suitable conservation strategies for such a functionally important taxon requires specifically designed long-term studies to enhance our understanding of potential drivers of diversity loss.

The few long-term trapping studies of carabids have focused mostly on heathland and grassland species (e.g. Hallmann *et al.*, 2018; van Noordwijk *et al.*, 2017). On local and country level, long-term studies on carabids demonstrate in general a declining trend of species numbers and biomass (Hallmann *et al.*, 2018; Kotze *et al.*, 2011). Brooks *et al.* (2012) revealed a similar trend for open habitat types in Great Britain and presume land-use intensification in agricultural landscapes to be the main driver of species and biomass decline in carabids. In less intensively used forests and hedgerows, however, carabid abundance increased significantly (Brooks *et al.*, 2012). Since forest management in some regions (e.g. Central Europe) has developed to be less intensive and more sustainable than in previous centuries (Brang *et al.*, 2014; Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Forsten, 1997), carabid diversity and abundance may have increased also in Central European woodlands. In contrast, other arthropod taxa indicate a poor conservation status of Central European forests (Seibold *et al.*, 2015).

Traits suggest a mechanistic explanation for many ecological processes which cause extinction processes of species or the decrease of population densities as a

consequence of land-use changes, especially of insect species (Birkhofer *et al.*, 2017; Davies *et al.*, 2000; Nolte *et al.*, 2017). Identifying the characteristics which are common in those species which decline may enhance our understanding of the drivers of species loss.

Here, we analysed a long-term data set on ground beetles from 24 years of continuous pitfall trapping. Our study site 'Hofgehölz Möhr' is located in an ancient woodland within the oldest nature reserve and largest inland conservation area of northern Germany, the Lüneburg Heath. Since the 1990s, the studied forest site is extensively used. Pitfall traps to inventory carabids were installed in 1994 and have been monitored continuously since then (cf. Günther & Assmann, 2004). Thus, the site is well suited to record long-term population trends and to study if the findings from British woodlands (Brooks *et al.*, 2012) also apply to this specific area in mainland Europe, especially in long-term stable and sustainably managed woodlands. We specifically address the following research questions: (i) Have diversity, abundance and biomass of forest carabids changed over the last 24 years? (ii) If there are changes, which traits are characteristic for the increasing or decreasing species? We expect stable environments, such as forests, to be advantageous for large-bodied and flightless carabid beetle species (Homburg *et al.*, 2013) but also other traits might explain species occurrence and abundance (Nolte *et al.*, 2017, 2019).

As the few existing studies do not show coherent patterns and moreover use different measures of biodiversity (e.g. biomass, abundance or species numbers), it is difficult to derive reliable conservation strategies for ground beetles in woodland habitats. Thus, our study contributes to a better understanding of long-term dynamics of ground beetle communities for our region.

Material and methods

Study site

The study was initiated in 1994 at the 'Hofgehölz Möhr', an ancient woodland in Northern Germany near the town of Schneverdingen (cf. Günther & Assmann, 2004). The site was already labelled as 'woodland' on historical maps dating back to the 18th century ('Kurhannoversche Landesaufnahme' 1774–1786), as well as on following ones, and as such is assumed to have been continuously wooded since the last ice age. 'Hofgehölz Möhr' is located in the Lüneburg Heath Nature Reserve which was first designated in 1921 (219 km²) and expanded to its current size of 231.5 km² in 1993. Until the 1960s, the surrounding heathland, bog and fen areas were used for extensive agriculture, especially peat cutting and grazing. Since then, the utilisation has been further reduced and some restoration measures (e.g. blocking of drainage ditches near the study area) occurred in 2003 and 2004. Nevertheless, the study site is not directly influenced by groundwater table changes as the sites are

located about one metre higher than the forest-adjacent open sites. The ancient woodland 'Hofgehölz Möhr' is about 4 ha in size but is today included in a forest of approximately 70 ha. The canopy layer of the studied Pericycleno-Fagetum forest is dominated by beech (*Fagus sylvatica*) and common oak (*Quercus robur*), the litter layer and humus have a relative low pH value (cf. von Oheimb *et al.*, 2008). During the study period, the forest site was completely left to natural development and did not experience any disturbance, with the exception of the removal of some Norway spruce (*Picea abies*) tree individuals in 2007 (Verein Naturschutzpark e.V., pers. comm.).

Trapping

Since 1994, continuous trapping of ground beetles has been carried out with eight pitfall traps being open throughout each year. The traps (plastic cups, 10 cm diameter, 10.3 cm depth and 500 ml volume) were placed in a transect from North to South with 10–12 m distance between traps. The traps contained a mixture of ethanol (40%), water (30%), glycerol (20%) and acetic acid (10%) (cf. Renner, 1980). Between March and October, the traps were emptied fortnightly, between November and February monthly. Carabids from each trap were identified to species level and the number of individuals per species per trapping period counted. Our analysis is based on data gathered from June 1994 until December 2017.

Data analysis

All statistical analyses were run in R (version 3.3.2, R Development Core Team, 2016). Graphs were drawn using the 'ggplot2' package (version 2.2.1, Wickham & Chang, 2016) in R. The number of species in a sample (or, in this case: year) is highly dependent on the number of individuals in this sample. Therefore, we calculated the species richness using a rarefaction approach based on the minimum number of individuals trapped in a year (425 in the year 2004). Species richness was calculated using the package 'vegan' (version 2.4-5, Oksanen *et al.*, 2017).

For calculating functional diversity, we compiled traits typically used for ground beetles (Birkhofer *et al.*, 2017; Homburg *et al.*, 2014; Nolte *et al.*, 2017) (Table 1). Traits were compiled from www.carabids.org (Homburg *et al.*, 2014), amended by information from Turin (2000) and Nolte *et al.* (2017) and from Gesellschaft für Angewandte Carabidologie (2009) for the habitat preferences. Functional diversity was calculated after Petchey and Gaston (2002, 2006) using the 'Gower' distance metric for building the cluster dendrogram (UPGMA method, package 'cluster' (version 2.0.5, Maechler *et al.*, 2016) in R) based on a set of variables in which the levels of each trait variable were coded using two variables (Table 1). From the resulting cluster dendrogram, the sum of the vertical cluster branch lengths for all occurring species (weighed by their

abundance) represents the functional diversity of a specific community (here: the species set of a certain year).

We calculated the phylogenetic diversity for each year by calculation Rao's quadratic entropy (Rao's Q; Rao, 1982) from a species-by-species taxonomic distance matrix (Euclidean distances) and a species-abundance matrix. Rao's Q is calculated as the variance in pairwise species dissimilarities (e.g. phylogenetic or functional) among the relative species abundances of all individuals in a community (de Bello *et al.*, 2010; Schuldt *et al.*, 2014). The taxonomic distances were calculated using taxonomical hierarchies according to the Catalogue of Palearctic Coleoptera (Löbl & Smetana, 2003; Nolte *et al.*, 2017). Since for many species no DNA sequences are available yet, a molecular phylogeny, as described in phylogenetic trees, was not applicable. Nevertheless in carabids, taxonomic hierarchies are highly supported by molecular phylogenies (for genus level, see Ober & Maddison, 2008; for subgenus level within the *Carabus* group, see Deuve *et al.*, 2012).

Species biomass was calculated from mean body length after Booij *et al.* (1994) and multiplied by the number of individuals per year. The total biomass per year over all species was then calculated.

The calculated measures of diversity may not be independent from, but correlated to, each other. To assess relationships between them, Spearman Rank correlations were conducted. Resulting correlation probabilities were corrected for repeated testing using the False Discovery Rate (Benjamini *et al.*, 2001). Likewise, trait variables can be related to each other, that is the occurring sets of trait variable levels may not always be independent of each other. We thus checked for possible associations between the analysed trait variables by a set of χ^2 contingency tests (for sets of two nominal variables) or ANOVA with subsequent Tukey's post hoc tests (combination of numeric and nominal variables). The post hoc tests were run in the R package 'multcomp' (version 1.4.8, Hothorn *et al.*, 2017). Repeated testing was accounted for by using the False Discovery Rate.

We tested for possible temporal linear changes in species numbers, species richness, phylogenetic and functional diversity as well as numbers of individuals and biomass using general linear models with 'Year' as the only explanatory variable. Model assumptions were checked graphically using diagnostic plots.

To test whether trait variables explained changes over time in the species occurrence (presence/absence), generalised linear mixed effects models (GLMMs) with binomial errors and 'Species' as random term was used. Analysing the interaction between 'Year' and each of the following trait variables 'Body size', 'Food preference' and 'Hibernation type' allowed us to assess a possible change across time in the relative occurrence of species with a respective trait level. All other traits were significantly associated with the three chosen trait variables (Table 2), and, thus, not incorporated into the model. Models were run using the 'lme4' package (version 1.1.15,

Table 1. Trait variables and their levels for the 55 recorded ground beetle species. For different analyses, the trait variables were coded in different ways, as can be seen from the third and fourth column.

| Trait variable | Explanation | Variable type and level(s) for calculation of functional diversity | Variable type and level(s) for analyses of relationships between trait variables | No. species in a trait level group |
|--------------------|--|---|---|------------------------------------|
| Body size, mean | Mean body length from tip of mandible to tip of elytra, in mm. | - | Continuous | 55 |
| Body size, minimum | Minimal body length, measured as above, in mm | Continuous | - | 55 |
| Body size, maximum | Maximal body length, measures as above, in mm | Continuous | - | 55 |
| Wing development | Development of the alae, that is the second pair of wings | 2 variables, nominal: 1 – 0: brachypterous 1 – 1: dimorphic 0 – 1: macropterous | Nominal, 3 levels: • brachypterous • dimorphic • macropterous | 11 18 26 |
| Habitat preference | Preferred habitat after Gesellschaft für Angewandte Carabidologie (2009) | 2 variables, nominal: 1 – 0: forest species 1 – 1: eurytopic 0 – 1: other habitats | Nominal, 3 levels: • forest species • eurytopic • specialists for other habitats | 15 18 22 |
| Food preference | Preferred type of food | 2 variables, nominal: 1 – 0: predator 1 – 1: omnivorous 0 – 1: herbivorous | Nominal, 3 levels: • predator • omnivorous • herbivorous | 38 9 8 |
| Hibernation type | Developmental stage in which species hibernates | 2 variables, nominal: 1 – 0: imagines 1 – 1: both stages 0 – 1: larvae | Nominal, 3 levels: • imagines • both stages • larvae | 34 9 12 |
| Reproduction time | Season in which species reproduces | 2 variables, nominal: 1 – 0: spring 1 – 1: indifferent 0 – 1: autumn 0 – 0: other | Nominal, 4 levels: • spring • both seasons • autumn • other | 33 4 16 2 |

Bates *et al.*, 2015). Models were simplified step-wise using likelihood ratio tests, starting with the two-way interactions, until only significant terms (or those included in significant interactions) remained (Crawley, 2007).

Results

Between June 1994 and December 2017, a total of 29 829 ground beetle individuals from 55 species were caught. Fifteen species were recorded with only one individual each (Table S1). Fifteen species were forest specialists, 18 species were eurytopic, and 22 were specialists for other, adjacent habitat types. The number of species trapped in a year ranged from 11 (2016) to 31 (1998), with a median of 17.5 (interquartile range: 16–21) species per year.

Measures of diversity

Both the number of species and the species richness (Fig. 1a) declined significantly across years, and there was a trend for a reduction in functional diversity (Table 3). In addition, the phylogenetic diversity decreased significantly over time (Table 3, Fig. 1b). While the number of

species, species richness and functional diversity were significantly positively correlated to each other, the phylogenetic diversity was not correlated to either the species richness or the functional diversity (Table 4).

In contrast, there was no significant change in the total number of individuals (across all species) caught over the years (Table 3), which ranged from 425 (2004) to 2244 (1998). Likewise, the total biomass did not vary systematically over time (Table 3, Fig. 1c). The yearly total biomass varied between 140 g (2004) and 963 g (2008). Both measures (number of individuals and total biomass) were highly positively correlated (Table 4).

Trait relationships and affected traits

The recorded beetle species differ in their life-history traits. However, not all of the traits varied independently from each other but were related in a certain way (Table 2). For instance, average body size of a species was significantly related to its wing development (larger beetle species are less likely to fly, Fig. S1a in Supplement) and to its habitat preference (forest species were significantly larger, Fig. S1b). The spring breeders were significantly smaller than the autumn breeders, while the

Table 2. Relationships between traits of the captured 55 species were assessed using contingency tables (exception: for relationships with the continuous variable 'Body size', ANOVAS were used). Indicated in bold are those test-statistics that remain significant after correction for multiple testing (False Discovery Rate after Benjamini *et al.*, 2001). Underlined trait variables were used for further analysis.

| | Wing development | Habitat preference | <u>Food preference</u> | <u>Hibernation type</u> | Reproduction time |
|-------------------------|-------------------------------------|---|--|---|--|
| <u>Body size</u> | $F_{2,52} = 49.78$, $P < 0.001$ | $F_{2,52} = 9.58$, $P < 0.001$ | $F_{2,52} = 1.03$, $P = 0.365$ | $F_{2,52} = 6.80$, $P = 0.002$ | $F_{3,51} = 3.74$, $P = 0.017$ |
| Wing development | | $\chi^2 = 24.95$, d.f. = 4 $P < 0.001$ | $\chi^2 = 10.63$, d.f. = 4 $P = 0.031$ | $\chi^2 = 8.84$, d.f. = 4 $P = 0.065$ | $\chi^2 = 9.55$, d.f. = 6 $P = 0.145$ |
| Habitat preference | | | $\chi^2 = 3.11$, d.f. = 4 $P = 0.539$ | $\chi^2 = 7.87$, d.f. = 4 $P = 0.094$ | $\chi^2 = 8.85$, d.f. = 6 $P = 0.182$ |
| <u>Food preference</u> | | | | $\chi^2 = 3.68$, d.f. = 4 $P = 0.452$ | $\chi^2 = 6.43$, d.f. = 6 $P = 0.377$ |
| <u>Hibernation type</u> | | | | | $\chi^2 = 64.52$, d.f. = 6 $P < 0.001$ |

other species showed intermediate body sizes (Fig S1c). Likewise, the reproduction time was significantly related to the hibernation type (most of the spring breeding species hibernated as adult beetles, Fig. S1d). The food preference was not significantly related to any of the other studied traits.

The likelihood of a species being present declined differently depending on its body size (GLMM, 'Body size : Year', $\chi^2 = 10.26$, d.f. = 1, $P = 0.001$; Fig. 2a): the smaller the species, the more pronounced was its decline (Fig. 2a). In addition, the decline in the likelihood of species' occurrence over time was explained by the developmental stage at hibernation (GLMM, 'Hibernation type : Year', $\chi^2 = 7.42$, d.f. = 2, $P = 0.024$; Fig. 2b): those species that hibernated as larvae were less likely to disappear over time than those hibernating as imagines or as both stages ($\chi^2 = 7.03$, d.f. = 1, $P = 0.008$); the latter did not differ over time in their occurrence probability ($\chi^2 = 1.41$, d.f. = 2, $P = 0.493$; Fig. 2b). The food preference of a species did not predict the likelihood of its occurrence across time (GLMM, 'Food preference: Year', $\chi^2 = 2.88$, d.f. = 2, $P = 0.236$) or its presence independently of time (GLMM, 'Food preference', $\chi^2 = 3.60$, d.f. = 2, $P = 0.166$). A model, in which the variable 'Wing development' was additionally included, resulted in the same outcome as the before-mentioned model (not shown).

Discussion

In contrast to recently published long-term studies of flying insect diversity in Germany and the Netherlands (e.g. Hallmann *et al.*, 2017, 2018), we did not observe a decline in biomass, but in species richness and phylogenetic diversity, and a declining trend in functional diversity in carabids at our study site. Our results of decreasing diversity measures are in accordance with surveys on many other studied insect taxa, such as butterflies, moths and solitary bees (Fox *et al.*, 2014; Habel *et al.*, 2016; Potts *et al.*, 2010). In summary, the

assumption that insect diversity is undoubtedly threatened is supported by this data.

However, it is difficult to infer that long-term insect decline appears as a uniform global trend over all regions, habitats and taxa, as the referred British study on carabid species concluded a positive population trend of carabids in woodland and hedges (Brooks *et al.*, 2012). The development of populations and community composition tends to be driven by more complex processes which are biased by local, regional and global factors such as land use (change) and disturbance regimes (e.g. agricultural and forestry activities, including the usage of pesticides: Geiger *et al.*, 2010; Nilsson *et al.*, 2008; Woodcock *et al.*, 2016), climate conditions and changes (Brandmayr & Pizzolotto, 2016; Habel *et al.*, 2016; Thom *et al.*, 2017), species traits (this study; Brooks *et al.*, 2012; Nolte *et al.*, 2017) and the interactions between these factors. Since it is difficult to disentangle the different mechanisms, we focus on the following main aspects.

Habitat

In their study of carabid species, Brooks *et al.* (2012) found carabids occurring in woodland and hedgerow habitats to be the only group with increasing abundance and richness trends. The authors assume habitat stability in woodland habitats to be a buffer against perturbations. As changes in forest management practices in Central Europe have put a better focus on preserving the ecological functions over the last decades (Brang *et al.*, 2014), we expected similar results for our study area, which is located in an ancient woodland and protected as nature reserve for almost a century. However, the extent of external effects is unknown, as the following example illustrates: East of the Lüneburg Heath Nature Reserve, insecticides against caterpillars feeding on oaks [e.g. the oak processionary (*Thaumetopoea processionea*), winter moth (*Operophtera brumata*) and green oak moth (*Tortrix viridana*)] have been applied between 2012

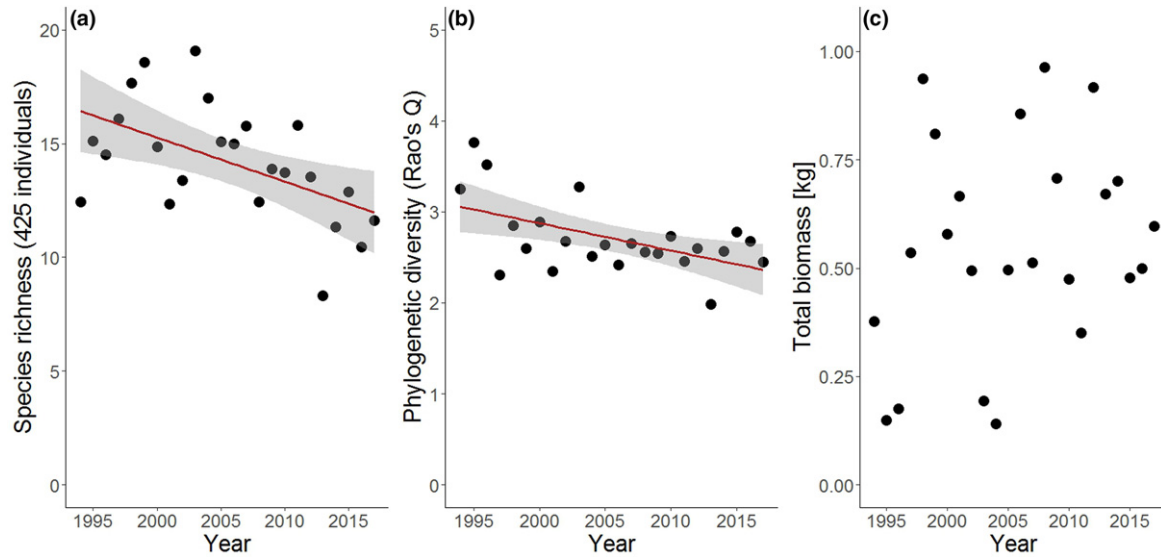


Fig. 1. Rarefied species richness (a), phylogenetic diversity (b) and total biomass (c) across 24 years of study. The lines and the shaded areas indicate significant declines over time (GLM, 95% confidence interval). For further details, see Table 3. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 3. Results from GLMs testing for changes in community characteristics across 24 years for the complete species pool (55 species) and for woodland species (15 species) only. Intercepts represent averages for the year 1994. Significant effects are marked in bold.

| Response | | Coefficient | $F_{1,22}$ | P | R^2 |
|--|-------------|--------------|-------------|--------------|--------------|
| All species: 55 species, 29 829 individuals | | | | | |
| No. species | Intercept | 22.53 | | | |
| | Year | -0.31 | 5.38 | 0.030 | 0.197 |
| Species richness (rarefied to 425 individuals) | Intercept | 16.62 | | | |
| | Year | -0.19 | 8.84 | 0.007 | 0.289 |
| Functional diversity | Intercept | 4.81 | | | |
| | Year | -0.04 | 3.69 | 0.068 | 0.144 |
| Phylogenetic diversity | Intercept | 3.09 | | | |
| | Year | -0.03 | 8.99 | 0.007 | 0.290 |
| No. individuals | Intercept | 1204.8 | | | |
| | Year | 3.19 | 0.04 | 0.846 | 0.002 |
| Total biomass [kg] | Intercept | 0.44 | | | |
| | Year | 0.009 | 1.63 | 0.215 | 0.069 |

(‘Landeszeitung’, April 25, 2012) and 2018. The agent used, Diflubenzuron, is known to have negative effects also on non-target species, especially on other herbivorous species and their predators (Hassan *et al.*, 1994). Klenner (1994) found for Diflubenzuron-treated woodlands a reduced number of carabid individuals, especially of spring breeders. These carabids reproduce and have early larval instars during the application time of Diflubenzuron. The synchrony of the agent application and the occurrence of early larval instars imply causal negative effects of the insecticide on these non-target species. For agro-ecosystems, Geiger *et al.* (2010) already showed that

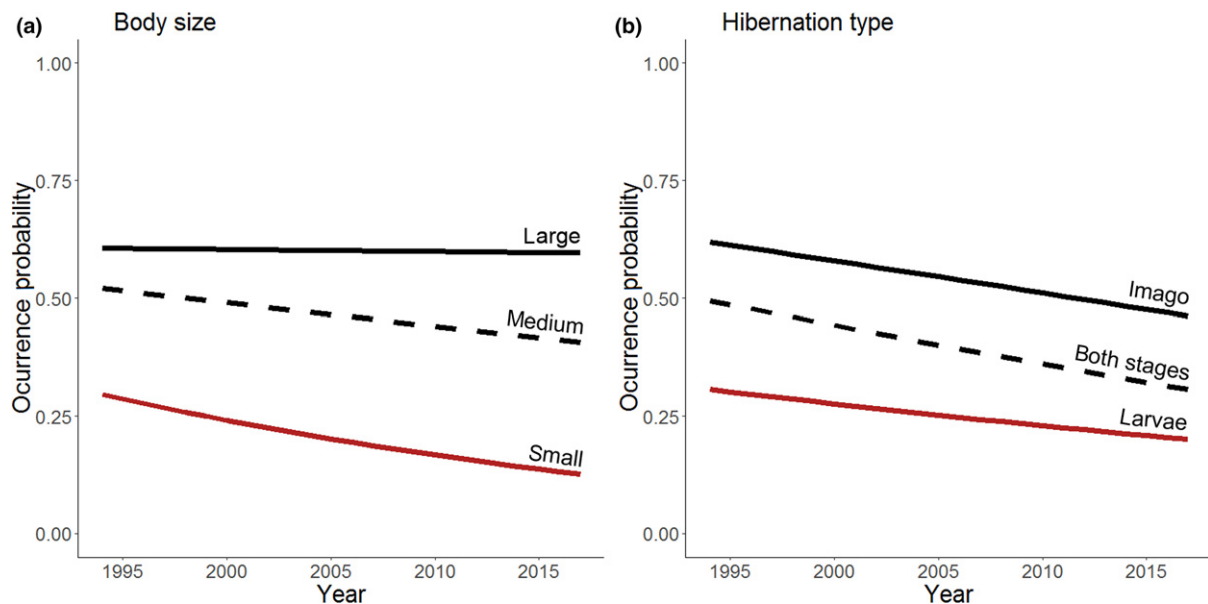
pesticides, such as insecticides used for crop protection, do not only harm the target organisms. These products even have an immense negative effect on other insects (including those providing biological control, e.g. carabids) and thus are one driver of biodiversity loss (Purtauf *et al.*, 2005; Scherney, 1959; Thiele, 1977). The exact influence of pesticide applications in surrounding areas can only be assumed, since we are lacking data on precise insecticide usage near the nature reserve and measures of chemical influences on the study plot. Specific research designs would be required to identify, for example, the drifting effects and their impacts on species and ecosystems.

Species traits

As our results show species loss in an ancient habitat type, habitat stability may not be the most important factor shaping long-term trends of species abundances and occurrences. Trait-based studies are increasingly used to test hypotheses on species occurrence and extinction probabilities (e.g. Nolte *et al.*, 2017). In times of dramatic insect decline, traits may be used to improve the understanding of extinction processes. However, the study of species traits cannot be made simply by consolidation or differentiating species by each trait independently. Species characteristics can be strongly correlated but not in a linear relationship over all species (cf. Davies *et al.*, 2004; Laube *et al.*, 2013). Our results show high correlation values between reproduction and hind wing development, the latter being the more obvious trait in carabid species but apparently not the one having the stronger effect on occurrence probability. Nolte *et al.* (2017) showed for a large-scale data set that

Table 4. Spearman rank correlations between different biodiversity measures. Significant correlations (after correction for multiple testing, cf. Benjamini *et al.*, 2001) are indicated in bold; *P*-values are given in brackets.

| | Species richness | Functional diversity | Phylogenetic diversity | No. individuals | Total biomass |
|------------------------|--------------------------|--------------------------|------------------------|-----------------------|--------------------------|
| No. species | 0.785 (<0.001) | 0.944 (<0.001) | −0.099 (0.644) | 0.397 (0.055) | 0.338 (0.106) |
| Species richness | | 0.723 (<0.001) | 0.203 (0.341) | −0.110 (0.609) | −0.213 (0.316) |
| Functional diversity | | | −0.101 (0.618) | 0.417 (0.044) | 0.328 0.118 |
| Phylogenetic diversity | | | | −0.493 (0.015) | −0.446 (0.030) |
| No. individuals | | | | | 0.877 (<0.001) |

**Fig. 2.** Changes in species occurrence probabilities depending on their body size (a) and hibernation type (b). For simplification of the presentation, two separate GLMMs with only the interaction between ‘Body size : Year’ and ‘Hibernation : Year’, respectively, and the main effects included in the interaction were run to create prediction lines for (a) and (b). A three-level variable ‘Body size class’ was built from the continuous variable ‘Body size’ (statistics reported in the main text were based on the continuous variable): Small species [< 10 mm]; medium sized species [$10 - <20$ mm]; large species [≥ 20 mm]. [Colour figure can be viewed at wileyonlinelibrary.com]

dispersal ability is a suitable predictor for the extinction risk of woodland species, with dimorphic carabids being less vulnerable to extinction. In our study on the local level, however, species’ dispersal ability represented by hind wing development appears to be the weaker predictor in contrast to reproduction period.

In addition, we found other species characteristics such as body size or hibernation type to be good predictors for occurrence probability of species. In our study, diversity loss is represented by a decreasing number of small species, whereas the occurrence probability of large species was stable over time. This may be due to the fact that woodland specialists, at least in our study, were significantly larger than species specialised to other habitats and eurytopic species. This may also explain that we did not find a decline in biomass over time as only the smaller species showed a decrease. Other studies, however, found large carabids to be more prone to species decline (Brooks *et al.*, 2012; Kotze & O’Hara, 2003; Nolte *et al.*, 2019).

As spring breeders may also be affected by insecticide applications in woodlands (Klenner, 1994) or arable fields in the surrounding, our recent results cannot disentangle which factor – global climate change or local pesticide application or both factors – is responsible for the observed species diversity trends.

Climate change

In addition, we detected hibernation stage as a significant predictor of occurrence probability of carabids. Nevertheless, the traits hibernation stage and reproduction time of the species were closely associated. Species hibernating as imagines or both imagines and larval instars tend to face a stronger decline than species hibernating as larval instars only (this study; Lindroth, 1949). Since species of these two hibernation types are more likely to be spring breeders, this trend is also true for this group of

species. The larvae of spring breeders are active in summer and have to face higher temperatures and mostly lower humidity than species reproducing in autumn and hibernating as larvae. For instance, in habitats with a Mediterranean climate (low precipitation, but high temperatures during summer and mild, but rainy winters), spring breeders seem to be completely absent in woodlands (Brandmayr *et al.*, 1983; Timm, 2010). This is probably a consequence of the drought stress of larvae during summer, as larval instars are the most sensitive part of the life cycle in ground beetles (Lövei & Sunderland, 1996).

As a consequence of climate warming, some spring breeders tend to follow suitable climate conditions and show an uphill shift of their occurrences (Brandmayr & Pizzolotto, 2016). During the last seven decades, mean annual temperature increased by 1.9°C and summer precipitation decreased by 5 to 10 per cent in Lower Saxony. Moreover, heat waves and drought periods during summer increased significantly (Umweltbundesamt, 2018). Consequently, the strong declining trend of spring breeders can be the result of ongoing climate change. Further investigations linking species abundance and occurrence data to local climate conditions are required and planned for this sample in order to improve the knowledge on above-mentioned interrelations.

Conclusions

Our long-term study shows a decline of species numbers and phylogenetic diversity of carabids in the oldest nature reserve of northern Germany. The study highlights the importance of long-term studies in which the individuals are identified to a low taxonomic (ideally down to species) level. Only this allows a deeper insight and, thus, the understanding of mechanisms driving local and global patterns of insect diversity and abundance.

In order to understand these patterns and the underlying mechanisms, we need to design and, more importantly, carry out standardised and comparable long-term studies in different habitats (not only in protected areas but also intensively used agricultural and forestry landscapes): a large-scale and long-time insect monitoring would be necessary. This is of crucial importance when it comes to further enhancing the knowledge whether or not a global trend of an insect decline applies to all species and habitats. To support (or falsify) such a hypothesis, data availability, especially long-term approaches with standardised and comparable research designs and analytical approaches, must be improved or developed. From a conservation perspective, we also require better evidence on population trends of specific species groups in nature reserves in order to distinguish between local and global drivers for, for example, insect decline and to evaluate the success of conservation measures and interventions.

Using trait-based approaches to predict species occurrence probabilities appears very promising. Nevertheless, statistical analyses always have to account for trait correlations and ecological background knowledge has to validate model results.

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Supporting Information

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

Table S1. Species caught in the study area with their habitat preference, traits and average total body size (min and max) and weight (calculated after Booij *et al.*, 1994).

Figure S1. Relationships between significantly related trait variables: Body size and wing development (a), body size and habitat preference (b), body size and reproduction (c), and reproduction and hibernation (d). In the box-whisker-plots different letters indicate significant differences (Tukey post-hoc tests, $p < 0.05$).

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