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Trends in monthly abundance and species richness of carabids over 33 years at the Kaiserstuhl, southwest Germany

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Abstract

Recent studies hint at consistent declines of insect abundance across taxa. However, detailed data from long-term surveys are rare in ecological studies, and yet are required in order to accurately infer trends and their causes. In the following, we analyse a dataset from pitfall traps sampled at a monthly resolution over a 33-year period (1979−2011) to investigate the activity density and species richness of ground beetles (Carabidae). The study site, an unmanaged xerophytic grassland amidst intensively managed vineyards in southwest Germany, underwent terracing for viticulture just before data collection began, which led the early community composition to be defined by succession. As this ecological situation initially conflates succession and other long-term trends, we define three successional phases (initial, early, and late), allowing us to separate trends over time. We use a generalised additive modelling approach to factor in the main drivers of the community trends in ground beetles, noticeably vegetation and climate. Both vegetation cover and climatic conditions had a small effect on carabid counts and species richness, and there was a notable decrease in both counts and species richness of 60% and 32%, respectively, during the late successional phase. An analysis of functional traits revealed an overall increase in community weighted mean biomass and a correlation of habitat preference with annual precipitation. Our results add to the growing volume of evidence pointing to a decline in insect populations both in central Europe and globally.

Keywords: Carabid beetles; Community ecology; GAM; Insect decline; Long-term survey; Xerophytic grassland

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Introduction

Long-term data sets are necessary in ecology in order to reveal species responses to changes in the environment (Dornelas et al., 2013). As many ecological processes take place over relatively long periods of time, their effects can only be revealed if the study period is long enough to encompass a wide enough range of environmental changes (Franklin, 1989). Ecosystem management also benefits from a greater understanding of ecological processes that occur over longer time scales (Lindenmayer et al., 2012). Recent interest in data relating to insect populations has increased since "insect decline" has become an unavoidable buzzword in the field of ecology as well as in the public sphere.

Due to the cost and logistics associated with long-term ecological surveys, very few such data sets exist. In the past few years, however, data collected over long periods of time investigating insect populations have been analysed and

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published (Hallmann et al., 2017; Homburg et al., 2019; van Klink et al., 2020; Powney et al., 2019; Schuch, Bock, Krause, Wesche & Schaefer, 2012). These studies, including the Rothamsted Insect Survey, which has been monitoring moth and aphid populations in the UK since 1964, have helped us better understand trends in insect abundance, species richness of certain insect groups as well as occupancy patterns (Bell et al., 2015; Conrad, Woiwod, Parsons, Fox & Warren, 2004; Shortall et al., 2009). Of the few such data sets that exist, however, many compare data from disparate years or locations, sometimes with non-standardised sampling schemes. To reduce dependence of results on a single year (Seibold et al., 2019), it is also important to ensure the study period is long enough to show robust trends. Even standardised annual sampling, such as in the 4th of July butterfly counts in the United States (Swengel, 1990) or the mid-January African-Eurasian waterbird census (Wetlands International, 2010), is potentially affected by phenological shifts, adding noise to any existing trend, compared to full-year counts. An additional challenge of insect surveys is the sheer volume of individuals collected, so that it is often only possible to measure them using a proxy for abundance, such as biomass (e.g. Hallmann et al., 2017), without being able to come to any conclusions about the change in species richness or shifts in dominant species or functional traits. This may also lead to a misinterpretation of certain trends if, for example, many small individuals are replaced by few larger ones or vice versa. This can be especially problematic if there is a large range of body sizes in the taxa being investigated, adding additional variance to the data.

Data from spatially limited, but temporally extensive standardised studies are important in that they can help uncover patterns at a local scale that can then be scaled up to investigate trends at larger spatial scales. The high resolution of these data sets (i.e. the intensity of the sampling effort and sample identification to species-level), such as a survey of hoverflies in England where samples from Malaise traps were collected weekly over 30 years (Owen & Gilbert, 1989), make them invaluable for uncovering local patterns that may be indicative of more widespread trends. amongst insect orders, ground beetles (Carabidae) have been particularly well investigated throughout Europe over the past century, with a number of studies describing changes in their abundance and range (Brooks et al., 2012; Desender & Turin, 1989; Kotze et al., 2011; Nolte, Boutaud, Kotze, Schuldt & Assmann, 2019; Turin & Den Boer, 1988). Ground beetles are also of importance to humans as biological control agents of pests and weed seeds in agricultural systems (Bohan, Boursault, Brooks & Petit, 2011; Kromp, 1999), show sensitivity to environmental changes, have a nearly global distribution (Lövei & Sunderland, 1996) and a stable taxonomy that allows for accurate identification (Kotze & O’Hara, 2003). These characteristics make them a common and appealing study organism for long term analyses, especially in temperate Central Europe.

Although short-term surveys might suffice to gain insights on individual species, as most carabids have short lifespans (mostly annual life cycles, but up to four years; Lövei & Sunderland, 1996), community-level changes are often only apparent after longer time periods. This is especially true in systems that undergo succession. Primary succession creates a rapid increase of resources and attracts different faunas. This of course also affects ground beetle populations, as they fulfil multiple functions at different trophic levels within an ecosystem (Lövei & Sunderland, 1996). Indeed, species traits reflect these functions and help us to interpret the causes as well as consequences of species turnover (Homburg et al., 2019; Nolte et al., 2019). Though weather patterns may change from year to year, the effects of climate on carabid populations can also only be revealed at longer time scales (see Thomsen et al., 2016).

Using data on a ground beetle assemblage collected in pitfall traps as part of a long-term survey over a period of 33 years (1979−2011) in Southwest Germany, we aimed to disentangle the effects of changes in climate and vegetation cover from long-term trends in ground beetle activity density (number of individuals trapped) and species richness (number of species trapped). The data were collected at the request of the state government to monitor the floral and faunal succession of a transformed landscape that was restructured to increase productivity for viticulture. The terracing that took place can be likened to lignite strip mining, where an area of 200 ha was stripped of topsoil leaving behind a surface devoid of most plant and animal life. The aeolian loess that remained has some properties, such as high water capacity and favourable soil structure, that resemble more mature soils and led to a rather rapid succession. After 6 years of monitoring large fallow slopes between terraces, a single slope was chosen as representative for the successional changes and was continuously monitored for a further 27 years.

For our analysis, we were guided by the following questions:

1. How has the activity density (henceforth also referred to as “counts”) and species richness of ground beetles changed over time after accounting for the effects of climate and vegetation cover?
2. Does the trend in ground beetle species richness follow that of activity density?
3. Is there a shift in functional traits over time that may help explain trends in ground beetle species richness and individual counts?

Materials and methods

Study area

Data were collected in the wine growing region of the Kaiserstuhl near the village of Oberbergen in the southwestern federal German state of Baden-Württemberg (Figs. A1 and A2). The Kaiserstuhl is a low mountain range with an area of 100 km^2 and the highest elevations around 500 m. With its location in the Upper Rhine plain, the Kaiserstuhl is one of the warmest areas in Germany (mean annual temperature of 10 °C with around 650 mm annual precipitation). In 1978–1979 the study site underwent reterracing designed to increase and improve the area available for modern viticulture. The Pleistocene loess cover, which is several metres thick (up to 40 m in some areas), and a defining feature of the landscape (Wilmanns, Wimmenauer, Fuchs, Rasbach & K., 1989), was removed or added to different areas in order to form the terraces (from here on referred to as loess removal or loess addition areas). After an initial study of 21 slopes between 1978 and 1984, one representative southern exposed slope was selected for continued observation of the floral and faunal succession. The data for the study presented here were collected on this slope located between two terraces. Due to their steep inclination and high erodibility of the loess, slopes in this area are unsuitable for agricultural production and have fallen fallow. This has led to a unique habitat of patches of steep, fallow land surrounded by intensively used agricultural land.

Data collection methods

Data collection using pitfall traps at this site began as an ecological monitoring project to document the primary succession on unmanaged areas after reterracing (Gack & Kobel-Lamparski, 1985; Kobel-Lamparski, 1987; Kobel-Lamparski & Lamparski, 1997). In July 1979, 15 pitfall traps (Fig. A3) were set up on a south-south east exposed slope (30°) between two terraces over an area of 250 *m*×20 m (Fig. A3). A transparent polyester resin cover was set up 15 cm above each trap to allow light to penetrate to the trap, but keep out any precipitation. Traps were set up in five rows of three traps each, with 25 m between each row (Fig. A4). Of the 15 traps, nine were located in loess removal areas and six in loess addition areas. The pitfall traps were emptied on a monthly basis for 33 years (until December 2011). In 2009, nine traps were abandoned for logistical reasons, leaving four in loess removal and two in loess addition areas for 2009–2011. Ground beetles were identified to the species level.

Vegetation composition was recorded at each trap in a 2 × 2 m quadrat each year according to the Braun-Blanquet cover abundance scale, as well as the relative vegetation cover, which we used as a proxy for succession after the reterracing. No vegetation data were collected from 1986 to 1991.

Weather data were taken from the nearest weather stations at Oberrotweil/Vogtsburg (1979–2003) and Blankenhornsberg (2004–2011), about 1 and 5 km from the study site, respectively. In addition to mean monthly temperature, mean annual temperature during the vegetation period and precipitation (mm/month), we also considered the number of ice days in the previous winter (days with maximum temperatures <0 °C), as this may be an important predictor for the survival of some beetles or beetle larvae (Bale & Hayward, 2010). The monthly mean temperature at the study site increased, although not significantly, over the survey period with the lowest temperatures recorded in 1980 and 1984 and the highest in 2003. However, according to a linear regression, the growing season mean temperature did increase significantly over the study period by around 1.65 °C (SE = ± 0.2 °C, *n* = 32). Despite the increase in temperature, there were no clear trends in the number of ice days per winter. There was also no significant change in monthly precipitation, although summers became wetter and winters drier.

Due to the unique conditions that prevailed at the beginning of the data collection, we classified three distinct periods that relate to the post-terracing succession. The *initial successional phase* (1979–1983) refers to the first years of the study, when vegetation was sparse and colonising carabid species dominated. The *early successional phase* (1984–1989) refers to the period in which the dry grassland habitat slowly established itself and new carabid species were found in the community year after year. The *late successional phase* (1989–2011) refers to the period in which the carabid community had stabilised and there were no successional shifts in carabid species composition. These phases were determined using an NMDS analysis of the yearly carabid species composition (Fig. 1) and are used to discuss the findings throughout this paper.

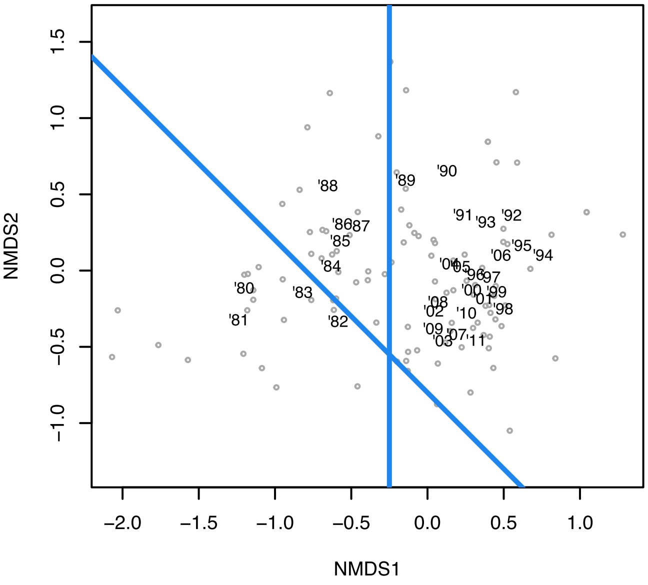

Fig. 1. Non-metric multidimensional scaling of row-wise normalised species composition. This figure forms the basis for identifying the three successional phases observed over the study period. The clearest dividing line would be vertical at approximately −0.3, i.e. to the left of 1989. Another dividing line can be drawn diagonally between 1983 and 1984, separating the first decade of sampling into initial succession (i.e. colonisation) and early successional phases. Open circles in grey represent single carabid species.

Data handling

All statistical analyses were performed using R 3.5.0 (R Core Team, 2019). Some data processing was required in order to fill gaps in the data. Vegetation cover data from 1986 to 1991 were interpolated using predictions from a linear model, as vegetation cover had increased rather linearly both before and after the period where data were missing. As only 6 of the 15 traps were sampled from 2009 to 2011, we imputed the missing trap level counts (for 324 of 5634 data points) to help inform our species richness model and calculate the rate of change in carabid counts over time. Since we analysed the counts at the level of the individual trap (see below), the model allowed us to predict the expected number of individuals for the traps with missing data. This imputation did not affect our results qualitatively, as we also fit a model only for the 6 continuously sampled traps, which yielded similar results, albeit with much higher residual error, due to the smaller number of data points. Monthly species richness values for 2009−2011 were estimated from the total monthly counts (observed trap counts for six traps plus the imputed counts for nine traps) using incidence-based species accumulation curves (Robert K. Colwell, Mao & Chang, 2004) calculated using the ‘rarecurve’ function from the R package ‘vegan’ (Oksanen et al., 2018). We used the monthly curves from 1986 - 2008 (period after initial vegetation succession) to estimate the respective monthly species richness for 2009−2011. See Appendix A for more details and code regarding data handling.

Statistical analysis

Activity density (counts)

We fitted GAMs using the R package ‘mgcv’ (Wood, 2011) to represent effects of different predictors on both the counts and species richness of ground beetles. The GAM framework was chosen as it allows us to model population trends with flexible smoothing terms (splines) to fit multiple nonlinear predictors. This is especially useful as the population data have a nonlinear seasonal trend that can be accounted for with such a modelling approach.

We analysed the monthly counts of carabid beetles in each trap using a mixed-effect GAM with negative binomial error distribution. The individual traps were represented as random effects, while mean monthly temperature, monthly precipitation, number of ice days, vegetation cover, mean growing season temperature and year were fitted with thin-plate regression splines (Table A1). Month of the year was fitted using a 12-month-cyclic cubic spline, forcing December and January values to smoothly connect. Moreover, we used loess addition (yes, no) as a categorical predictor in this model. As GAMs use shrinkage to reduce overfitting, the predictors “year” and “month” only contribute an effect not represented by climate and vegetation data. This minimises the probability of wrongly detecting a trend over time that could actually be attributed to variation in climate or vegetation, respectively.

Predictions of this model are presented by summing the expected count values for each trap for each month. The effects of model terms on counts are presented at the trap level, i.e. for an average trap, thereby removing the random variation across traps.

Given the high level of explained variance, we can provide reasonable carabid count estimates for the discontinued traps during the last three years of the study (2009−2011). Summing over these nine estimated and six observed values, we are thus able to extend the analysis for species numbers based on incidence based species accumulation curves as described in the previous section.

Species richness

To model species richness, we fit three separate GAMs in order to determine to what extent ground beetle counts determine species richness. Their comparison allows us to disentangle the trend in counts from a trend in species richness. The first model contained the same predictors as the count model, plus log carabid counts. It investigates trends *beyond* those in the carabid counts, which are used as a covariate. The second model contained all predictors except for log carabid counts, thus modelling the trend in species richness. The third model contained only log carabid counts as a predictor, largely to gauge how much variation can be explained without an additional trend in species richness. The species richness models were run at the level of the month (aggregated across all traps).

Functional traits

Trait data were compiled for all species from Trautner (2017). We considered commonly collected ground beetle traits including wing morphology (brachypterous, macropterous or dimorphic), biomass (calculated from body length following Sabo, Bastow & Power, 2002), habitat preference (xerophilic, non-xerophilic), trophic level (predator, herbivore, omnivore), breeding behaviour (spring, autumn, indifferent) and peak activity time (single peaks in spring, summer, autumn, or winter, double peaks, and year round). We used the ‘dbFD’ and ‘functcomp’ functions from the R package ‘FD’ (Laliberté, Legendre, Shipley & Laliberté, 2014) to calculate community weighted means (CWM), i.e. yearly trait values weighted by species activity density, for each of the traits and plotted each CWM over time to examine any visible trends or shifts in dominant traits over time.

Results

In total, 22 410 ground beetle individuals from 107 species in 37 genera were collected and identified over the 33-

year survey period. Singletons were recorded for sixteen of the 107 species.

Activity density (counts)

Trap counts varied according to month of year and also showed pronounced trends over the years (Fig. 2). Accordingly, month and year had the greatest effect in our count analysis, which explained 48% of the deviance, with the other predictors contributing only marginally (Fig. 3, see also Fig. A5 and Table A2). We did not find an apparent shift in phenology of carabid counts across the years, with peaks in counts occurring between April and May and a second, smaller peak in September (Fig. A10). A principal component analysis of climatic predictors (see Fig. A6) found no directionality in the overall climate on the basis of the climate variables used in our analysis.

We can report an overall decline in ground beetle counts over the study period following comparatively high counts during the first years of sampling (Figs. 2 and A7). The high counts at the beginning of the study coincide with the initial successional period after the terracing of the landscape. The early successional period ended in 1989 (Fig. 1) and from 1989 to 2011 a decrease in carabid counts of around 3.8% (± 2%) per annum, or 60% ([34%, 74%] 95%- confidence interval) over these 23 years was observed.

Species richness

Species richness largely followed the pattern of the carabid counts (Fig. 2B). The count-only model was as good as the environment-only model (see Appendix A), both accounting for 77% of the variance, while environment *plus* carabid counts explained only an additional 9% (total of 86%). Indeed, activity density was the most important predictor of species richness (Fig. 4), followed by phenology (i.e. month), year and temperature. The data show a loss of species richness over time, with a decrease of 1.6% (± 0.5%) per annum, or 31% ([25%,39%] 95%-confidence interval) fewer species present in 2011 than in 1989. Twenty-four species were collected in at least 25 of the 33 years of the study period, constituting a stable core community. The mean number of species collected per year was 45, with a mean annual absolute species turnover of 18 species (Fig. 5).

Traits

We looked at the community weighted means (CWM) of a number of commonly collected ground beetle traits over time to investigate shifts in dominance of functionally important traits. We found an increase in CWM biomass over time (Fig. A8). Interestingly, however, yearly total

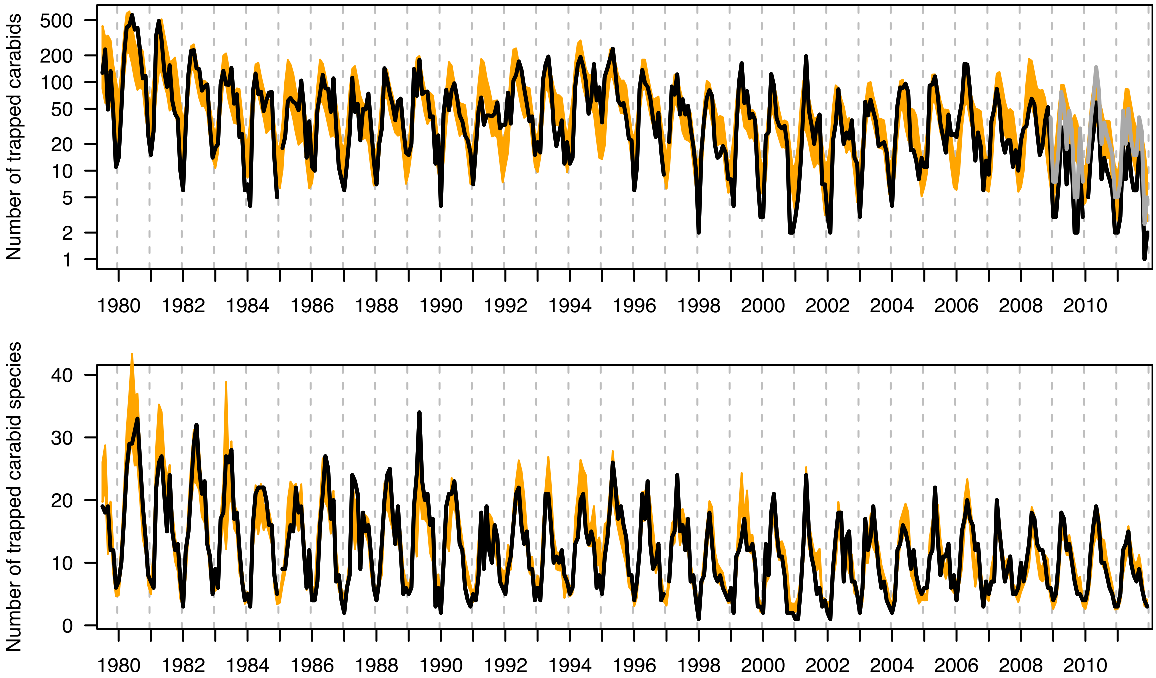

Fig. 2. Monthly individual (top) and species counts (bottom) of carabid beetles across 33 years from 15 pitfall traps in the Kaiserstuhl. Observed counts (black line) and model predictions (95% confidence interval, orange) are shown. For the individual counts, observed data for 2009−2011 (black) were multiplied by 15/6 to give an approximation of counts to be comparable to the other years (grey), as only 6 of 15 traps were sampled. For species richness, the interpolated richness values for 2009−2011 were used in the model. Both plots are on the response scale. (**Print in colour**). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

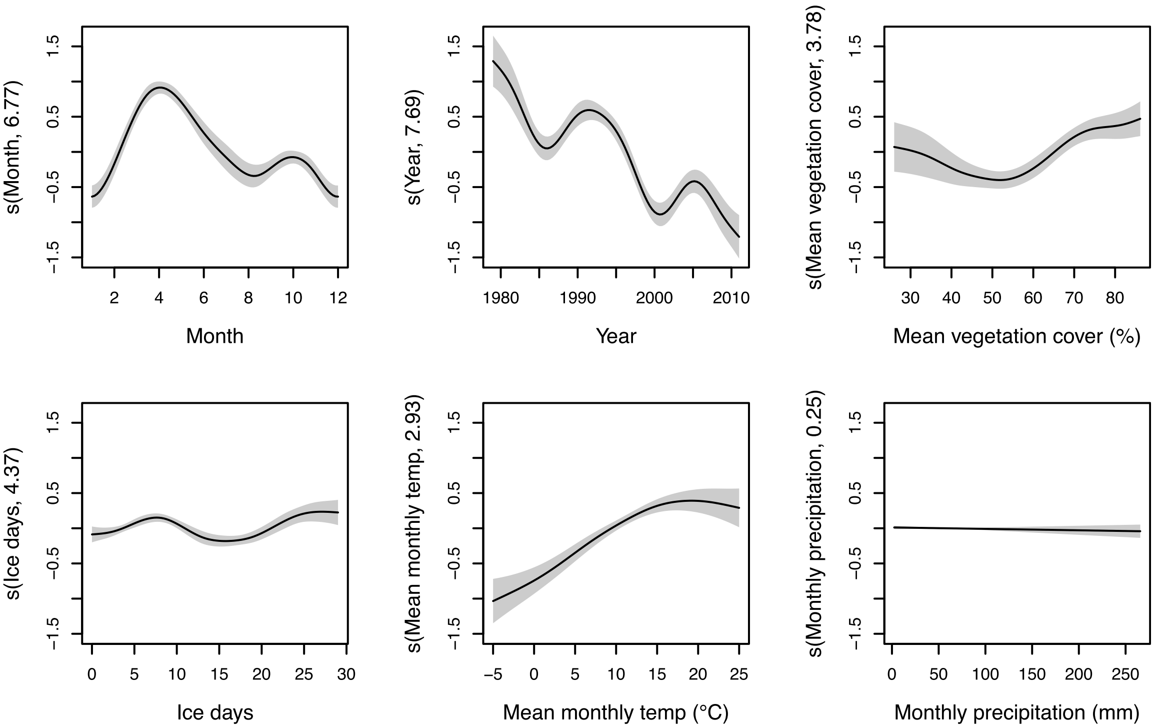

Fig. 3. GAM spline plots for effects on carabid counts with 95% confidence interval (grey). Shown here are the partial effects of month, year, annual mean vegetation cover, ice days, mean monthly temperature and monthly precipitation. Essentially, these plots show the change in individual counts (on the link scale) due to the respective model term, holding all other model terms at their mean value. Month and year clearly have the strongest effect on carabid counts.

biomass (sum of all individuals) still declined during the late succession period (annual loss of around 6%), showing that the decrease in counts more than compensated for the increase in CWM biomass over the same period (Fig. A9). The habitat preference showed clear patterns, with xerophilic species experiencing peaks in the mid 1990s and mid 2000s (Fig. 6). All other traits showed no overall trends other than during the early succession period.

Discussion

In this study, our long-term dataset of ground beetle counts and species richness at a site in southwestern Germany shows a decline in both species richness (−32%) and counts (−60%) over the last 23 years of the study period. Climate and vegetation cover could only explain a small amount of the variation in carabid beetle counts, with month (i.e. phenology) and year, a temporal variable encompassing non-measured environmental variation, being the most important predictors in our model. Our results add to the growing volume of evidence pointing to a large-scale decline in terrestrial insect populations both in central Europe (Brooks et al., 2012; Hallmann et al., 2017, 2019; Kotze & O'Hara, 2003; Seibold et al., 2019) and globally (van Klink et al., 2020). We also show a rate of change in carabid counts similar to that from a long-term pitfall trap study in the Netherlands by Hallmann et al. (2019), where traps were sampled over a period of 27 years, albeit not continuously. They found a mean annual decline in carabid activity density of 4.3%, just 0.5% points greater than the annual decline found in our study. They also found an even greater annual decline in species richness of 7%, which is four times greater than what we observed in our study. Another recent study from Seibold et al. (2019) shows a decline in grassland arthropod abundance of 78% over 10 years at sites in three regions in Germany, though this trend is largely due to a particularly high number of individuals in the first year of sampling.

We also show that the decline in carabid species richness is first and foremost dependant on the counts of carabid beetles. This was expected, as the probability of finding more species increases with the sample size, i.e. with higher activity density (Bunge & Fitzpatrick, 1993; Gotelli & Colwell, 2001). Ground beetle species richness declined at a rate only half as fast as the activity density in our study area, which also makes sense when looking at species accumulation curves, which rapidly increase with more individuals and then gradually level off. As the relationship between species richness and the number of individuals is typically log-normal (Colwell et al., 2012), we would expect the decline in richness to be less than the decline in activity density, a trend which we also find in our data. This result is in contrast to findings from Homburg et al. (2019), the only other long-term pitfall trap carabid study in Central Europe. In their study, they observed a decline in carabid species

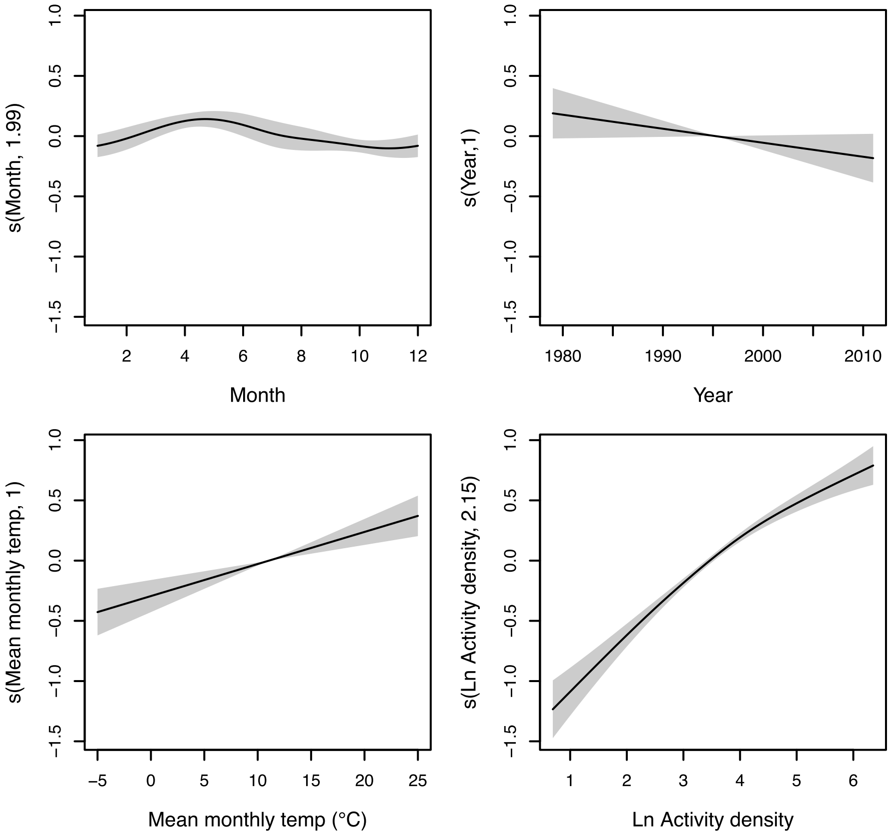

Fig. 4. GAM spline plots for species richness with 95% confidence interval (grey). Shown are the partial effects of month, year, mean monthly temperature and carabid activity density (on the link scale) due to the respective model term, holding all other model terms at their mean value. Monthly carabid activity density (counts) has by far the largest effect on the species richness.

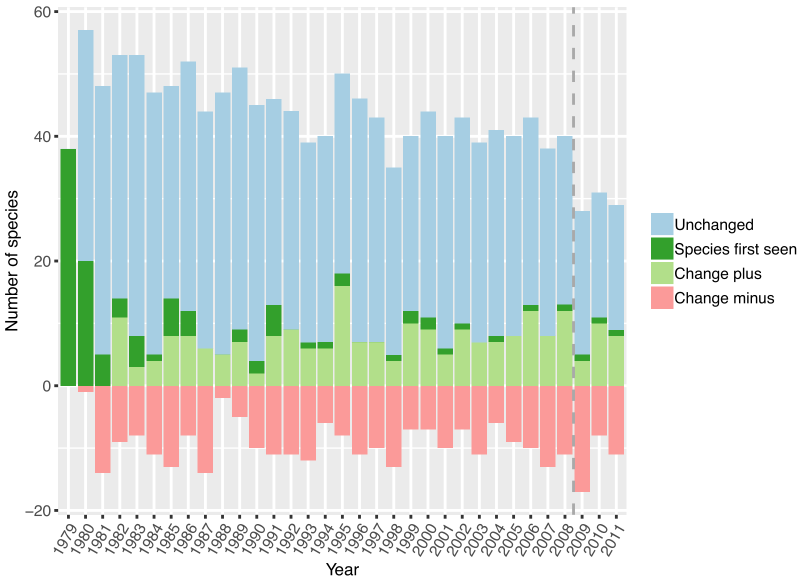

Fig. 5. Observed annual species turnover. After the first three years, few new species were encountered (dark green), while on average around 10 species were lost (red) and 9 gained (light green and dark green) from one year to the next, with half of the species remaining (around 50%). Note that 2009 - 2011 only six out of 15 traps were sampled, yielding the drop in species numbers and proportion unchanged (to the right of dashed grey line). **(Print in colour)**. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

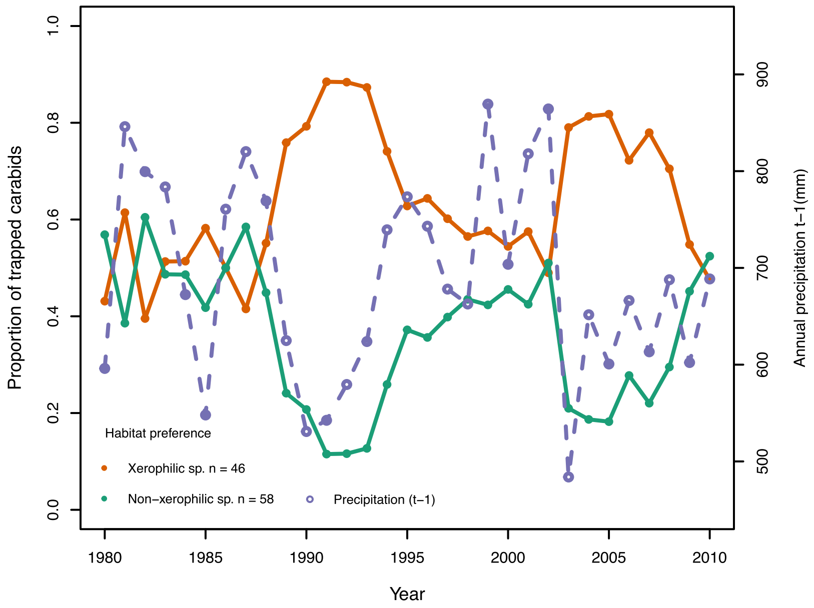

Fig. 6. Proportion of xero-thermophilic (red) and non-xero-thermophilic (green) carabid individuals collected in each year (right y-axis). Also shown is the total annual precipitation (mm) for the previous year (t-1) over the study period (right y-axis), since, for example, the precipitation in 1985 will affect the carrabid populations in the following year. In drier years, the proportion of carabids preferring xerophilic habitats increases dramatically, especially during the drought period of the early 1990s and mid 2000s. **(Print in colour)**. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

richness without an apparent decrease in the trap counts of carabids in a protected forest in North Germany over 24 years. This difference between our study and theirs is interesting as it suggests that there may be disparate trends in carabid communities depending on the ecosystem in question.

Another result of our analysis was the significant effect of temperature on species richness in excess of the other explanatory variables. It is likely that this effect can simply be attributed to an “activity effect” (e.g., Honek, 1997; Nève, 1994), where ground beetles are more active, for example, in an exceptionally warm April, leading to more individuals, and hence more species, to be caught by chance. This does not necessarily mean that there were actually more species in the system during these months, only that more were trapped.

Perhaps the most interesting development in our investigation of traits was exhibited in the trend of biomass. The increase in community weighted mean biomass over time can be attributed to only a handful of especially large (up to 5 cm) *Carabus* species, whose weight is nearly 200 times that of some of the most common ground beetles. There was a high number of small carabid beetles during the early successional stage, which is consistent with other studies that found an increase in ground beetle body size in later stages of vegetation succession (Barber, Lamagdeleine-Dent, Willand, Jones & McCravy, 2017; Schirmel, Blindow & Buchholz, 2012). If the *Carabus* individuals were removed from the analysis, no change in CWM biomass was visible (see Fig. A8).

If we consider the total biomass over time, a measure used by Hallmann et al. (2017) to quantify flying insect population size, we still see a decline, with high year-to year variation, again driven by large *Carabus* individuals. However, if we look at the late successional phase and exclude *Carabus* species (Fig. A9), we see a stronger significant decline in biomass that follows the trend in counts, although again the standard error for this estimate is rather high (67% loss, [14%, 80%] 95%- confidence interval). In this study, we can say with high certainty that the decrease in biomass follows the decrease in counts over long periods of time. However, we also show that biomass in relatively small samples can be a rather unreliable measurement, as it exhibits substantial fluctuations based on few large individuals. In particular, small taxa that include some large-bodied species are vulnerable to such fluctuations. This can be especially problematic under circumstances where sampling is not continuous or comparisons are made between disparate years. amongst the other traits, the only one to show a discernible pattern was habitat preference. The proportion of xerophilic carabids was notably higher from 1990 to 1995 and 2004−2008. The same pattern is reflected in the climate data - the years with a high proportion of xerophilic carabids followed years that were particularly dry. The year of lag time is likely due to the effect on larval development of carabids in dry years (Fig 6). This is in line with (Buchholz, Hannig & Schirmel, 2013), who found strong correlations between soil moisture and carabid species composition at dry grassland sites under different successional regimes. As open habitat carabid species tend to be xerophilic, the patchy vegetation during dry years likely benefitted these species.

The high counts of carabid beetles at the beginning of the study was expected, as the study site had just undergone a dramatic transformation which can be likened to a large-scale surface mine (see photo in Appendix 1) and early successional conditions dominated the study site. Both Parmenter and Macmahon (1987) and Small, Sadler and Telfer (2002) report similar findings regarding carabid beetle populations at early successional sites (restored mining sites in Wyoming and brownfields in England, respectively), with an initial increase in numbers of individuals and richness in the first few years after disturbance and a subsequent decline. As a consequence, in our analysis we distinguish between the initial and early successional phase and thereafter, and only calculated rates of decline for the late successional phase. Our definition of the successional phases is based on the carabid community composition, and at least for the time period that we investigated, we found no major changes in the community composition in the last 23 years of the study. This suggests a certain stability in the core carabid community (see Fig. 1), through which the counts and species richness nonetheless continued to decline. While our model reveals that increasing vegetation cover drives carabid counts and composition in the early period, perhaps due to an increase in resources, the drivers of decline in the later period, post 1989, remain unclear. However, as succession is a continuous process, it is possible that some of the variation in our model captured by the “year” variable is attributable to successional change.

Climate change, as quantified by weather variables, seems to have had a minimal effect on the ground beetle community at our site up to this point. While our model revealed a positive effect of increasing temperatures on ground beetle species richness, we still observed a strong overall decline in ground beetle species richness. A long-term study (18 years, April-November) in Denmark (Thomsen et al., 2016) also showed that increasing summer temperature had a positive effect on ground beetle richness and abundance. This effect, however, was not apparent when considering ground beetle activity density at our site. The annual precipitation, however, was influential in determining the proportion of xerophilic and non-xerophilic individuals, as described above. In light of the dry spells captured in our data set, we can speculate that under drought conditions, the carabid community would likely experience a shift in the species occurring at the study site, as non-xerophilic species would struggle to persist.

There are of course other potential forces at play which we did not explicitly measure that may affect ground beetle populations. Vele, Holusa, Frouz and Konvicka (2011) found that landscape-scale drivers were more important for ground beetles than small-scale succession in a spruce clear cut, while Aviron, Burel, Baudry and Schermann (2005) show that large-scale landscape patterns and farming intensity affected carabid assemblages, with larger carabids being disproportionately affected by intensive agriculture and a lack of permanent landscape structures. Though we only included local vegetation cover as a predictor of succession, the surrounding landscape remained unchanged in its use over the study period, making it improbable that landscape scale change affected the ground beetle population. While we lack hard data on pesticide use at the study site, which may generally play a role in ground beetle diversity (Geiger et al., 2010), it is unlikely that it played a role at our study site. From personal communication with the vintners in the vicinity of the study site, pesticide use has declined and become more targeted over time and has been largely replaced by integrated pest management (IPM) techniques such as mating disruption targeting specific pests.

Conclusions

Our data show a continuous decline in both species richness and activity density of ground beetles over the 33-year study period, even after accounting for the effects of climate and vegetation cover, although the underlying reasons for the decline remain unclear. Additionally, identification at a high taxonomic resolution allowed us to gain a better understanding of how the community changed over time in terms of prevailing functional traits. Interestingly, many traits showed no significant changes over the time period and therefore provide little insight into the loss of species and lower trap counts observed.

All near-natural systems are currently, and since decades, experiencing environmental change, be it atmospheric N-deposition, increased use of agrochemicals, which also drift into adjacent habitats, or more severe weather conditions. The vegetation change at the study site after the early successional phase is a modest change relative to the loss of species in former extensively, now intensively managed agricultural habitats.

Small-scale long-term studies are valuable and can be used to help reveal patterns on a larger scale (e.g. through meta-analysis), however, a more comprehensive picture would require establishing standardised long-term monitoring in a variety of habitats and ecosystem management regimes. While this is often a logistical challenge, it is essential if we hope to corroborate (or contradict) patterns found at local scales.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

AKL collected the original data, organised the species identification, provided the digitised data and metadata for further statistical analysis and provided input about the study site, data collection, and biology of the sampled organisms. CJS and CFD performed the statistical analysis and created the figures. CJS led the writing of the manuscript. All authors provided critical input to all drafts and approved the final manuscript.

Data availability statement

Data will be archived in the online repository Dryad.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2020.11.003.

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