Strong decline in grasshopper abundance over 20 years without major land-use changes: Is soil drying one of the drivers?

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ABSTRACT

Strong declines in insect numbers have been described for different taxa and regions. These observations are of great concern such that broad scientific and public attention has been raised. Among other urgencies, the need for long-term insect data has been identified. Here, we present data on grasshopper (Caelifera) abundances recorded between 1992 and 2011 at over 600 sites in north-western Switzerland. While vegetation type, often semi-natural grasslands, had remained largely constant, total grasshopper abundance declined by around 50 % (while many other taxa showed much less decline). Numbers in July remained relatively stable until about 2003 but then declined similar to the declines seen in August–October already before. Greatest losses were observed for drier habitats and steeper slopes, suggesting that soil drying might be an important factor for the decline. Second, more nutrient-rich habitats suffered greater losses; possible reasons for this include small-scale vegetation changes in these habitats e.g. due to atmospheric nitrogen deposition, or isolation of sites. Other than abundance, species richness decreased much less, illustrating that important ecological changes may be strongly underestimated when only species lists are available. The strong declines at our sites, which often are in an agri-environmental scheme, is alarming. Apart from being yet another call to fight climate change, our results also point to the urgent need to reduce atmospheric nitrogen deposition and to continue extensive farming, but also to adapt it in preparation of expected effects of climate change, with the aim to favour a divers, ecologically robust insect community.

1. Introduction

In the past years, a number of publications reported strong declines in different insect taxa (e.g. Conrad et al., 2006; Habel et al., 2019; Hallmann et al., 2017; Wagner, 2020). There is a lively ongoing debate about the generality of declines across regions, habitat types and taxa (Komonen et al., 2019; Saunders et al., 2020; Wagner et al., 2021; Crossley et al., 2020; van Klink et al., 2020) and about methodological challenges in studies reporting insect trends (Didham et al., 2020; Montgomery et al., 2020). For example, studies often only started once a decline was indicated by unstructured observations (Bonebrake et al., 2010; Didham et al., 2020), causing a bias in the available data sets. Also, studies comparing old and new censuses are often based on presence-absence data, thereby not detecting changes in abundances especially of common species (Gaston and Fuller, 2007), which may be most relevant for ecological processes. Irrespective of such difficulties, there is a consensus about the enormous potential risks of a large insect extinction wave (Cardoso et al., 2020) and the topic has moved into the scientific and public spotlight. A prerequisite to understand the problem of insect declines is reliable data on population trends and, for that, long-term studies (Fox et al., 2019; Harvey et al., 2020). New monitoring initiatives have been started (e.g. Fischer et al., 2010), but additional data from past decades are of specific interest to improve our understanding of the overall insect development Such data exists from a limited number of large long-term monitoring programs such as the UK Butterfly Monitoring Scheme (www.ukbms.org), but additional data, including data from outside scientific entomology and conservation biology, should be made available and analysed (Montgomery et al., 2020).

In the 1980s, Georg Artmann-Graf (GA) began systematically observing insects of various taxa in the area of Olten, north-western Switzerland, due to his interest in field biology (and not based on previous information on any local trends). This voluntary engagement resulted in >15'000 visits to >750 sites between 1992 and 2021, with

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>320′000 records of insects from 38 taxa (mostly families; Artmann-Graf, 2022). In view of the urgent need for long-term insect monitoring, this data set is of great value, as also identified by Widmer et al. (2021). For the analyses presented here, we selected grasshoppers (suborder Caelifera) due to the long time series with expert knowledge by GA on this taxon. Also, grasshoppers are relatively abundant, and they are good indicators of changes in the environment (Fartmann et al., 2012; Hochkirch et al., 2016; Löffler et al., 2019). With their comparatively large biomass, grasshoppers can constitute an important food resource for larger animals, e.g. for different bird species (Ingrisch and Köhler, 1998; Wilson et al., 1999).

Presumed important drivers of changes in insect numbers are changes in climate and habitat characteristics induced e.g. by fertilisation, intensive pasturing, abandonment or afforestation (Cardoso et al., 2020, Rumohr et al., 2023, Raven and Wager, 2021, Wagner et al., 2021, Outhwaite et al., 2022; for grasshoppers: Löffler et al., 2019, Poniatowski et al., 2020). On agricultural land, survival may be drastically reduced by the use of pesticides and modern machinery, such as fast grass cutting by rotary mowers followed by mechanical chopping and silage packing (Humbert et al., 2010). Climate change effects include increased temperature, but also increased evapotranspiration and more fluctuating and extreme weather conditions, including drought.

From his extensive experience in the field, GA postulated that a critical factor for grasshopper population trends could be the humidity of the soil, especially of the upper layer, where several species live during sensitive life stages (eggs and young nymphs; Poniatowski et al., 2018, Tingjuan et al., 2021). Fartmann et al. (2021) found increasing occupancy rates for most of 23 grasshopper species between 1995 and 2012 in NW Germany, but *Omocestus viridulus*, a species considered susceptible to summer drought, decreased strongly. The authors formulate the hypothesis that other hygrophilous species could also be threatened because climate change leads to warmer summer temperatures and higher evapotranspiration, which reduces soil moisture in summer, even if precipitation remains constant throughout the year.

Because there was little change in the vegetation types in our study area (see results), we did not expect that vegetation changes (as measured by us) could explain changes in grasshopper abundances. However, small-scale changes in the vegetation might play a role. Especially airborne nitrogen deposition may affect habitat quality even if overall vegetation remained similar (Bobbink et al., 1998; Nijssen et al., 2017).

Weather during specific time periods preceding the summer census might be a driver for changes in grasshopper abundances (Marshall et al., 2020). Effects of winter conditions on insect survival have e.g. been suspected by Harris et al. (2019), who observed a steep decline in abundance and diversity of different beetle taxa in a natural forest habitat in New Hampshire, USA, over the last 45 years and linked this to reduced snow cover in the preceding winters. In an experimental setup simulating increasing winter temperatures, larvae of the butterfly *Erebia medusa* were heavier but had lower survival (Stuhldreher et al., 2014).

Here, we first analyse changes in total grasshopper abundance across years (1992–2011) in Jura Mountains in north-western Switzerland, overall as well as separately per month which may indicate shifts in phenology. We then discuss relationships between observed trends on the one hand and habitat and topography on the other hand, possibly indicating reasons for changes. For example, if soil desiccation is an important driver, we might expect less changes in wet habitats but more changes in dry sites with a southern aspect where evapotranspiration is strongest. We also explore correlations with weather parameters to find potential weather effects during different time periods of the year.

2. Methods

2.1. Study area

The study area covered around 350 km^2 between Aarau and Solothurn in north-western Switzerland (47°21′N, 7°54′E), with flat areas at 400–440 m a.s.l. and hilly areas in the Jura Mountains raising up to 1100 m a.s.l. (Fig. 1). The landscape is composed of a mix of forests and open areas with settlements and often intensive agriculture (grassland and arable land). Especially on slopes, semi-natural open habitats, often listed in communal conservation inventories, were still present in the 1980s and were selected for the study; agricultural land used intensively was not included in the study. Concomitant with the beginning of the study, federal subsidies for the conservation and recreation of semi-natural and extensive farmland started. This spared many of our study sites from intensification or abandonment, as they were included in the agri-environmental scheme.

From 1985 to 2021, mean annual temperature in the study area increased by 1.38 °C (from 8.71 to 9.40 °C), while annual precipitation remained unchanged (1113 mm per year; Table S 3; data from the MeteoSwiss weather station "Wynau", Fig. 1). For the focus period of 1992 to 2011, temperature increased by 0.24 °C with considerable variability among years such that the overall trend for this time period was uncertain; six of the monthly trends increased, six decreased, with only April being statistically robust (+2.34 °C). Precipitation showed no clear trend between 1992 and 2011, but rather large variability, also between months (Fig. S 3).

2.2. Study sites

We included 629 study sites with at least one grasshopper registration during the years 1992 to 2011. Sites were 44 ares (1 a = 10 × 10 m) on average (1 a to 150 a, interquartile range 9–47 a) and were composed of a vegetation type distinctively different from the surroundings. About 20 % of all sites were linear structures, such as hedges or riverine vegetation (for these, a width of 2.6 m was used to calculate an area). Typically, sites consisted of more or less extensive grassland mown once or twice per year, some with autumn grazing. Some sites contained scattered bushes or trees. Habitats adjacent to our study sites were often hedges, forest edges, intensively used agricultural land, or settlements.

The vegetation type of each study site was assessed once per decade according to the criteria given in Delarze et al. (1999), i.e. based on the presence of characteristic plant species. From these vegetation types, we deduced a humidity, a nutrient, and a structure index (Table S 1, Table S 2). The humidity index was extracted from the corresponding graphs in Delarze et al. (2015) on a scale from 1 to 5: arid, dry, mesic, humid, and swampy. The nutrient and structure index were averages from independent estimates by three ecologists, with values from 1 to 4 (nutrient
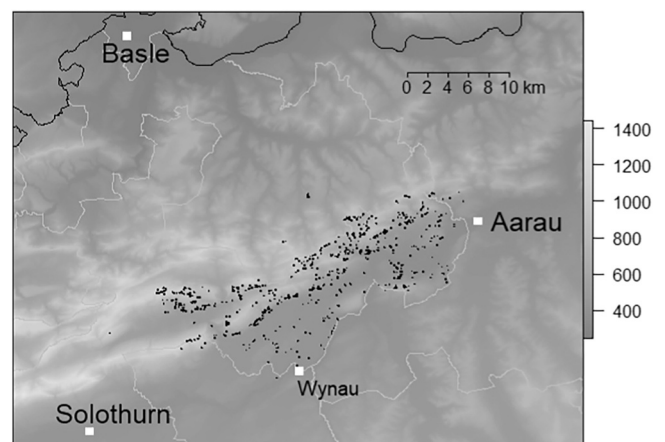

Fig. 1. Study sites (black areas, *N* = 629) in north-western Switzerland (dark line = national border, light lines = borders of cantons). The background shows the elevation in m a.s.l., with flatter parts to the south of a line drawn between Aarau and Solothurn, and hilly Jura Mountain areas to the north (background: ©Swisstopo).

poor, mesic, rich, and very rich) and from 1 to 5 (none [i.e. grassland], tall herbs, some bushes, bushes, forest), respectively. For 83 % of vegetation assessments, a second vegetation type was assigned, for 2 % a third type. In these cases, humidity, nutrient, and structural indices were averaged across the two or three vegetation types, with weights 2:1 and 4:2:1, respectively.

2.3. Censuses

We analysed data from 3855 visits to the study sites during the months July to October. Visits were organized by decade: 1992–2001 and 2002–2011. 626 of the 629 sites were visited in the first and 628 in the second decade.

Per decade, each study site was visited 2–4 times (some only once, others 4–8 times, few cases with even more visits) from July to October during one or two years (few sites had visits in more years). Visits were conducted during sunny weather and at a temperature of at least 13 °C. The entire area was walked slowly in 5–10 m wide transects; linear elements were walked from one end to the other and back. On average, a visit lasted 1 h 18 min (90 % between 15 min and 3 h 20 min depending on the area of the site).

Grasshopper imagos were registered visually and acoustically, including individuals at the edge of adjacent hedges or forests if present. Abundance per species was registered in classes: 1–2, 3–9, 10–25, 26–100, and > 100 imagos on the site. For most analyses, we used the middle value of these classes (150 for the last class), summed across species to yield a total abundance per visit.

Hearing capacity of GA (born 1942) declined with age, especially for species with high-pitched song. Therefore, we focused our analyses on the time up to 2011 (end of second decade, with good hearing capacity).

2.4. Statistical analyses

Total grasshopper abundance was analysed on the level of the single visits ($N = 3855$). With a first model called "overall change", we aim to describe the overall development of total abundance of imagos across years. For that, we fitted an N-mixture model that allows to separately estimate abundance and detection probability. Thereby, we aim to account for changes in detection probability e.g. due to a change in singing activity of the grasshoppers or the detection efficiency by GA over the years. The model makes the assumption of a closed population across the visits per site and year ("closure"); individuals in nymphal stages that later survive to the imago stage are assumed to be present but not detectable. For this model, we back-transformed the total abundance (across species) to the original abundance classes and fitted a Poisson N-mixture model for interval-censored data (Kéry and Royle, 2021; model code in the supporting file). We used the data from 1992 to 2011 and fitted the model with the software jags via the package rjags 4–14 (Plummer, 2023) of R statistical software (R Core Team, 2023).

In the second model, called "change per month", we estimate the development over years of grasshopper abundance separately per month, using a normal additive linear mixed effects model (function stan_gamm4 of package rstanarm, Goodrich et al., 2023) and log-transformed total abundance. Since there were generally no repeated visits within a month, no model accounting for detection probability could be fitted, but we used the detection probability estimated in the first model to approximately correct the abundance estimates for the change in detection over years (estimate/detection probability). We included year as smoothed predictor, in interaction with month, site area as a covariate (linear and quadratic, to account for variable site areas), and site as a random factor with random year slopes.

With the third model, called "habitat model", we estimate potential effects of environmental parameters on total abundance and especially on its change. We fitted a normal linear mixed model (function lmer of package lme4, Bates et al., 2015) with log-transformed total abundance as outcome variable. Predictors were, as in the second model, month and

site area, plus six environmental variables: three habitat variables (humidity, nutrient and structures index as described above) and three topographic variables (elevation a.s.l., slope, and aspect with 5 levels: flat, i.e. <5° slope, S, W, E and N), including quadratic effects. Year was included as a further covariate, in interaction with all six environmental variables. Site was included as a random factor with random year-slopes. As we were mainly interested in effects of the predictors on the trend, i.e. on the year-effect, we created, for each predictor, an effect plot with the estimated trend per study site vs. the predictor. To estimate the trend per site, we added, to the overall year effect, the random slope per site plus the interaction effect (using the site-specific value of the predictor). We describe the pattern in such a figure using a smoother (using function gam from package mgcv, Wood, 2017). To propagate the error from the linear mixed model to the smoother, we used sim (package arm, Gelman and Su, 2022) to get 5000 draws from the joint posterior distribution. Each draw was used to calculate the site-specific trends as explained, including the smoother; mean and 95 % range of these 5000 smoothers represent the point estimate and 95 % uncertainty interval of the connection between habitat values and trends.

We fitted analogous models using weather parameters from different time periods of the year. However, while we observed strong correlations between weather and abundance changes, these were mostly difficult to interpret, so that this aspect of the analyses was moved to the supporting file (chapter S 7).

3. Results

3.1. Vegetation types

Vegetation types according to Delarze et al. (1999) did not change between the two decades (1992–2001 and 2002–2011) in 95 % of our 629 study sites, the other sites mostly changed to similar vegetation types (Fig. S 1 and Fig. S 2). The average humidity index (5 levels from arid to swampy, see Table S 1) was 2.87, mean nutrient richness (4 levels from poor to very rich) was 2.52, and mean vertical structures (5 levels from none to forest) 1.78. Up to the precision given here, these values were the same for both decades, hence, the vegetation types remained largely unchanged. Also, there was no general major change in agricultural usage in our study sites (pers. obs.), as many of them are in an agri-environmental scheme.

3.2. Grasshopper abundance and richness

Overall, 23 grasshopper species were registered (Table S 4). The overall abundance of imagos, corrected for detection probability, decreased to about 50 % between 1992 and 2011 according to the N-mixture model (model "overall change"; Fig. 2A). Detection probability was estimated to have decreased somewhat since year 2000 (Fig. 2B). Detection probability increased between July and August and decreased again until October, reflecting the peak presence of imagos in August. Across years, total abundance decreased in all months, albeit in July only after about 2003 (model "change per month", Fig. 3; for analogous models per species, see Fig. S 6 in the supporting file). In the raw data, the proportion of the two abundance classes with most individuals (26–100 and >100) decreased continuously, while the proportion of the class with 1–2 individuals increased (Fig. 4). There was no obvious spatial pattern of the trends in our study area (Fig. S 4).

The number of species decreased less strongly than abundance, from a mean of 4.75 species per site in the first decade to 4.19 species in the second decade (richness per site and decade, but using only the 587 sites with at least 2 visits in both decades; Fig. 5).

3.3. Changes in relation to environmental parameters

The decline in grasshopper abundance correlated with the humidity and nutrient index of the habitat, with stronger declines in drier and
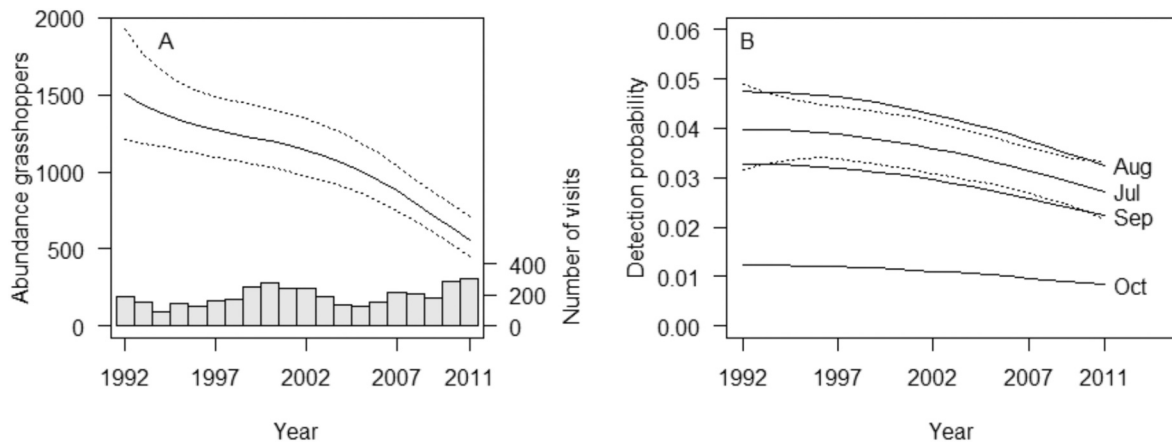
Fig. 2. Results from the N-mixture model estimating true abundance (A) and detection probability (B) of grasshopper imagos. Solid lines are the estimates, dotted lines 95 % uncertainty intervals (only shown for July in B for better readability, with similar uncertainties for the other months). In A, the estimate is for a site area of 50 ares; in B, the detection probability of an individual grasshopper is shown (an individual that later survived to the imago stage, or already was imago). The histogram in A shows the number of visited sites per year (right y-axis).
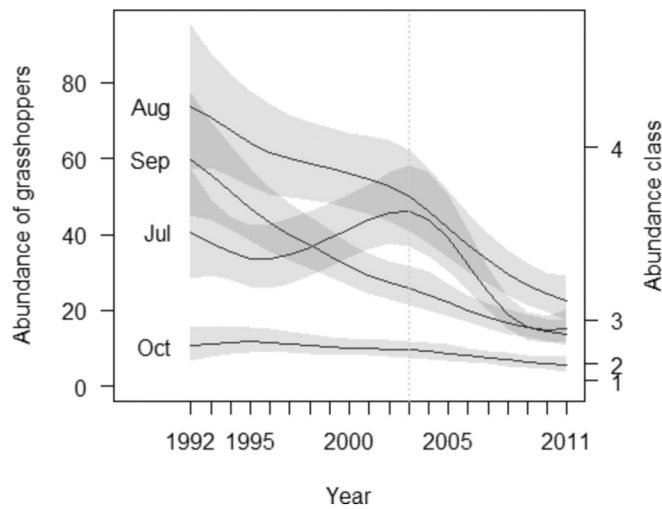

Fig. 3. Mean observed total grasshopper abundance over the years, separately per month. Year 2003 is marked with a dotted line. Estimates and 95 % uncertainty intervals (grey shades) from an additive linear model corrected for detection probability using the estimates in Fig. 2B.
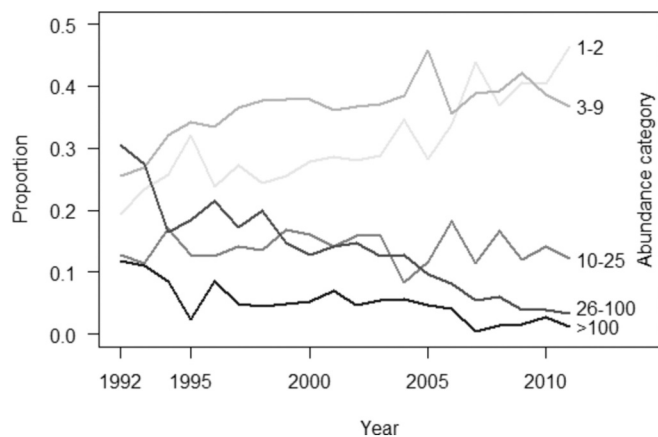

Fig. 5. Number of species of grasshoppers registered per study site and decade. Representation of the raw data, with boxplots showing the mean, 50 % range (box), 95 % range (whiskers) and more extreme values (dots, jittered sideways to reduce overlap). Only sites included that were visited at least twice in each decade.

Fig. 4. Changes in the proportions of abundance classes between 1992 and 2011 (grey scales) in the raw data. 249–817 class values per year (one value per visit and observed species). Per year, the five lines add up to 1.
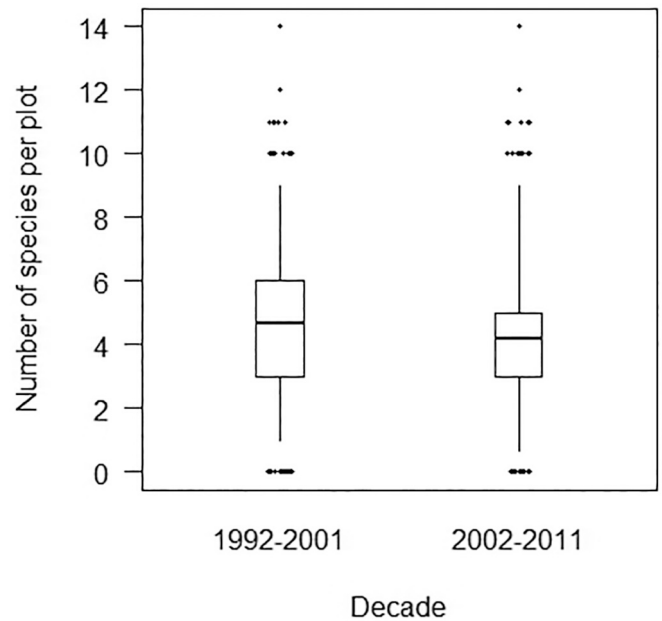
more nutrient rich habitats (from the "habitat model", Fig. 6A and B; for coefficient estimates and additional effect plots, see Table S 5 and Fig. S 7 and S 8 in the supporting file). The amount of vertical structures showed no effect on the trend (Fig. 6C). Regarding topography, more negative developments were observed at lower elevations and steeper slopes (Fig. 6D and E; the latter with more positive trends for the steepest slopes, but this is based on very few sites). Sites with a western aspect had slightly better trends, but the effect of aspect was rather limited (the level "flat" should be interpreted with care due to its correlation with slope). Note that in these figures, trends for almost all sites are estimated to be negative, while in the raw data, this pertains to only 76 % of all sites (compare Fig. S 4); this is due to statistical shrinkage, but the main information in these figures is the pattern of the smooth line.
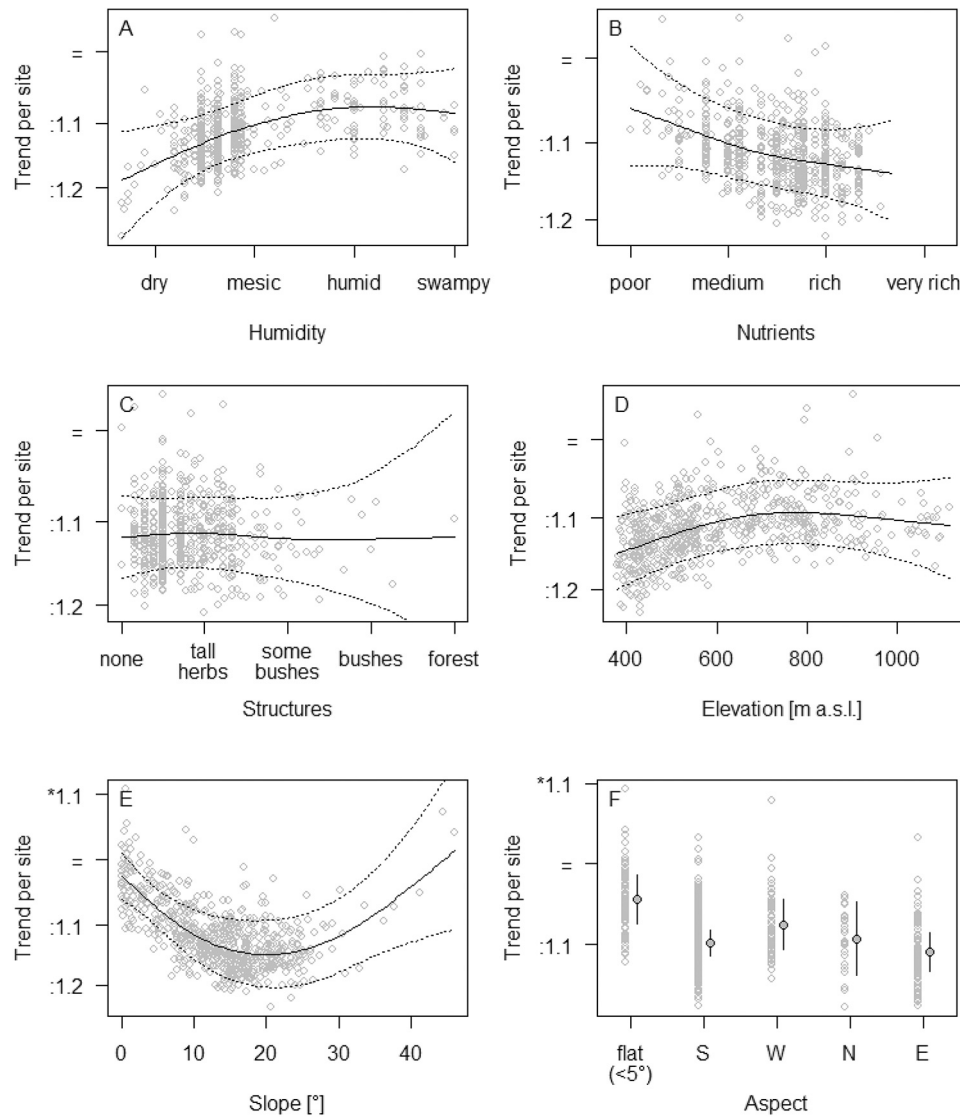
Fig. 6. Multiplicative trends in grasshopper abundance 1992–2011 vs. habitat (A-C) and topographic (D-F) variables. "="means no change. Each grey circle is a study site (*N* = 629; trend estimated from the «habitat model»). The black line is a smoother through the grey circles (from a general additive model), with 95 % uncertainty interval (including uncertainty in the estimates of the grey circles). Continuous predictors not shown in a figure were set to their average (site area rounded to 50 ares), month to July and aspect to W (west); except in F, where slope was set to the mean slope per aspect level (an overall mean slope would make no sense for level «flat»).

4. Discussion

We observed a strong decline by around 50 % in total grasshopper abundance in our study plots between 1992 and 2011. In the context of the current discussion regarding the insect biodiversity crisis, it is important to note that the grasshoppers showed one of the strongest declines among the over 30 taxa (mostly families) GA observed. Hence, our results should not be extrapolated to assume an equally strong decline in overall insect biomass. Not all data from other taxa is currently prepared for detailed analyses, but Artmann-Graf (2022) compiled summary tables of the number of records per taxa, decade (1992–2001, 2002–2011) and abundance class. From these, and taking the number of visits per decade into account, we can roughly estimate that the total insect abundance (summed across taxa) excluding Orthoptera decreased by around 25 % between the first and second decade. Also, within the Orthoptera, Caelifera (grasshoppers and relatives) decreased much stronger than Ensifera (crickets and relatives). Declines comparable to the grasshoppers were observed for Carabidae and Staphylinidae, to a lesser extent also for Chrysomelidae, Panorpidae

and Tipulidae, while most other taxa showed more or less constant numbers; no taxa showed an increase as strong as the decrease in grasshoppers. Hence, overall, it seems clear that the total insect biomass surveyed by GA did decrease between 1992 and 2011, but not as strongly as seen for the grasshoppers. Fürst et al. (2023) observed roughly stable total abundances across the years 1987, 1997 and 2019 for ground dwelling and flying insects of different families (but not Orthoptera) in the Limpach valley, only 10 km south of our study site, which concurs with our finding that the loss of insects as a whole was likely <50 %.

A strength of our data set is that it was recorded by the same person (GA). Study sites censused in a given year were visited repeatedly over the season rather than only once or twice – the latter can lead to biased estimates of abundance changes if phenology changed strongly. Also, the transect method used by GA is a standard and useful method for counting grasshoppers (Gardiner et al., 2005). Nevertheless, long-term counts may suffer from subtle shifts, e.g. in methodology, that potentially affect detection probability and, thereby, bias abundance values. With our first model, using the different visits at a site within a year as

repeated counts of a closed population, we aim to correct the abundance estimates for changes in detection (Fig. 2). Furthermore, relationships we find between abundance change and habitat characteristics (e.g. humidity and nutrients) would not be expected if the decline would not largely be real.

With climate warming, it may be expected that in temperate central Europe, insects as a whole would be winners, rather than losers. Indeed, a number of studies reported range expansions, also of grasshoppers and especially of warm adapted species, into central Europe during the last decades (e.g. Fumy et al., 2020; Poniatowski et al., 2020; Fartmann et al., 2021). However, it is important to make the distinction between species richness (based on presence-absence data, also reflected in the range of a species) and abundance. With strong changes of the environmental parameters, such as the long-term temperature increase also seen in our study area, the ensuing change in species composition may, at first, mainly lead to the collapse of the numbers of the previously most abundant species, which is illustrated in our data by the decline of the two largest abundance classes (Fig. 4). As total abundance mainly reflects what happens with the populations of the few most abundant species, it is not necessarily a contradiction to find a strong decline of the total abundance and, at the same time, a stable or increasing richness (Gaston and Fuller, 2007) or range expansions.

Few other studies present abundance trends for Orthopterans in central Europe. Schuch et al. (2012) compared historical abundance estimates from 1951 of Auchenorrhyncha, Orthoptera and Heteroptera at nine sites in Germany. For the Orthoptera, richness increased but abundance decreased by about 60 %. Other than in our study site, the vegetation types changed markedly, hence the reasons for the decline likely differed. The authors discuss a possible effect of reduced moister conditions on egg survival for Auchenorrhyncha, an effect that might also play a role in Orthoptera as discussed below. Schlegel and Schnetzler (2018) re-censused 100 sites in the Swiss hills at the edge of the Alps from which abundance values were known from 1990 and 2000; similar to our sites, vegetation types did not fundamentally change. Where possible, we have added their values to the species-specific trends from our study site (Fig. S 6), from which we see a much less dramatic development in their numbers. One reason for the difference may be that our study site is mostly on calcareous soils that dry out much faster than the sites of Schlegel & Schnetzler, which lay in a region that also harbours different wet meadow habitat. But the authors also mention a possible effect of dryer conditions, based on the observed increase of *Chorthippus biguttulus* and decrease of *C. dorsatus*. Abundance measures of Orthopterans from the Jura mountains (i.e. the same region as our study site) are presented by Braschler et al. (2009), who found increasing densities of grasshoppers. However, these values stem from an experimental setup where the habitat was manipulated to simulate different degrees of isolation; also, their data only cover the years 1993–1999. Illich and Zuna-Kratky (2022) observed strongly fluctuating but overall stable abundances of five grasshopper species between 1991 and 2020, but this study is also not easy to compare with ours as their study plots were in a much cooler habitat (not south-facing and mostly over 2000 m a.s.l. in the Austrian Alps).

Until about 2003, we observed a shift in phenology with numbers in July remaining roughly stable while numbers in August and September declined steadily (Fig. 3). Therefore, phenology seemed to have advanced for this time, with more grasshopper individuals appearing earlier in summer. With higher temperatures, this is an expected pattern for ectotherm animals where temperature strongly influences the speed of development. Note that from Fig. 3 the question arises whether the phenological change just continued such that now the large numbers of grasshoppers appear even before July, but this is not the case: An analogous model including also May and June estimates lower abundances for these two months than for October for all years (data not shown).

A key element for the interpretation of the observed strong decline in grasshopper numbers are the correlations between abundance changes and habitat characteristics. More negative trends were observed in dryer habitats (Fig. 6A), in lower-laying sites (with higher mean temperatures; Fig. 6D) and also in steeper sites (Fig. 6E) which, given the mostly southerly aspect, relates to more solar radiation (however, using a measure for solar radiation instead of slope and aspect did not improve the models). These relationships may suggest that the grasshopper community at our sites struggled with a lack of soil moisture. From our correlative study, it is not possible to exactly pinpoint the critical parameters. Precipitation did not decrease at our study sites, and even mean temperature did not increase systematically between 1992 and 2011, but temperature increased in a longer time window (Fig. S 3, Table S 3, Fig. S 5). Possibly, average soil moisture during relevant times of the year has decreased, which may negatively affect grasshopper species that previously were abundant. Other research groups also suspect soil humidity to be of critical relevance for a number of grasshopper species (Ingrisch, 1983; Poniatowski et al., 2020; Fartmann et al., 2021), e.g. for *Omocestus viridulus*, one among several species that seems to be highly susceptible to drought conditions (especially its eggs; Holtmann, 2013, Gardiner, 2010, Poniatowski et al., 2018, Fartmann et al., 2021). van Wingerden et al. (1991) find an increasing hatching success with temperature for a number of grasshopper species, but as temperatures rise above 30 °C, most species show strong declines in egg survival. Löffler et al. (2019) found no decline in the range of hygrophilous grasshopper species in the Eiffel area in Germany between 1994 and 2015, but they predict that such species will face an increasing local extinction risk with climate warming. Hochkirch et al. (2016) stress the potential negative effect of drought, but state that the knowledge about the effects of drought on grasshoppers are still limited, and that drought has been explicitly identified as a threat for only 23 of the over 1000 European Orthoptera species in their red list.

A general trend in soil moisture is one possible critical factor for the change in our grasshopper community. Another potentially critical factor are extreme weather conditions, especially heat-waves such as during summer 2003. Grasshopper numbers in our study area did not immediately decline drastically during this summer or thereafter (Fig. S 5), but there might be indirect, longer-lasting effects of the heat-wave, e. g. on ground water or the vegetation. Fartmann et al. (2022) observed strong effects of summer heat-waves on the vegetation, which likely led to food shortage for the grasshoppers.

We might expect that less soil moisture and heat-waves would favour warm-adapted grasshopper species. However, such species (as identified by a larger species temperature index STI, Poniatowski et al., 2020) did not generally show positive trends at our study sites (Fig. S 6), e.g. *Mecosthethus parapleurus* first increased, but later decreased. However, this species needs mesic to humid microclimatic conditions especially for reproduction, hence soil drying likely caused or contributed to its negative development.

Total grasshopper abundance in our study area decreased more in nutrient-rich compared to nutrient-poor habitat (Fig. 6B). Abundance was not systematically higher in more nutrient-rich sites at the beginning of our study period, such that the numbers at these sites could have decreased more strongly. The overall intensity of usage (e.g. number of cuts) probably did not change markedly during our study period (pers. obs). However, mowing techniques might have changed, for example mechanical chopping and mowing speed might have increased (though silage is not allowed on most of our study sites). Such changes might be more likely on more productive grassland, hence this could be a cause for the stronger declines in more nutrient-rich vegetation types. Also, more nutrient-rich sites may lay in a matrix of more intensively used neighbouring fields, such that stronger isolation might be a reason for the unfavourable development in such sites (Helbig et al., 2017). Another critical factor is the deposition of considerable amounts of airborne nitrogen in Switzerland (Rihm and Achermann, 2016). Nitrogen inputs as well as other factors, e.g. climate change, likely led to vegetation changes too small to be detected by our vegetation type classification but with important consequences for some grasshopper

species. Roth et al. (2021) postulate a microclimatic cooling effect because atmospheric nitrogen deposition leads to a denser vegetation. Their argument is based on an observed negative correlation between atmospheric nitrogen deposition and butterfly richness and abundance in Switzerland. Such an effect may contribute to the development in grasshopper abundances in our study, but it seems rather unlikely to be the main driver. Total grasshopper abundance was mostly determined by species with a wide ecological tolerance (e.g. *Chorthippus biguttulus*, *C. parallelus*, Fig. S 6), able to live in more intensively used grassland than the typical grassland in our study sites.

If our study suggests that soil drying may be an important factor for grasshopper abundances, this should not be extrapolated to explain the scarcity of grasshoppers in intensively used agricultural areas. In such areas, it is evident that scarcity is due to the dense and uniform vegetation together with regular mechanical disturbances (cutting, chopping, silage; e.g. Poniatowski et al., 2020, and literature cited in the introduction).

5. Conclusion

We observed a striking decline of total grasshopper abundance in apparently largely unchanged agricultural, often semi-natural grassland between 1992 and 2011. We interpret our observations as a species-turnover in progress, with species optimally adapted to the past conditions strongly declining in number. Drivers potentially responsible for this trend may be overall and summer temperatures, soil humidity and drought conditions, fine-scale vegetation characteristics that changed due to atmospheric nitrogen deposition and climate change, and possibly also winter temperatures, snow cover and slight changes in land-use, albeit the relevant factors cannot be identified with certainty from our correlational data. We expect that in the future, warm-adapted species will become more common or will newly arrive. Whether they will be super-abundant as some of the now less common species once were (at least in some years) will depend on many factors, with consequences for higher trophic levels. Also, climate change likely alters productivity of the grasslands, potentially increasing the risk of abandonment and overgrowth that have negative effects on species richness (Marini et al., 2009). Therefore, it will be critical to retain and adapt measures that ensure a continuous and extensive usage to promote a rich insect and overall biodiversity. Regarding biodiversity monitoring, our study, as many others, illustrates the urgent need for standardized long-term monitoring of abundances, including censuses at different times of the year, in combination with measurements of relevant environmental factors (e.g. for grasshoppers: soil humidity and vegetation density), to improve our understanding of the current massive biodiversity changes inflicted by mankind, and to develop efficient tools to promote biodiversity in this changing world.

CRediT authorship contribution statement

Georg Artmann-Graf: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Pius Korner:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110816.

Data availability

Data and R-code can be found at https://doi.org/10.5281/zenodo.13933230.

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