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Contributed Paper

Butterfly community shifts over 2 centuries

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Abstract: *Environmental changes strongly impact the distribution of species and subsequently the composition of species assemblages. Although most community ecology studies represent temporal snap shots, long-term observations are rather rare. However, only such time series allow the identification of species composition shifts over several decades or even centuries. We analyzed changes in the species composition of a southeastern German butterfly and burnet moth community over nearly 2 centuries (1840–2013). We classified all species observed over this period according to their ecological tolerance, thereby assessing their degree of habitat specialisation. This classification was based on traits of the butterfly and burnet moth species and on their larval host plants. We collected data on temperature and precipitation for our study area over the same period. The number of species declined substantially from 1840 (117 species) to 2013 (71 species). The proportion of habitat specialists decreased, and most of these are currently endangered. In contrast, the proportion of habitat generalists increased. Species with restricted dispersal behavior and species in need of areas poor in soil nutrients had severe losses. Furthermore, our data indicated a decrease in species composition similarity between different decades over time. These data on species composition changes and the general trends of modifications may reflect effects from climate change and atmospheric nitrogen loads, as indicated by the ecological characteristics of host plant species and local changes in habitat configuration with increasing fragmentation. Our observation of major declines over time of currently threatened and protected species shows the importance of efficient conservation strategies.*

Keywords: atmospheric nitrogen, community structure, dispersal behavior, ecological tolerance, Rhopalocera, stochastic processes, temporal species turnover, time series

Cambios en las Comunidades de Mariposas a través de Dos Siglos

Resumen: *Los cambios ambientales impactan fuertemente la distribución de las especies y en consecuencia a la composición de los conjuntos de especies. Aunque la mayoría de los estudios de ecología de comunidades representan panoramas temporales, las series de tiempo a largo plazo son bastante raras. Sin embargo, sólo este tipo de información a largo plazo permite la identificación de los cambios en la composición de especies a través de varias décadas o incluso siglos. Analizamos los cambios en la composición de especies en las comunidades de una mariposa del sureste alemán y una polilla ziygena a lo largo de casi dos siglos (1840–2013). Clasificamos todas las especies observadas en este periodo de acuerdo a sus características ecológicas, para así evaluar su grado de especialización de hábitat. Esta clasificación se basó en los caracteres de las especies de mariposa y de polilla o en las plantas hospederas de sus fases larvales. Para nuestro estudio colectamos datos del mismo periodo de tiempo sobre la temperatura y la precipitación en nuestra área de estudio. El número de especies declinó sustancialmente de 1840 (117 especies) a 2013 (71 especies). La proporción de especialistas de hábitat disminuyó y la mayoría de estos se encuentran actualmente en peligro de extinción. En contraste, la proporción de generalistas de hábitat incrementó. Las*

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especies con un comportamiento de dispersión restringido y las especies que requieren de áreas pobres en nutrientes del suelo tuvieron pérdidas severas. Además de esto, nuestros datos indicaron una disminución en la similitud de la composición de especies entre décadas diferentes en el tiempo. Estos datos sobre los cambios en la composición de especies y las tendencias generales de las modificaciones pueden reflejar los efectos del cambio climático y las cargas de nitrógeno atmosférico, como fue indicado por las características de las especies de plantas hospederas y los cambios locales en la configuración de hábitat con la fragmentación creciente. Nuestra observación de grandes declinaciones de especies amenazadas y protegidas a través del tiempo muestra la importancia de las estrategias eficientes de conservación.

Palabras Clave: comportamiento de dispersión, estructura comunitaria, nitrógeno atmosférico, procesos estocásticos, remplazo temporal de especies, Rhopalocera, serie de tiempo

Introduction

Species are strongly influenced by environmental changes at different spatial scales. Climate change and atmospheric nitrogen loads act at a large geographic scale, whereas increasing destruction or fragmentation of formerly interconnected habitats and decreasing habitat quality act at regional and local scales. Species react to environmental modifications either through local adaptations (Karl et al. 2009) or modifications of their distributions (Berg et al. 2010). Thus, studies reveal range contractions of cold-resistant species and range expansions of warm-loving species over elevational and latitudinal gradients in response to climate change (Parmesan et al. 1999; Scriber 2014). Furthermore, increasing atmospheric nitrogen loads already have caused remarkable changes in community assemblages; habitat generalists have become more dominant and there are fewer species with specific habitat demands, for example, species adapted to habitats poor in nutrients or monophagous taxa. Such rapid large-scale modifications may strongly affect local species assemblages and hence affect interactions among species (Blois et al. 2013), for example, geographic mismatches between hosts and host plants (Schweiger et al. 2008; Bowman et al. 2006; Phoenix et al. 2006; Duprè et al. 2010; Filz et al. 2013*a*).

In addition to these large-scale impacts, locally driven factors in combination with the ecological demands of taxa may significantly impact the composition of communities. Many land-cover types today are represented only by comparatively small and isolated remnants, wherein many negative effects on a population level persist (Fahrig 2003). Such small and isolated populations are highly and negatively affected by environmental and demographic stochasticity (Melbourne & Hastings 2008) and thus are particularly subject to extirpation (Reed & Frankham 2003). Here, the ecological amplitudes of species play a pivotal role in the persistence of taxa over time. Species with specific ecological demands and species with low dispersal abilities are assumed to be more prone to extirpation than highly mobile species and habitat generalists. This situation underlines the necessity to balance potential negative population trends on the landscape level (Schloss et al. 2012; Polic et al. 2014).

Comparative studies of potential changes in the composition of communities, based on data sets collected at least at 2 points in time, provide valuable insights into trends of the local biota. Although long-term data sets on single species are available (reviewed in Müller et al. 2010), few studies trace potential changes of community compositions and structures over longer periods (e.g., Wenzel et al. 2006; Augenstein et al. 2012; Filz et al. 2013*a*). Such time series mainly cover relatively short periods of a few years or decades, are limited to 2 or 3 points in time, and do not include the preindustrialization period. Thus, most data sets cannot be used to study the entire transformation process from the time of preindustrial farming through the high-productivity industrialized agriculture of today (Wenzel et al. 2006; Augenstein et al. 2012). An exception is the recent work of Ollerton et al. (2014), who found that extinction pulses are related to changes in agricultural practices. Therefore, the integration of community data collected prior to the onset of the focal drivers of environmental change is essential to set appropriate temporal baselines for community comparisons (cf. Papworth et al. 2009). This will allow for a more comprehensive evaluation of potential responses of taxa and communities to environmental changes over time and allow the evaluation of the efficiency of recent conservation strategies.

We analyzed a data set of butterflies and burnet moths that covers the past 2 centuries. These data consist of decades of species records collected at protected calcareous grasslands in the vicinity of the city of Regensburg in southeastern Germany. We considered the ecological characteristics and biology of each species based on its habitat demands, dispersal behavior, and larval ecology (Weidemann 1986, 1988; Bink 1992; Bräu et al. 2013). We further assessed the ecological needs of the main larval host plants from all Lepidoptera species observed relative to soil moisture, soil nutrients, temperature, and sunlight and shade requirements. Furthermore, we integrated local climatic conditions, which were recorded from the same region and for the same period. Based on these data, we analyzed the quantitative and qualitative trends of species (i.e., species losses, species gains, and changes in the composition of species). We interpreted our results against the background of ongoing, rapid abiotic and biotic changes, as well as modifications of the landscape structure.

Methods

Study Area

Our study area, located near the city of Regensburg, Bavaria (southeastern Germany), has been a nature reserve since 1992. The current conservation area consists of about 45.4 ha of grassland and stretches about 3.5 km on south-facing slopes of the Danube River. It comprises our grassland study site consisting of 3 local patches, Am Keilstein, Schwabelweiser Hänge, and Fellinger Berg (Segerer 2012). These seminatural calcareous grasslands have continuously existed for several centuries and currently represent important habitat remnants of many oligotrophic and xerothermophilic plant and animal species.

Species Data Set

We compiled records of butterflies and burnet moths from articles published in international, national, and regional journals and from data stored in the Zoological State Collection Munich (ZSM). Data sets from the past 10 years were provided by one of the authors (AS). We obtained an occurrence matrix of butterflies (Rhopalocera) and burnet moths (Zygaenidae) that ranged from 1770 to 2013. An overview of all resources used is in Supporting Information.

We used data from 10-year periods during which reliable surveys were conducted. Ten-year periods for which various abundant and widespread species were missing, a clear indication of insufficient surveying, were excluded. Thus, we removed the pre-1840s data and data from the decades from 1880 to 1899. We also discarded data from the decades between 1930 and 1969, when recorded species numbers were unreliably low (Table 1). Recorders applied different methods of data collection (observing, netting, transect counts), so we confined our entire data set to a simple presence-absence matrix. Information about species′ abundance and density was disregarded. Our final data set contained eleven decades of well-documented species records that covered 3 larger time windows: 1840–1879, 1900–1929, and 1970–2013. Our full data set is in Supporting Information.

Ecological Classification of Species

To determine the ecological significance of changes in community composition, we categorized all butterfly and burnet moth species according to various ecological and behavioral traits. We assessed biotope preference, habitat type, moisture and temperature preference, degree of openness of the habitat, ecological requirements of larval host plants, and dispersal behavior of imagoes. Hence, each species falls into one of two general groups habitat generalists and habitat specialists. Information on ecological classification was taken from Weidemann (1986, 1988), Bink (1992), and Bräu et al. (2013). We considered the degree of endangerment following the species' classifications in the Red List of Bavaria (Geyer & Bücker 1992). Details on these classifications and assignments of the individual species to categories are in Supporting Information.

Climate Data

Time series for the local climatic conditions, including monthly temperature and precipitation data, were taken from the annual records of the German Weather Service (DWD) and covered the period 1871–2013. We used the mean (SD) temperature and precipitation for each decade. The year-wise climatic data records are in Supporting Information. Mean temperature and precipitation were highly and positively correlated during the study period (Pearson $r = 0.87$, $P < 0.001$). Nevertheless, we used both data sets separately because both parameters affect potential trends in community shifts independently and may impact population trends in different ways.

Ecological Classification of Larval Host Plants

In addition to the ecological classifications of our studied butterfly and burnet moth species, we determined the ecological requirements of all the main larval host plants used by the recorded lepidopteran species in our study region. We considered 4 parameters: soil moisture, soil nutrients, temperature, and sunlight requirements. We applied Ellenberg's (1992) system of values to determine the ecological tolerance of each Central European vascular plant species based on a number of biotic and abiotic characteristics (for further details see Schaffers & Sýkora 2000 and Wamelink et al. 2002). These data provide valuable information relative to the potential effects from atmospheric nitrogen loads and other factors that occur at an interregional scale. We excluded potential host plant species if they did not occur in our study region according to a plant-species assessment by Segerer (2012). We calculated mean values of the ecological niche of the respective host-plant species and hence for the butterfly and burnet moth species. Ellenberg's indicator values were averaged over all larval host plants potentially used by the respective lepidopteran species in our study region. Further details and an overview of the ecological classification and species-specific values are in Supporting Information.

Table 1. Changes in butterfly and burnet moth species richness and species gains and losses and changes in numbers of generalist species, xerothermophilic species, and endangered species.

Period	*Species richness*	*Species gains*	*Species losses*	*Generalist species*	*Xerothermophilic species*	*Endangered species*
1840–1849	117			60	39	60
1850–1859	120	8	5	60	40	62
1870–1879	123	6	3	61	41	64
1900–1909	114	8	17	59	36	61
1910–1919	63	6	57	31	27	35
1920–1929	73	32	22	29	36	44
1970–1979	78	41	36	45	21	29
1980–1989	107	33	4	58	34	49
1990–1999	89	7	25	51	29	39
2000–2009	92	13	10	55	31	39
2010–2013	71	6	27	48	22	24

Note: Species gains and losses refer to new species and lost species with respect to the previous study decade.

Statistical Analyses

We organized the entire data set in a presence–absence matrix with species in rows and time intervals in columns (Supporting Information). We assessed the degree of ordered species loss over time (the nested subset pattern; Ulrich et al. 2009) and the temporal change in community composition (β diversity). We used the approach of Baselga et al. (2007) and Baselga (2010) and partitioned the overall β diversity (β_{sor}) among sites into multisite nestedness (β_{nest}) and turnover (β_{sim}) components. In this respect, multisite nestedness quantified the part of compositional change caused by ordered species loss, whereas turnover was related to the exchange in faunal composition caused by the local trade-off between extinction and immigration. To quantify the total degree of nestedness, we used standard nestedness derived from the overlap and decreasing fill (NODF) metric, which is a normalized count of the degree of species overlap among the sequence of plots ordered according to decreasing species richness (Almeida-Neto et al. 2008).

Metrics of species co-occurrences, such as NODF and beta diversity, are constrained by matrix geometry (Gotelli & Ulrich 2012) and cannot be used directly to assess degree of nestedness and β diversity. To assess whether observed patterns deviated from random expectation, we used a null model approach for statistical inference (Gotelli & Ulrich 2012) and compared observed scores with those obtained through randomization. Because species differ in regional abundances and therefore in colonization abilities (mass effects in the sense of Ulrich et al. 2009 and Gotelli & Ulrich 2012), we calculated the expected metric scores from a null model that randomized the focal matrix by placing species into the cells proportional to observed total occurrences (the fixed row-equiprobable column model) as recommended by Gotelli (2000). Low NODF and high values of β diversity relative to the null expectations imply pronounced temporal changes in species composition and therefore point to dispersal as a major factor that shapes butterfly communities (Ulrich et al. 2009).

We used one-way distance-matrix-based permutation analysis of variance (PERMANOVA) (Anderson 2001) based on Sørensen dissimilarities β_{sor} to link changes in species occurrences to the ecological classification of species. To relate average decade temperatures and precipitation to the ecological classification, the matrix was multiplied by the temporal vectors to obtain average climate scores for each species. These served as the metric input in a subsequent one-way ANOVA with ecological classifications as categorical variables. We used Sørensen dissimilarities to assess the degree of temporal exchange in faunal composition between the 3 time windows. We used ordinary least-squares linear regression to infer general temporal trends in butterfly community composition.

Similarly, we summed single values for the ecological requirements calculated for the host plant species to obtain average scores for light, moisture, temperature, and nutrient requirements for each decade. We used these scores to assess whether observed changes in habitat conditions translated into differences in species composition.

Results

In total, 136 butterfly and burnet moth species were recorded in the study area from 1840 to 2013. The highest species numbers (117 to 123 species per decade) were observed from 1840 to 1880 (130 species for the entire period; Table 1). Species temporal turnover was low during this period (mean $\beta_{\mathrm{sor}} = 0.07$ [SE 0.01]). A lower species number per decade (63–114) but a considerably higher degree of temporal species turnover ($\beta_{\mathrm{sor}} = 0.57$ [0.06]) was observed for the period 1900–1929 (Table 1). However, the total species number during this period was 133 and thus even slightly higher than

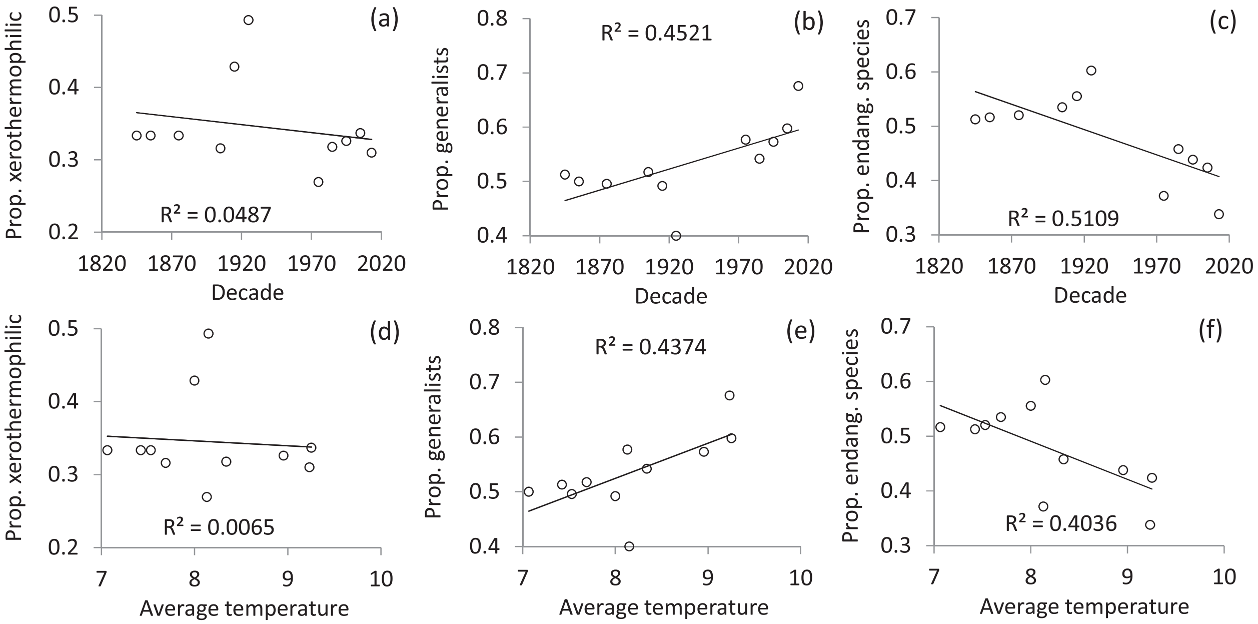

Figure 1. Changes in the proportion of (a) xerothermophilic, (b) generalist, and (c) currently endangered species from 1840 to 2013 and changes in the proportion of (d) xerothermophilic, (e) generalist, and (f) endangered species relative to average temperature scores.

Table 2. The NODF, total β diversity (β_{sor}), and the respective nestedness (β_{nest}) and species turnover components (β_{sim}) of the butterflies and burnet moths matrix of decade presences and absences.

Metric	*Score*[a]	*Lower null model CL*[b]	*Upper null model CL*[b]
NODF	0.76	0.71	0.73
β_{sor}	0.59	0.59	0.64
β_{nest}	0.40	0.53	0.58
β_{sim}	0.19	0.01	0.06

Note: Standard nestedness derived from the overlap and decreasing fill.

[a] *Significance: P < 0.001.*

[b] *Upper and lower 99.9% confidence limits of the fixed-equiprobable null model.*

observed from 1840 to 1880. The period 1970–2013 had the lowest total number of species (121; 71–107/decade) and a relatively high degree of temporal species turnover ($\beta_{sor} = 0.25$ [0.02]). From 1840 to 1880, temporal variability in species composition was significantly lower than in the latter 2 periods (one-way ANOVA $P < 0.05$). The proportion of xerothermophilic species did not significantly change over time (Fig. 1a), whereas the proportion of generalist species increased significantly (Fig. 1b) and the proportion of (today) endangered species decreased (Fig. 1c).

The species × decade matrix was significantly nested and showed a lower temporal species turnover (β_{sor}) than expected from our null hypothesis (Table 2), although species (Sørensen) similarity decreased exponentially as temporal distance increased (slope $z = -0.16 \pm 0.06$; $r^2 = 0.29$, $n = 17$, permutation $P = 0.03$). Consequently, the partitioning pointed to nestedness as being the major component of β diversity and species turnover as being of minor importance. Because species numbers were significantly negatively correlated with average decade temperature ($r^2 = 0.49$, $P = 0.01$), the degree of ordered species loss after ordering the decades according to average temperature was similar to the ordering according to species numbers and also highly significant (NODF = 0.76, $P < 0.001$, not shown).

The results of a PERMANOVA (Table 3) suggested generalism, endangerment, and, to a lesser degree, biology as changing with the species numbers and climatic conditions. In turn, land-cover type, larval host plants, and dispersal ability did not significantly covary with species numbers and climatic conditions (Table 3). The proportion of xerothermophilic species did not significantly correlate with temperature (Fig. 1d) and precipitation ($r^2 = 0.05$, not shown). The proportion of generalist species increased as average temperature increased (Fig. 1e) and as average precipitation increased ($r^2 = 0.56$, $P < 0.01$, not shown). The proportion of species endangered today correlated negatively with temperature (Fig. 1f) and precipitation ($r^2 = 0.50$, $P = 0.01$, not shown).

Average indicator values of the ecological requirements of larval host plants of the butterfly and burnet moth species supported our results for a general decrease of species with comparatively low ecological tolerance and rather oligotrophic and thermophilic habitat demands (Fig. 2). The proportions of xerothermophilic (Fig. 2a) and endangered species (Fig. 2g) increased and those of generalist species (Fig. 2d) decreased as

Table 3. Results of one-way permutation analysis of variance (species co-occurrences) and one-way analysis of variance (temperature and precipitation).

Factor	*df*	*Species co-occurrences*	*Temperature*	*Precipitation*
Biotope preference	3	<0.01	<0.01	0.01
Habitat type	9	0.10	0.42	0.30
Phagy	2	0.50	0.33	0.79
Dispersion	6	0.2	0.25	0.36
Trophic generalism	1	<0.01	<0.001	<0.001
Endangerment	5	<0.01	<0.001	<0.001

Note: Significant Bonferroni-corrected P values based on F statistics ($n = 136$ species) (Fig. 1). Changes in the proportion of (a) xerothermophilic, (b) generalist, and (c) currently endangered species from 1840 to 2013 and changes in the proportion of (d) xerothermophilic, (e) generalist, and (f) endangered species relative to average temperature scores.

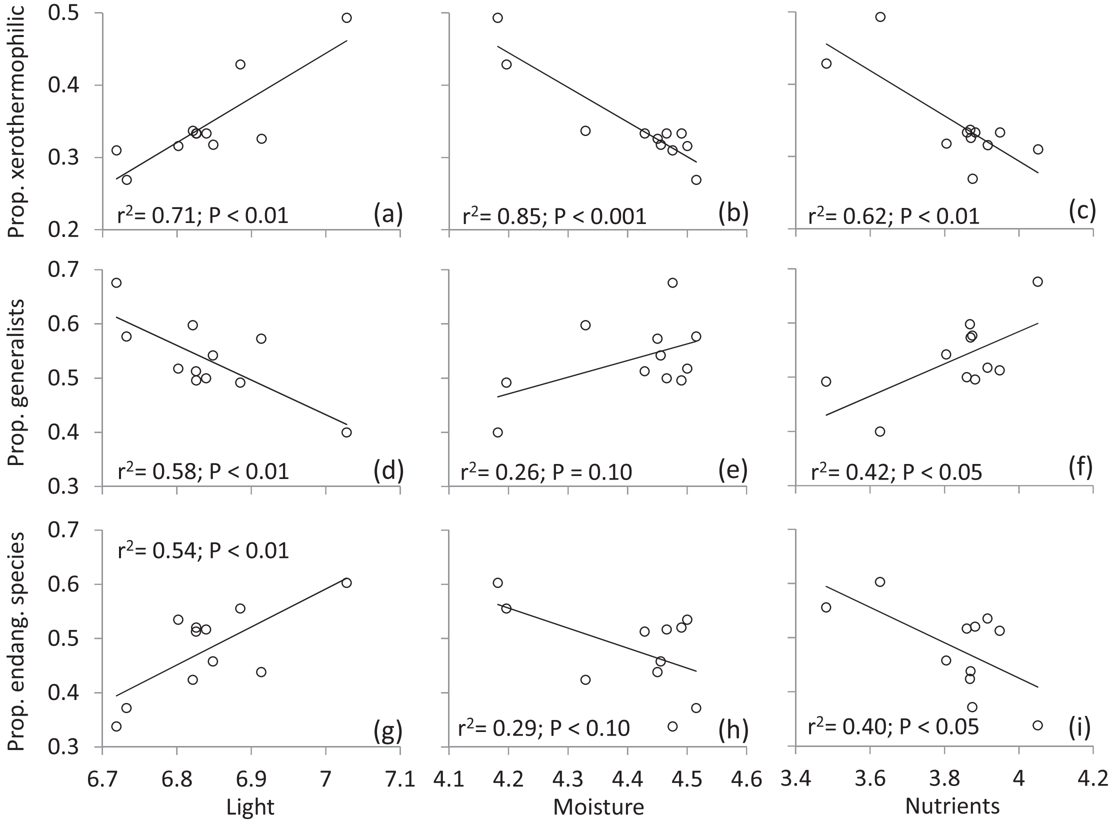

Figure 2. Proportions of xerothermophilic (a, b, c), generalist (d, e, f), and endangered species (g, h, i) in relation to average Ellenberg indicator values (i.e., values to express the ecological character of vascular plants) for light, moisture, and nutrient levels, as inferred from the larval host plants. Regression lines are for ordinary least-squares linear regressions.

light requirements of these plants increased. The opposite trends were observed with respect to soil moisture (Figs. 2b, e, and h) and nutrients (Figs. 2c, f, and i).

Discussion

Impoverishment of Communities

We found 3 frequently observed long-term phenomena: a significant loss in the total number of species (Table 1); major changes in beta diversity among consecutive decades; and a gradual transformation from a species assemblage hosting many habitat specialists to a community dominated by a few habitat generalist species (Fig. 1). Although the proportion of habitat generalists increased, many species with specific habitat demands, restricted dispersal behavior, and comparatively higher degrees of endangerment were extirpated (Fig. 1). This is apparently a general phenomenon, one that has also been observed in the recent past (e.g., Rodríguez et al. 2003; Phoenix et al. 2006; Augenstein et al. 2012).

This trend fits our data on larval host plants. The average nitrogen values of the principal host plants of the butterfly and burnet moth species present in each decade gradually shifted to higher nitrogen values over time. Thus, the average larval habitat requirements became increasingly eutrophic, which supported the observed trend from communities dominated by calcareous grassland specialists toward communities dominated by common, open-habitat species (Fig. 2).

The gradual extinction of species has resulted in a nested community structure over time, where the more recent species assemblages represent simple subsets of the older ones. This loss of species has been observed by others, who, in contrast, examined only the past few decades. Hence, frequently reported recent species' declines may be a general trend for animal and plant species that coincides with the beginning of industrialization, with its concomitant increases in atmospheric pollution and industrial fertilization of agricultural sites. The biodiversity losses over the last few decades may consequently represent only a small portion of a dramatic biodiversity decrease that has been ongoing for a much longer period than most studies. A combination of large-scale global effects, such as rapid climate change, increasing atmospheric nitrogen loads, and small-scale local effects, such as land-use changes and in particular land-use intensification, may be responsible for these negative trends.

Global Change and Local Species Communities

High deposition rates of atmospheric nitrogen have detrimental effects on nutrient-poor ecosystems such as bogs, calcareous oligotrophic grasslands (our study site), and heathlands (Stevens et al. 2004; de Vries et al. 2007). Atmospheric fertilization affects the growth potential of plants, greatly changing phytosociological structures (de Vries et al. 2007). In the successional process, plant species typical of nutrient-poor habitats are replaced over time by species of eutrophic sites. This ultimately results in plant communities dominated by few nitrophilic species, and these species are highly successful if they have a sufficient nutrient supply (de Vries et al. 2007). These processes primarily result in large alterations to vegetation that subsequently affect all animal species that rely on specific vegetation structures, for example, butterflies and burnet moths (Filz et al. 2013*a*, 2013*b*). Thus, it is mostly species of oligotrophic habitats that are negatively affected by increases in atmospheric nitrogen (Wenzel et al. 2006). Consistent with this contention, we found a significant negative correlation between the nutrient requirements of host plants and the proportion of endangered butterfly and burnet moth species, most of which depend on plants of nutrient poor sites. Furthermore, dominance of a few habitat generalists adapted to nitrophilic host plants increased (Fig. 2f).

In contrast, for example, to Chen et al. (2011), we detected only comparatively moderate effects of climate change on the butterfly and burnet moth community we analyzed. However, our data suggest that habitat generalists have benefited from increasing temperatures, whereas habitat specialists have been negatively affected by increasing temperatures (Fig. 1) and precipitation. These effects may be explained by increased vegetation growth rates triggered by the combination of increased moisture, temperature, and atmospheric nitrogen (Filz et al. 2013*b*). Greatly increased vegetation growth may also explain the apparently paradoxical situation that thermophilic species are also undergoing substantial declines in response to increased temperatures. However, higher vegetation growth rates, fostered by the combination of increasing plant nutrients, precipitation, and higher temperatures may produce a cooler and more humid microclimate close to the soil. The environment just above the soil is of particular importance in the development of many butterfly and burnet moth caterpillars (Weidemann 1986, 1988; Ebert & Rennwald 1991). Therefore, microclimatic conditions for larval development may be less favorable for xerothermophilic species in our study area today than several decades ago or even during the 19th century when average temperatures were still considerably lower (Filz et al. 2013*b*).

In contrast to the moderate effects from climate warming in our study area, other studies on butterflies detected stronger impacts, for example, rapid northward colonization of species (e.g., Parmesan et al. 1999; Asher et al. 2001) and colonization of higher elevations (Dieker et al. 2011). These effects are occurring mostly in northern Europe, in particular the British Isles (e.g., Asher et al. 2001) and Fennoscandia (e.g., Parmesan et al. 1999). Range expansions of butterfly and burnet moth species have been limited in Germany over the last 100 years (mostly *Pieris mannii* and *Brenthis daphne* in southwestern Germany) and have not been recorded in southeastern Germany. The large majority of these expansive species are habitat generalists, and because they have no specific habitat requirements, they simply follow their climatic envelope (Hill et al. 2002, 2011).

Habitat Configuration and Dominance of Habitat Generalists

Apart from large-scale global factors, local land-use intensification may have large impacts on the persistence of taxa and thus local species composition. Intensification of agriculture with subsequently increasing levels of habitat fragmentation strongly affects species assemblages via rising environmental and demographic stochasticity, particularly in small and isolated habitat remnants of relatively poor quality (Melbourne & Hastings 2008; Krauss et al. 2010). Such landscape transformations in particular affect species with specific habitat demands (Wenzel et al. 2006; Augenstein et al. 2012; Filz et al. 2013*a*) and hence affect many of the vanishing species in our study. Increasing temporal variability of species composition over time (expressed by Sørensen dissimilarity in our study) and the nested structure of the community we studied are warning signs of community impoverishment.

In our study area, the abundance of calcareous grasslands and thus their characteristic species is rather low. In addition, these habitat specialists tend to have relatively low dispersal ability. Thus, the small and isolated populations of habitat specialist species without viable metapopulation structures in our study area are subject to inbreeding. Stochastic events may affect such species much more than habitat generalists that show higher abundances and stronger dispersal behaviour and thus exist in rather interconnected populations at the landscape level (Hanski 1999; Melbourne & Hastings 2008). Our results suggest that in our study area habitat specialists should be a major focus of conservation (Van Swaay et al. 2006, 2012; Van Dyck et al. 2009).

Temporal Nestedness and Shifting Baselines

The constant disappearance of species, representing a human cross-generational trend, is rather slow and gradual. In consequence, it is difficult to detect potential changes in the composition of species or a significant loss of taxa during one single human generation. Thus, a new baseline of species composition is created with each human generation (the so-called shifting baseline phenomenon; Pinnegar & Engelhard 2008; Papworth et al. 2009). Shifting baselines highlight the tremendous importance of data sets such as ours that span long periods, including several human generations, and extend from a preindustrialized period to today.

Acknowledgments

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Supporting Information

Overviews of all sources used to compile the data set (Appendix S1), of all butterfly and burnet moth observations (Appendix S2), and of the species-specific ecological characteristics of the lepidopterans (Appendix S3); ecological classifications of all species observed in the study region (Appendix S4); climate data used (Appendix S5); and an overview of the Ellenberg (1992) indicator values for the larval host plants for the Lepidoptera species observed in our study site (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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