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Host specificity and species colouration mediate the regional decline of nocturnal moths in central European forests

Nicolas Roth, Herrmann Heinrich Hacker, Lea Heidrich, Nicolas Friess, Enrique García-Barros, Jan Christian Habel, Simon Thorn and Jörg Müller

N. Roth (https://orcid.org/0000-0002-8423-7288) ✉ (nicolas.roth@bfh.ch), H. H. Hacker, L. Heidrich (https://orcid.org/0000-0002-3229-4758), S. Thorn (https://orcid.org/0000-0002-3062-3060) and J. Müller (https://orcid.org/0000-0002-1409-1586), Field Station Fabrikschleichach, Dept of Animal Ecology and Tropical Biology, Biocenter, Univ. of Würzburg, Rauhenebrach, Germany. NR also at: Bern Univ. of Applied Sciences School of Agricultural Forest and Food Sciences, Zollikofen, Switzerland. JM also at: Bavarian Forest National Park, Grafenau, Germany. – N. Friess (https://orcid.org/0000-0003-0517-3798), Faculty of Geography, Philipps-Univ. Marburg, Marburg, Germany. – E. García-Barros (https://orcid.org/0000-0003-2804-9626), Dept of Biology – CIBC, Univ. Autónoma de Madrid, Darwin 2, Madrid, Spain. – J. C. Habel (https://orcid.org/0000-0003-1378-9381), Evolutionary Zoology, Dept of Biosciences, Univ. of Salzburg, Salzburg, Austria.

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The high diversity of insects has limited the volume of long-term community data with a high taxonomic resolution and considerable geographic replications, especially in forests. Therefore, trends and causes of changes are poorly understood. Here we analyse trends in species richness, abundance and biomass of nocturnal macro moths in three quantitative data sets collected over four decades in forests in southern Germany. Two local data sets, one from coppiced oak forests and one from high oak forests included 125K and 48K specimens from 559 and 532 species, respectively. A third regional data set, representing all forest types in the temperate zone of central Europe comprised 735K specimens from 848 species. Generalized additive mixed models revealed temporal declines in species richness (−38%), abundance (−53%) and biomass (−57%) at the regional scale. These were more pronounced in plant host specialists and in dark coloured species. In contrast, the local coppiced oak forests showed an increase, in species richness (+62%), while the high oak forests showed no clear trends. Left and right censoring as well as cross validation confirmed the robustness of the analyses, which led to four conclusions. First, the decline in insects appears in hyper diverse insect groups in forests and affects species richness, abundance and biomass. Second, the pronounced decline in host specialists suggests habitat loss as an important driver of the observed decline. Third, the more severe decline in dark species might be an indication of global warming as a potential driver. Fourth, the trends in coppiced oak forests indicate that maintaining complex and diverse forest ecosystems through active management may be a promising conservation strategy in order to counteract negative trends in biodiversity, alongside rewilding approaches.

Keywords: climate change, colour patterns, global change, Lepidoptera, macro moths, specialists, time series

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Introduction

Recent studies have raised concerns about 'insect decline' as a worldwide phenomenon (Cardoso et al. 2020, Harvey et al. 2020, Samways et al. 2020). Insects have been shown to decrease in terms of species richness (Thomas et al. 2004), abundance (Conrad et al. 2006) and biomass (Hallmann et al. 2017). There are indications of diversity loss in Hymenoptera (Biesmeijer et al. 2006, Potts et al. 2010), Hemiptera (Schuch et al. 2011, 2012), Coleoptera (Desender et al. 2010, Brooks et al. 2012), Diptera (Gatter et al. 2020) and Lepidoptera (Conrad et al. 2006, Habel et al. 2016). Although many studies show that 'insect decline' is occurring, a recent review by Sánchez-Bayo and Wyckhuys (2019) predicting the extinction of 40% of the world's insect species over the next few decades raised criticism, as their approach is considered biased towards studies reporting declines and thus accused of drawing 'too alarmist' conclusions (Komonen et al. 2019). This criticism is supported by several studies showing no trends, increasing trends in insect biodiversity or positive trends for a considerable number of species (Fox et al. 2014, Boyes et al. 2019, Macgregor et al. 2019, Crossley et al. 2020). The trends of insect populations are complex and depend on the habitat types, the taxonomic group and the study sites (Shortall et al. 2009, Hallmann et al. 2018, Roth et al. 2020, Van Klink et al. 2020). In addition, long time-series featuring a high taxonomical resolution and a high number of replicates are lacking or neglect management gradients or certain habitats. Uncertainties about the trends in insect biodiversity have increased calls for more robust temporal data on insects, covering time spans that are relevant when investigating effects of climate change and replicated at large geographical scales (Habel et al. 2019a, Kunin 2019, Thomas et al. 2019). Additionally, there is rising concern about the accurate analysis of time series data and monitoring schemes in general (Didham et al. 2020). Shifting or false baseline effects may lead to non-robust conclusions, especially when time series do not feature at least 10–15 individually sampled years (Fournier et al. 2019, White 2019). Furthermore, the meta analyses of insect declines come with drawbacks such as non-standardized sampling by various entomologists and pooling of samplings at different scales. This makes the generalisability of the conclusions doubtful in certain instances (Welti et al. 2020).

Forest dwelling insect species are often thought to be less endangered, especially in Europe (Juslén et al. 2016, Potocky et al. 2018), as forest use intensity has not changed dramatically over recent decades in central Europe compared to agriculture, with its marked increase in pesticides and fertilizers (Reif et al. 2006). Previous studies have shown stable temporal trends in woodlands for moths and other insects (Brooks et al. 2012, Hunter et al. 2014) and increasing species richness has been observed at individual locations (Thomsen et al. 2015, but see Seibold et al. 2019). Moreover, modern forestry often promotes continuous forest cover (uneven-even aged forest management), creating a stable and homogenous habitat (Schall et al. 2017). However, this homogenization of forests might come with costs in terms of habitat heterogeneity and the related biodiversity (Merckx et al. 2012a, Thorn et al. 2015), as the forest stages with the highest canopy cover are usually quite species poor (Hilmers et al. 2018). Furthermore, threats like diverging trends in phenology between hosts and pollinators or herbivores (Asch and Visser 2007, Memmott et al. 2007), have reduced the nutritive value of the host plants due to rising CO_2 levels (Lincoln et al. 1986, Cornelissen 2011). Also, general nitrogen input and the accompanying homogenization in plants (Gilliam 2006) are likely to affect forests in a similar fashion to open habitats (Seibold et al. 2019). Although forests are a major habitat type in Europe, general trends in the diversity of forest insects are largely unknown. So far, most quantitative long term studies on insects have been conducted in open habitats, focused on mainly open-habitat groups such as butterflies, have been based on monitoring schemes which are not habitat specific, or featured temporal extents smaller than four decades (Conrad et al. 2006, Groenendijk and Ellis 2011, Hunter et al. 2014, Hallmann et al. 2017, 2019).

Furthermore, species traits can influence trends in insect populations, and may also lead to diverging patterns within taxa, especially if they are taxonomically rich (Stefanescu et al. 2011a, Habel et al. 2019b). Traits like large wingspans, nocturnal activity and preference for woody or herbaceous food sources have been associated with species declines in moths (Coulthard et al. 2019). More generally, species with a higher degree of feeding specialization have been shown to be more negatively affected by habitat degradation and loss because of the higher flexibility generalists show regarding their diets (Habel et al. 2016, Coulthard et al. 2019, Wölfling et al. 2019). This makes generalists potentially more resilient to deterioration of habitat quality. Another trait which may be associated with differentiated decline/increase is colour (Zeuss et al. 2014). The variability in colour pattern is associated with niche breadth and feeding specialization (Forsman et al. 2020), whereas the colour lightness of insects exhibits patterns along thermal gradients. Thus colour lightness decreases with latitude (Zeuss et al. 2014, Pinkert et al. 2017, Heidrich et al. 2018), elevation (Xing et al. 2018, Wu et al. 2019) and from open to shaded habitats (Xing et al. 2016). Although mechanisms driving these relationships are not fully understood, the incidence suggests that lighter colouration will be favoured under climate warming (Zeuss et al. 2014).

In order to address the issue of forest insect diversity we analysed a lifework moth data set with high taxonomic resolution collected by HHH over four decades, featuring plots located in all forest types typical for central Europe. Nocturnal moths make up 86% of Lepidoptera in Germany (Steiner et al. 2014) and constitute a model group of insects covering a large trait space and exhibiting varying life histories. Thus, they are suitable for identifying overall, functional or lineage specific response differences. Their taxonomy is largely understood in central Europe (Timmermans et al. 2014, Mitter et al. 2017) and there is substantial knowledge about their ecology (Potocky et al. 2018). However, while macro-moth diversity has been shown to decrease because of land use intensification, habitat loss, light pollution and climate change (Conrad et al. 2006, Merckx et al. 2012b, Fox 2013, Mangels et al. 2017, Boyes et al. 2020), trends in forests are still unclear. We distinguished between two local scale data sets and one regional scale data set from light trapping samples, in order to analyse the temporal trends of species richness, abundance and biomass. We used left and right censoring as well as cross validation to check the robustness of the results. In addition to overall trends of species richness, abundances and biomass of macro moths, we analysed the three most abundant macro-moth families (Geometridae, Noctuidae and Erebidae) to test if 1) species richness, abundance and biomass have declined during the last four decades and whether these responses apply to all main subtaxa. Furthermore, we split the dataset into opposite halves of trait spectra (light/dark – and generalist/specialist species) to test if, 2) dark and light species and 3) feeding specialists and generalists differ in their trends.

Material and methods

Study area

The study area is split into three. Two core areas were sampled regularly within the study period, as well as a regional data set featuring plots across the whole German federal state of Bavaria (70 550 km^2). The first core area is an oak forest characterized by a continuous coppice-with-standards management (coppicing wood-management method with several trees, which are allowed to grow bigger; subsequently named coppiced forest) and was sampled in 23 years from 1979 to 2018 (Fig. 1). Within an area of approximately 1 km radius, eight plots were sampled on a total of 283 plot dates. The minimum number of resamplings per plot was nine, the maximum was 80 resamplings. The second core area is an oak high forest (subsequently named high forest), which was sampled in 18 years from 1979 to 2018. Within an area of approximately 200 m radius, nine plots were sampled on 118 plot dates. The minimum number of resamplings per plot was 7, the maximum was 36. At the regional scale, all forest types typical for central Europe (for details on forest types see Müller 2005, Hacker and Müller 2006, 2009) were sampled on 531 plots in 41 years spanning 1978–2018 and an elevational range from 210 to 1740 m a.s.l. Ninety-eight of the plots were sampled only once, 50 twice. The maximum number of resamplings on one plot was 62. In total we analysed 2806 sample dates at the regional scale.

Moth sampling and classification

Moths were collected using light traps equipped with superactinic ultraviolet light tubes mounted above plastic funnels for one full night per sampling. The attracted moths were collected in plastic containers at the bottom of the traps and killed with chloroform (Müller et al. 2012). All moth specimens were counted and identified by HHH, if necessary by examining genital preparations, following the higher-rank taxonomy by Zahiri et al. (2013) for the Noctuoidea. We used only data on macro moths for this study, for which all families were completely determined in all years. We analysed the data across all species (overall), and for Geometridae, Noctuidae and Erebidae (including Acrtiinae and Lymantriinae) separately, as these were the most abundant families. We separated all the species into different subsets (light coloured or dark coloured and dietary specialist or generalist) to create groups for which species richness trends could be compared (see the Supporting information for values and thresholds). We grouped all species into two classes of food specialisation with monophagous and oligophagous species (feeding on one or a few plant species) as a proxy for host specialists and polyphagous species as a proxy for host generalists, based on the classification by Hacker and Müller (2006). Information about host specificity was available for 785 of the 861 species sampled. We excluded species without information on host specificity from the respective analyses.

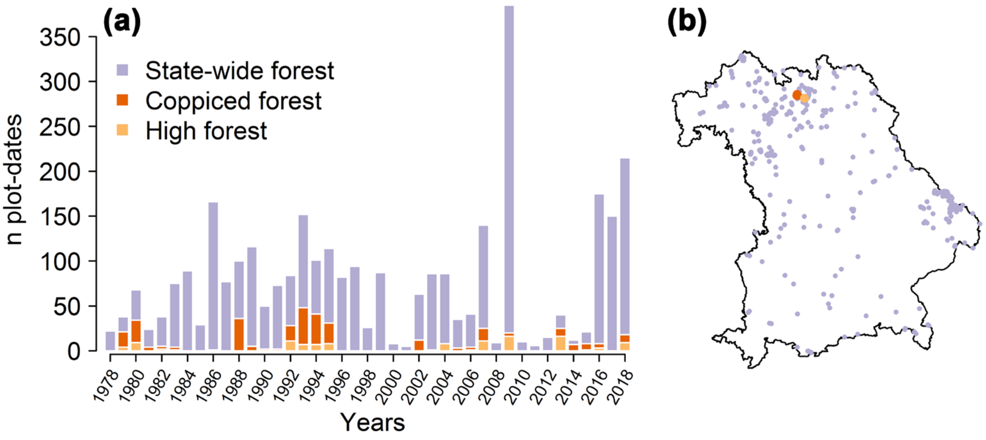

Figure 1. Sum of trapping nights per plot and year split according to the three analysed data sets (a), and plot locations within the federal state of Bavaria, Germany (b).

We assessed species colour lightness by analysing photos extracted from Segerer and Hausmann (2011) with a scanner (48 bits depth of colour). We removed the background and converted the images to eight-bit grey values (mean of the red green and blue values) following the protocol of Zeuss et al. (2014), and scaled colour lightness from zero (completely black) to one (completely white) using the software package 'png' (Urbanek 2013). We used the full dorsal surface area of the body and wings to calculate the colour lightness of species (Heidrich et al. 2018). We then separated species into light and dark according to the grey values, to estimate if trends in species richness are affected by colour lightness. Species above the median were categorized as 'light' species and species below as 'dark' species (see the Supporting information for values and thresholds). We chose this dichotomous approach to be able to analyse this trait in the same way as host specialization. Information about colour lightness was available for 853 of the total 861 sampled species. We excluded species without information on colour lightness from the respective analyses.

Statistical methods

We excluded 34 plot-dates on which only one species was sampled (numbers above refer to cleaned data). All statistical analyses were performed using R ver. 3.5.2 (<www.r-project.org>). We predicted the biomass of each sample using a model based on data published by García-Barros (2015). We modelled the dry weight as a function of the total area (mm^2) of the moth species reported by García-Barros (2015), using the 'lm' function from the 'stats' package (<www.r-project.org>). Based on this model, we then predicted the biomass of each species in our data set using the 'predict' function from the 'stats' package (see the Supporting information for details). For each sample, we added up the biomass of all species, multiplied by its respective number of individuals.

In order to account for nonlinear predictors (e.g. season and space), we used generalized additive mixed models (GAMMs; Wood 2004) to model species richness (e.g. the raw species number, negative binomial error-term), abundance (negative binomial error-term) and biomass (gaussian error-term), per plot and trapping night as dependent variables. We used the 'gam' function in the package 'mgcv' (Wood 2017) to model the dependent variables as a function of the year (as a numerical variable for all groups and additionally as a factor for overall species richness, abundance and biomass), season (calendar day) and elevation as well as latitude and longitude for the regional dataset. Latitude and longitude, and the season were included as smoothed variables (basis functions: splines on the sphere for latitude and longitude and cubic regression splines for the season; dimensions were set to default); plot id was included in the models as a random factor to account for replicated measurements on the same plot. We excluded latitude, longitude and elevation from the local models due to limited variation.

We predicted species richness, abundance and biomass using the 'predict.gam' function in the 'mgcv' package for each year between 1978 and 2018, in order to illustrate the results (Wood 2017). Latitude, longitude and elevation (regional data set only) as well as day of the year and the plot-id were set to null in the predictions in order to generate species richness, abundance and biomass trends independent of these variables. In order to test for robustness of the models we conducted left and right censoring as well as a cross validation of the models (Didham et al. 2020). For the left censoring models were recalculated by progressively removing the early time points from the data set until the year 2008 (Fournier et al. 2019). For the right censoring the latest years were progressively removed until the year 1988. For cross-validation models were calculated with only odd or even years, respectively. After prediction of species richness, abundance and biomass for the odd and even years, respectively, we calculated Pearson correlations between predicted and observed values.

We determined species richness, abundance (total number of specimens) and biomass per plot-date for light/dark and specialist/generalist species (subsequently called groups) and subsequently calculated GAMMs as described above with the group as an additional factor and an interaction term between group and years. We identified the group specific effects of the year and tested for significant interactions between groups.

Results

At the local scale, 125 078 specimens (mean 441.9 per sample, range 10–10 599) belonging to 559 macro-moth species (mean 49.6 per sample, range 6–164) in the coppiced forest and 58 270 specimens (mean 493.8 per sample, range 30–2932) belonging to 532 macro-moth species (average 61.8 per sample, range 12–133) in the high forest, were recorded. At the regional scale 735 483 (average 262.1 per sample, range 2–7321) belonging to 848 macro-moth species (average 37.9 per sample, range 2–176) were sampled in the state-wide forests, over the whole sampling period. Nine macro-moth families (Geometridae and Noctuidae being richest in specimens and species) were collected; 43 261 specimens from 260 species and 40 867 from 204 species, for Geometridae and Noctuidae, respectively were collected in the coppiced forest; 20 937 specimens from 212 species and 27 014 from 201 species, for Geometridae and Noctuidae, respectively in the high forest. At the regional scale 329 592 Geometridae specimens from 338 species and 200 506 Noctuidae specimens from 334 species were sampled in state-wide forests at the regional scale. The Erebidae family was the third group, which we analysed separately. 26 117/5321/130 833 specimens from 54/49/79 species were obtained from the coppiced, high and state-wide forests, respectively (see the Supporting information for complete species list).

We found that the season (day of the year, Fig. 2b), and space (latitude/longitude) were significantly correlated with species richness, abundance and biomass at the regional scale

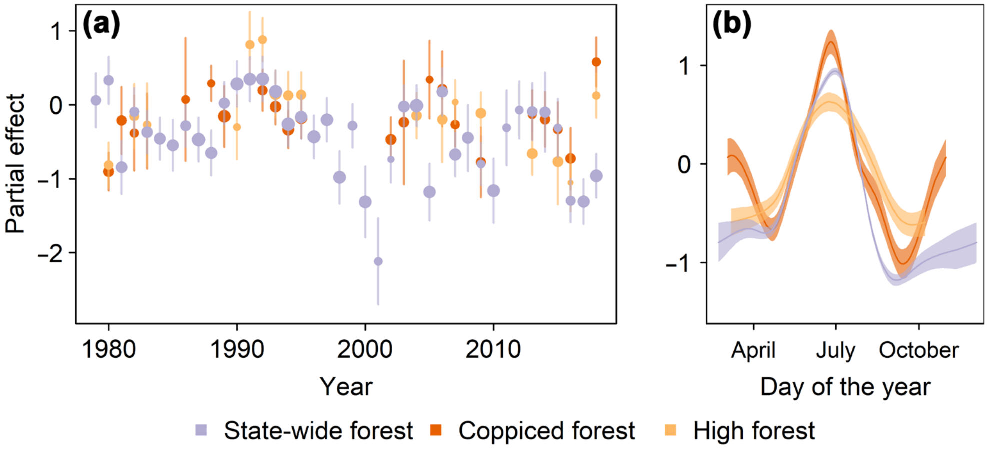

Figure 2. Partial effects the variable year scaled as a factor (a) and the season (b), day of the year as continuous variable) on the biomass. Colours indicate the three data sets. The size of the dots is relative to the number of sample events in the according year. All raw data in the Supporting information.

and at the local scale (season only) (Fig. 2, Table 1) except for Noctuidae biomass in the high forest (Supporting information). In state-wide forests we found elevation to have a significant negative effect on overall species richness (Table 1), and on Geometridae, and Erebidae abundance and biomass (Supporting information).

Long-term trend of macro moth diversity and biomass

We found pronounced temporal fluctuation (not the overall temporal trend) in species richness, abundance and biomass (Fig. 2a, see the Supporting information for raw data patterns). This fluctuation was consistent throughout the three datasets. Time as a linear predictor had a significant negative effect on the overall number of macro-moth species in the state-wide forests at the regional scale. We detected an overall decrease in species richness of 0.93% per year (predicted values decreased by 38% from 1978 to 2018, Supporting information) and abundance and biomass decreases of 1.3% and 1.4% per year, respectively (53% and 57% decrease over four decades, respectively Fig. 3b–c, Table 1). The decline in species richness, abundances and biomass in the state-wide forests affected Noctuidae the most followed by Geometridae. Erebidae showed a positive, significant temporal trend for all three biodiversity measures (Supporting information).

At the local scale we detected an increase in species richness of 1.5% per year (62% increase over four decades) on coppiced plots from 1978 to 2018 (Fig. 3a, Table 1). The species richness of all families (Geometridae, Noctuidae,

Table 1. Effect sizes of parametric and smoothed terms of GAMs for the state-wide (left), the coppiced (middle) and the high forest (right). Significances are indicated with * = <0.05, ** = <0.005, *** = <0.001; not significant where not indicated.

	State-wide forest		Coppiced forest		High forest		
	Estimate	z/F value	Estimate	z/F value	Estimate	z/F value	
Species richness							
Intercept	27.22	8.35***	−20.41	−2.98***	−0.48	−0.06	
Year	−0.01	−7.24***	0.01	3.52***	0	0.56	Parametric
Elevation	0	−4.04***					Parametric
Season	7.29	4308.46***	5.84	791.08***	5.53	382.87***	Smoothed
Lat/Lon	18.93	1593.56***					Smoothed
Abundance							
Intercept	43.05	7.34***	3.99	0.31	39.75	1.63	
Year	−0.02	−6.47***	0	0.14	−0.02	−1.38	Parametric
Elevation	0	−0.96					Parametric
Season	7.4	2160.57***	7.17	274.48***	4.56	132.41***	Smoothed
Lat/Lon	22.12	2259.99***					Smoothed
Biomass							
Intercept	51.11	7.89***	4.59	0.33	35.07	1.47	
Year	−0.02	−6.6***	0	0.31	−0.01	−1.08	Parametric
Elevation	0	−1.78					Parametric
Season	7.34	224.88***	6.68	26.39***	4.07	12.68***	Smoothed
Lat/Lon	22.62	26.96***					Smoothed

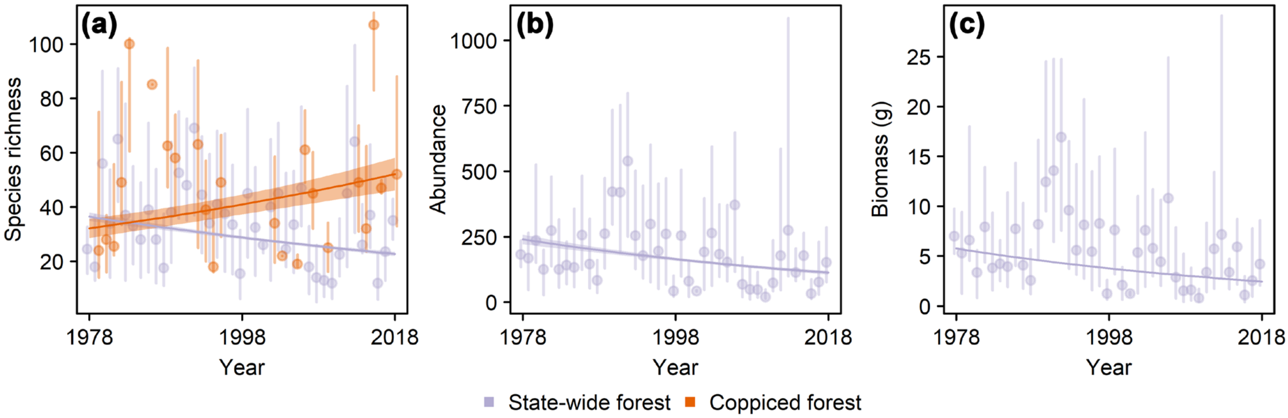

Figure 3. Trends of species richness (a), abundance (b) and biomass (c) between 1978 and 2018 at the local (coppiced forest) and regional scale (state-wide forest). The lines are based on predictions of the original models. Only significant trends are shown. Dots and lines in the background represent the median, the 25% and the 75% quantiles of the raw data.

Erebidae) increased significantly over time on coppiced forest plots, while only Erebidae increased in species richness and biomass in the high forest (Supporting information).

Left censoring showed the robustness of these results as the trends were constant in the state-wide forests for species richness (Fig. 4). Increases in species richness in coppiced forest were apparent until the removal of the sampling years up to the 1990s. In the high forest negative trends of abundance and biomass became apparent on removing the first three sampling years. Also, within the separately analysed families the trends were generally robust (Supporting information). However, left censoring indicated that the positive trends in Erebidae species richness, abundance and biomass, in the high forest, and species richness of Geometridae in the coppiced forest, were due to the first decade in the data set (Supporting information). Major deviations from the reported overall pattern were detected when excluding sampling years before 2003 (Fig. 4 light grey line). Right censoring showed that leaving out the years after 2005 would lead to non-significant trends or less pronounced trends (Supporting information). When all recent years until 1995 were removed, it resulted in the same patterns as with complete time-series data. Cross-validation showed that the predicted values correlate well with the measured ones especially at the regional scale at the order level (Supporting information). Species richness was predicted most accurately, while the strength of the correlations was partly weak (e.g. biomass and abundance predictions for single families at the regional level).

Association between species colouration, host specialisation and long-term trend

In the state-wide forests at the regional scale overall species richness, abundance and biomass decreased for dark and light species (Table 2, Supporting information). However,

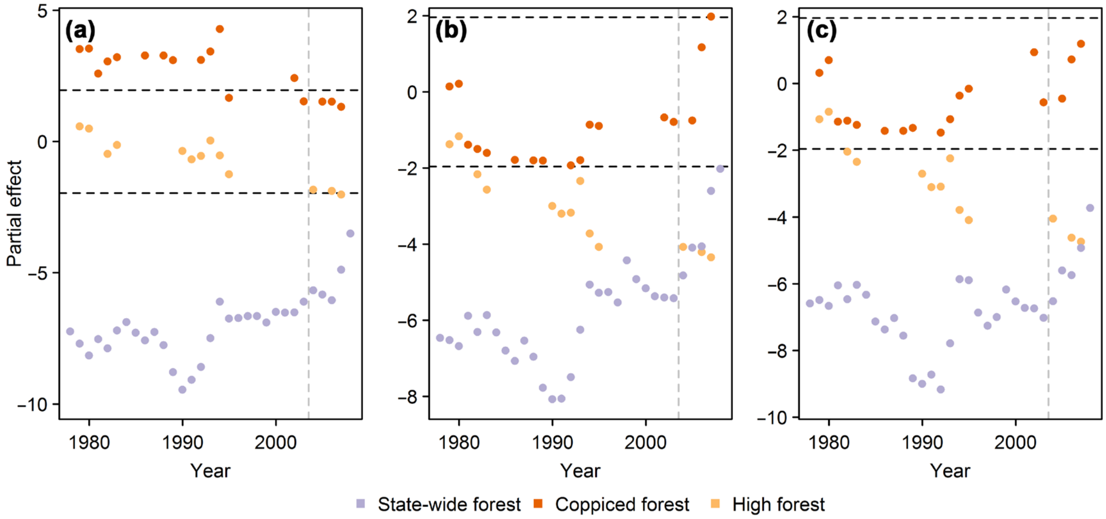

Figure 4. Left censoring of overall data (subsequent removal of the oldest year in the data set, and recalculation of the model), species richness (a), abundance (b) and biomass (c). Dashed black lines indicate significance threshold. The dashed grey line indicates subsets spanning less than 15 years, which may reduce the reliability of trend (White 2019).

Table 2. Partial effects of interaction terms of between dark/light and generalist/specialist species richness (negative binomial error distribution), abundance (negative binomial error distribution), biomass (gaussian error distribution) and the year, of GAMs calculated with the state-wide forest data set. Significances are indicated with * = <0.05, ** = <0.005, *** = <0.0001. Significant differences between the groups dark/light and generalists/specialists are indicated in grey.

State-wide forest			Coppiced forest			High forest		
Interaction	Estimate	z/F value		Estimate	z/F value		Estimate	z/F value
Color								
Species richness								
Dark	−0.01	−7.89***	Dark	0.01	3.62***	Dark	0	0.1
Light	−0.01	−3.56***	Light	0.01	3.73***	Light	0	0.83
Abundance								
Dark	−0.02	−8.31***	Dark	0	0.65	Dark	−0.03	−2.04*
Light	−0.01	−4.15***	Light	−0.01	−0.88	Light	−0.02	−1.54
Biomass								
Dark	−0.02	−7.67***	Dark	0.01	0.96	Dark	−0.02	−1.27
Light	−0.01	−4.61***	Light	0	0.36	Light	−0.01	−0.73
Feeding guild								
Species richness								
Generalists	0	−0.99	Generalists	0.01	3.75***	Generalists	0	1.09
Specialists	−0.01	−8.07***	Specialists	0.01	3.44***	Specialists	0	0.33
Abundance								
Generalists	0	0.69	Generalists	0	0.04	Generalists	−0.02	−1.09
Specialists	−0.03	−8.64***	Specialists	−0.01	−1.35	Specialists	−0.03	−2.19*
Biomass								
Generalists	0	−1.13	Generalists	0.01	1.44	Generalists	−0.01	−0.81
Specialists	−0.03	−9.62***	Specialists	0	−0.42	Specialists	−0.02	−1.68

the species richness, abundance and biomass of dark moths decreased significantly more than those of light moths. In the coppiced forest, we found increases in species richness in both light and dark groups, with no significant differences between the two functional groups (Table 2, Supporting information). In the high forest only the abundance of dark species decreased significantly.

In the state-wide forests at the regional scale, species richness, abundance and biomass of specialist species declined significantly, but not those of generalist species (Table 2 and Supporting information). In the coppiced forest, species richness of generalists and specialists increased with no significant difference between the two groups (Table 2). In high forest only the abundance of specialists decreased significantly.

Discussion

We found temporal fluctuation in species richness, abundance and biomass comparable to the fluctuations found in other insect biomass studies in Europe (Fig. 2a, Supporting information) (Hallmann et al. 2017, Macgregor et al. 2019). The decline in insect biomass in northern Germany from the mid-nineties to the year 2000 and the peak after the year 2000 (Hallmann et al. 2017) match the patterns we found particularly closely. Similarly, the decline in biomass from the late 1990s to present (Fig. 2) with local increases after the year 2000 matches the observations in moth biomass in Great Britain's forests (Macgregor et al. 2019). Fluctuations and tipping points of trends were also reflected in left and right censoring. There was a peak in species richness, abundance and biomass around 1990 at the regional scale as subsets excluding the sampling years before showed the steepest decline across the left-censoring (Fig. 4). Left-censoring also indicates that the increase in species richness in the coppiced forest happened before the year 2000. The non-significant trends of abundance and biomass in the high forest become negative on removing the early sampling years from the analyses. This suggests an increase until the early eighties followed by a decrease (Macgregor et al. 2019) and possibly a trend which is more strongly negative than the overall analyses suggests. However, we also found that the annual linear decline in moth biomass, of 1.3% within the sampled forests, did not occur in such drastic rates as those noted for Malaise traps sampled in open habitats (i.e. 6.1% in Hallmann et al. 2017) but was more pronounced than in moth biomass in forested habitat in Great Britain (i.e. 0.4% from 9 plots in Macgregor et al. 2019). This might be due to the fact that nocturnal moths in general did not show such a drastic decline as Diptera or Hymenoptera sampled predominantly with Malaise traps. This is supported by Macgregor et al. (2019) who found only a gradual decline with phases of net gains in moth biomass over the past 50 years (Macgregor et al. 2019). This may also be linked to a higher resilience of forests in comparison to open lands where intensification including inputs of pesticides, mowing and fertilizers are higher (Simon-Delso et al. 2017), and to the fact that forest may moderate responses to climate warming due to a microclimate buffered significantly by the canopy cover (Frenne et al. 2013). In a direct comparison, Seibold et al. (2019) also observed a steeper decline in insects in grasslands than in forests over one decade.

As species richness, abundance and biomass decreased at comparable magnitudes at the regional scale, this is an indication that the reported declines in biomass (Hallmann et al. 2017, Macgregor et al. 2019) might also mirror declines in species richness of insects (Seibold et al. 2019). In the forests at the regional scale we found a decline in moth richness in line with previous studies (Conrad et al. 2006, Groenendijk and Ellis 2011, Van Langevelde et al. 2018). The possible reasons for biodiversity declines are manifold, including climate change, light pollution, habitat loss and combinations of both (Fox 2013, Boyes et al. 2020). Rising CO_2 levels and changing air quality can lead to reduced nutritive value in leaves and thus negatively influence herbivore diversity (Lincoln et al. 1986, Cornelissen 2011, Pescott et al. 2015) through a higher mortality rate (Fajer 1989, Stiling et al. 2003). Also, differing changes in phenology between host and herbivores might result in a biodiversity decrease (Asch and Visser 2007, Memmott et al. 2007). Additionally, stressors might vary locally which adds to complex patterns of changes in moths (Wagner et al. 2021). In woodlands, the degradation of the structural complexity and the preference for closed canopy in silviculture (Vilén et al. 2012) have been discussed as possible factors driving population and species losses of Lepidoptera (Jeffries et al. 2006, Hilmers et al. 2018). However, there is an increasing number of studies showing constant diversity across recent decades (Crossley et al. 2020, Van Klink et al. 2020). Note that in contrast to numerous case studies, it is often meta-analyses, which report constant or increasing trends in insect communities. However, these studies tend to assemble data on a multitude of taxa, sampled on different scales, with inconsistent sampling of the different habitats (Welti et al. 2020). This might be a reason for undirected trends and conclusions which might not apply generally. In this study we cannot rule out that the different results at the regional and the local scales are partly due to the difference in sampling intensity per plot (Weiser et al. 2019, Wainwright et al. 2020). However, we analysed data from one taxon sampled only in forested habitats over a long time span. This should assure a certain degree of reliability of the trends we report. Different results at the regional and the local scales can also be due to the scale itself, as regional species richness is not only a product of α-diversity, but also of β-diversity (Chase et al. 2019).

Effects of habitat structure and silvicultural practices on moth communities

We observed stable moth diversity in oak high forest plots and increasing species richness in coppice with standards plots. The latter forest management type has already been shown to be beneficial to common but declining species (Merckx et al. 2012a). It implies the regular creation of gaps which undergo succession until trees are cut down again after 20–30 years. The resulting small-scale mosaic of different stages allows coexistence of shade-tolerant and light demanding species and may have positive effect on the moth diversity (Weiss et al. 2020). This is in contrast to most other forests in our study region that are kept in an optimum phase with continuous forest cover and thus feature less dynamics (Vilén et al. 2012). This lack of dynamics in forests may be one reason why these forest types cannot compensate for habitat alteration leading to subsequent species losses through, for example, nitrogen input (De Schrijver et al. 2011) and/or insecticides. The observed increase in insect biodiversity in coppice with standards plots may be connected to the expansion of range sizes of species from lower latitudes (Pateman et al. 2012). However, it is most likely a combination of temperature rise, which enables warm adapted and non-forest species to colonize the area, and the positive effects of the successional mosaic, which outweigh regional, negative effects in our coppice with standards plots. In order to corroborate these indications, broader scale analyses of differences in diversity trends with different management techniques would be necessary.

We also found the Erebidae to thrive at a regional scale in the regional data set with the present forestry practice. This may be due to the Lymantriinae (Erebidae) subfamily, which harbours several pest species (e.g. *L. dispar*, *L. monacha*), some of which have increased significantly in population over recent decades (Klapwijk et al. 2013). This is in line with other pest species which are increasing as a consequence of global warming (Klapwijk et al. 2013, Seidl et al. 2014, Seidl and Rammer 2017, Thompson et al. 2017) and the fact that not all taxa within moths show negative trends in Europe (Wagner et al. 2021). Our finding on Erebidae found broad support in the long-term data from different habitats in Great Britain (Macgregor et al. 2019). In Macgregor et al (2019), Erebidae were the only group increasing in biomass since the 1980ies. This might be an indication of a general pattern in Erebidae in Europe, although further analyses would be needed in order to confirm this.

Association between host specialisation and long-term trend

Habitat loss and degradation have negative effects on Lepidoptera diversity, especially on species dependent on a restricted number of host species (Stefanescu et al. 2011b). The general declines found in our data are most pronounced in specialist species which is in line with other recent studies on Lepidoptera (Stefanescu et al. 2011b, Habel et al. 2016, 2019c, Wölfling et al. 2019). Beyond the faster decline of specialists, we found that generalists typically increased in diversity, abundance and biomass. This will lead to a major shift in community composition, as shown by Habel et al. (2016, 2019b) at one site over 200 years for butterflies and three decades for moths, in addition to the stated loss of macro-moth diversity. This tendency is possibly caused by a homogenization of forest vegetation (Keith et al. 2009, Dirnböck et al. 2014) which is partly due to nitrogen input (De Schrijver et al. 2011) and increasingly homogenous canopy densities resulting from increasing growing stock (Schelhaas et al. 2003). In our study, however, the local data indicated either no change for specialists or generalists (oak high forest), or an increase in both groups on coppice with standards plots. Thus, there seem to be certain forest types where specialists survive or increase. Nonetheless, note that forest specialists remain vulnerable especially because of intense forest fragmentation (Slade et al. 2013).

Association between colour lightness and long-term trend

Climate change may impact species population dynamics and survival if ambient temperatures approach thermal thresholds of species' climate niches. We found dark species to decline faster than light ones, which is in line with ecological findings that the expected climate change favours light coloured insects (Zeuss et al. 2014). Furthermore, this matches the colour distribution of insects at broader elevational and geographical scales (Bässler et al. 2013, Pinkert et al. 2017, Heidrich et al. 2018, Wu et al. 2019), though the mechanisms remain unclear for nocturnal insects. Thus, we hypothesize that light colouration is beneficial for forest dwelling moths under the current development of the climate, although factors other than temperature may have a bearing on driving colour trends. These might include passive defence against visual predators (e.g. background matching, Kettlewell 1959, Wilson et al. 2001) and unexpected consequences due to pleiotropism in the induction of pigment production (Dubovskiy et al. 2013, Roulin 2014). However, we detected differences between the richness of light and dark species in the state-wide forests predominantly at the regional scale, which means the differences in these trait trends seem to be detectable only at a broad scale.

Implications for conservation and prospects

The diversity responses of hyperdiverse taxa over time and to changes in the environment are complex, habitat dependent and scale dependent. Our data set indicates that insect decline also occurs in these insect groups in forests, supporting the recent findings by Seibold et al. (2019) over the last decade for other insects. A more pronounced loss of habitat specialists and dark species indicates that, similarly to open land, habitat loss and temperature effects due to global warming are potentially the main drivers of loss in forests. However, we would like to stress that in practice these drivers act differently in forest than in open land. While open land is especially affected by direct effects of pesticides and intensification (Simon-Delso et al. 2017), habitat loss in the forest is most probably mediated by indirect effects of, for example, nitrogen input and changes in microclimates (De Schrijver et al. 2011). The same applies to global warming.

The increasing biodiversity in coppice with standards forests shows that forest landscapes with a high diversity of tree species and succession stages are still able to buffer negative trends. This is especially interesting in the light of increasing disturbance intensities (Seidl et al. 2014), which create heterogeneous patterns in landscapes, which in turn increase biodiversity (Beudert et al. 2015). Coppicing might be a way to emulate natural disturbance in order to maintain diversities. Note that rewilding and the abandonment of management may be alternative or complementary approaches to create structural heterogeneity in forests for insect conservation (Müller et al. 2010, Merckx and Pereira 2015, Dantas de Miranda et al. 2019).

We finally note that all our data are observational data collected over long periods. Although we have accounted for the season and the geographic location, the whole study area was not sampled constantly throughout the sampling years. Cross validation also showed that predictions for the odd and the even years was generally good but not always as accurate as desirable ($R^2 << 0.5$, Supporting information). This is possibly due to the fluctuating nature of the samplings, i.e. samplings did not follow a regular sampling scheme on all plots. However, left-censoring (Didham et al. 2020) showed that the trends are nevertheless quite robust when some sampling years were removed subsequently starting with the oldest (Fig. 4). Right-censoring showed the importance of the latest three to five sampling years identifying the significant trends we report. We conclude that although the sampling design has its flaws, the analyses and the reported results are robust. However, in order to develop evidence-based conservation strategies in forests under a changing climate, we need more evidence from spatially and temporally replicated silviculture-biodiversity experiments.

Data availability statement

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.kwh70rz35 (Roth et al. 2021).

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Author contributions

Nicolas Roth: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Hermann H. Hacker**: Data curation (supporting); Investigation (lead); Writing – review and editing (equal). **Lea Heidrich**: Data curation (supporting); Investigation (supporting); Writing – review and editing (equal). **Nicolas Friess**: Data curation (supporting); Investigation (supporting); Writing – review and editing (equal). **Enrique García-Barros**: Data curation (supporting); Writing – review and editing (equal). **Jan C. Habel**: Data curation (supporting); Writing – review and editing (equal).

Simon Thorn: Visualization (supporting); Writing – review and editing (equal). **Jörg Muller**: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal).

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