RESEARCH ARTICLE

Global Change Biology WILEY

Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in central Europe

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Abstract

Recent climate and land-use changes are having substantial impacts on biodiversity, including population declines, range shifts, and changes in community composition. However, few studies have compared these impacts among multiple taxa, particularly because of a lack of standardized time series data over long periods. Existing data sets are typically of low resolution or poor coverage, both spatially and temporally, thereby limiting the inferences that can be drawn from such studies. Here, we compare climate and land-use driven occupancy changes in butterflies, grasshoppers, and dragonflies using an extensive data set of highly heterogeneous observation data collected in the central European region of Bavaria (Germany) over a 40-year period. Using occupancy models, we find occupancies (the proportion of sites occupied by a species in each year) of 37% of species have decreased, 30% have increased and 33% showed no significant trend. Butterflies and grasshoppers show strongest declines with 41% of species each. By contrast, 52% of dragonfly species increased. Temperature preference and habitat

Diana E. Bowler and Christian Hof should be considered joint senior author.

specificity appear as significant drivers of species trends. We show that cold-adapted species across all taxa have declined, whereas warm-adapted species have increased. In butterflies, habitat specialists have decreased, while generalists increased or remained stable. The trends of habitat generalists and specialists both in grasshoppers and semi-aquatic dragonflies, however did not differ. Our findings indicate strong and consistent effects of climate warming across insect taxa. The decrease of butterfly specialists could hint towards a threat from land-use change, as especially butterfly specialists' occurrence depends mostly on habitat quality and area. Our study not only illustrates how these taxa showed differing trends in the past but also provides hints on how we might mitigate the detrimental effects of human development on their diversity in the future.

KEYWORDS
arthropod, biodiversity, climate change, cross-taxon, long term, monitoring, occupancy model, specialization, trait, trend

Zusammenfassung

Jüngste Klima- und Landnutzungsänderungen haben erhebliche Auswirkungen auf die biologische Vielfalt, wie z. B. Populationsrückgänge, Verlagerung von Verbreitungsgebieten sowie Veränderungen in der Zusammensetzung von Lebensgemeinschaften. Nur wenige Studien bisher haben diese Auswirkungen auf unterschiedliche Taxa verglichen, insbesondere in Ermangelung an standardisierten Zeitreihendaten über lange Zeiträume. Vorhandene Datensätze sind räumlich und zeitlich oft wenig umfangreich, was Rückschlüsse, die aus solchen Studien gezogen werden können, einschränkt. Hier vergleichen wir klimatisch und landnutzungsbedingte Vorkommensänderungen bei Schmetterlingen, Heuschrecken und Libellen anhand eines umfangreichen Datensatzes mit sehr heterogenen Beobachtungsdaten, die in der mitteleuropäischen Region Bayern (Deutschland) über einen Zeitraum von 40 Jahren gesammelt wurden. Anhand von Occupancy-Modellen stellten wir fest, dass die Occupancy (Anteil der von einer Art besetzten Standorte pro Jahr) bei 37% der Arten abnahm, bei 30% zunahm und bei 33% keinen signifikanten Trend zeigte. Schmetterlinge und Heuschrecken wiesen mit jeweils 41% der Arten die stärksten Rückgänge auf. Dagegen nahmen 52% der Libellenarten zu. Temperaturpräferenz und Habitatspezifität scheinen die wichtigsten Faktoren für die Trendentwicklungen der Arten zu sein. Wir zeigen, dass kälteangepasste Arten in allen Taxa zurückgingen, während wärmeangepasste Arten zunahmen. Darüber hinaus nahmen bei Schmetterlingen Lebensraumspezialisten ab, während Generalisten zunahmen oder stabil blieben. Unsere Ergebnisse deuten auf starke und konsistente Auswirkungen der Klimaerwärmung auf alle untersuchten Insektentaxa hin. Der Rückgang von Schmetterlingsspezialisten (im Gegensatz zu den semiaquatischen Libellen, bei denen sowohl Generalisten als auch Spezialisten zunahmen) könnte auf eine Bedrohung in terrestrischen Lebensräumen hindeuten, da das Vorkommen insbesondere von Schmetterlingsspezialisten hauptsächlich von der Lebensraumqualität und -fläche abhängt. Beides hat sich in den letzten Jahrzehnten in aquatischen Lebensräumen verbessert, nicht jedoch in terrestrischen Lebensräumen. Unsere Studie veranschaulicht, warum diese Taxa in der Vergangenheit unterschiedliche Trends aufwiesen, und wie wir die nachteiligen Auswirkungen anthropogener Aktivitäten auf ihre Vielfalt in Zukunft abmildern können.

1 | INTRODUCTION

Recent reports of insect declines and community changes are receiving increasing attention around the globe (Brower et al., 2012; Cameron et al., 2011; Dirzo et al., 2014; Hallmann et al., 2017; Seibold et al., 2019; Wagner, 2020). Several studies have documented declines in insect biomass (Macgregor et al., 2019) and abundance (Habel, Samways, & Schmitt, 2019; Habel, Trusch, et al., 2019; Hallmann et al., 2020; Wepprich et al., 2019) across habitat types (Van Swaay et al., 2006), as well as range shifts poleward, range expansions and contractions in thermophilous taxa (Hickling et al., 2005; Poniatowski et al., 2020; Pöyry et al., 2009; Termaat et al., 2019). For instance, in the Netherlands, Hallmann et al. (2020) found declines in light-attracted macro-moths, beetles and caddisflies mirrored the declines detected in flying insects in Germany (Hallmann et al., 2017). However, Outhwaite et al. (2020) compared the national trends of different taxa in the United Kingdom and found strongly diverging trends between different insect taxa, especially terrestrial and freshwater insects. Hence, there is still a lack of understanding about the generality of insect declines across taxa.

Even though insect declines appear to be a general pattern, there is strong variation between study regions and time periods. Although many studies on responses of insects to environmental changes have focused on pollinators (Biesmeijer et al., 2006; Hanula et al., 2015; Mathiasson & Rehan, 2020; Potts et al., 2010), studies that simultaneously compare multiple insect groups with other ecological functions remain scarce (Habel, Samways, & Schmitt, 2019; Habel, Trusch, et al., 2019). In addition, studies that include multiple insect taxa typically use data with different temporal and spatial extent to infer general trends (e.g. Crossley et al., 2020).

Assessing insect species trends over large spatial and temporal extents is often impossible due to the lack of standardized monitoring or long-term time series data. Highly heterogeneous, opportunistic observation data are more common. New analytical methods, such as hierarchical Bayesian occupancy detection models, allow for reliable estimates of species occurrences from heterogeneous data sources (Outhwaite et al., 2020). In recent years, occupancy models have been used to show large-scale species-specific trends of several invertebrate groups across North America and Europe (Dennis, Brereton, et al., 2019; Jönsson et al., 2021; Outhwaite et al., 2019; Powney et al., 2019; Soroye et al., 2020). Distribution trends from occupancy models are similar to trends estimated from standardized monitoring data (Kéry et al., 2010; van Strien et al., 2010) and, therefore, allow to infer the factors that affect different insect groups across their habitats, for specific regions.

Although commonalities are difficult to derive across different temporal and spatial scales, previous studies suggest a range of possible common drivers of distributional changes of insects that explain similar trends of species in different taxonomic groups. Across taxa, warm-adapted species show more positive trends under recent climate warming than cold-adapted species, thus indicating the impact of climate change (Assandri, 2021; Bowler, Haase, et al., 2017; Bowler et al., 2015; Bowler, Hof, et al., 2017; Löffler et al., 2019;

Poniatowski et al., 2020; Zeuss et al., 2014). Another important factor shaping insect distributions is loss of habitat due to land-use change (Fartmann et al., 2021; Wagner et al., 2021; Warren et al., 2001). Some studies suggest that terrestrial insects show different trends compared with freshwater species (van Klink et al., 2020). Freshwater insects such as dragonflies, have recovered in Central Europe since the 1980s due to general improvements in water quality and wetland restoration (Termaat et al., 2015). Meanwhile, terrestrial insect taxa such as butterflies and grasshoppers are threatened by land-use change, including land-use intensification and abandonment, especially in agricultural landscapes in central Europe (Fumy et al., 2020; Habel, Ulrich, et al., 2019). Since the 1990s, there has been relatively little conversion of terrestrial habitats, but the intensity of agricultural and forestry land-use has increased (Carvalheiro et al., 2013; van Strien et al., 2019).

Species' attributes, such as life history and ecological preferences, allow inferences about the effects of different drivers on species' trends (Willis et al., 2015). Attributes can predict range shifts under climate change (MacLean & Beissinger, 2017), explain species' trends (e.g. Pöyry et al., 2009), and indicate community responses to climate and land-use change (Börschig et al., 2013; Vandewalle et al., 2010; Zografou et al., 2014). Hence, assessments of the effects of attributes on the trends of species within a community have become a popular way of understanding the effects of global change (Birkhofer et al., 2015; Habel, Samways, & Schmitt, 2019; Habel, Trusch, et al., 2019; Thomas, 2016). Some species attributes, such as a broad habitat breadth or geographic range size, may lower the vulnerability to anthropogenic changes (Breed et al., 2013; MacLean & Beissinger, 2017; Pöyry et al., 2009). In general, specialist species that are adapted to specific habitat types or food sources show stronger declines than generalists (Ball-Damerow et al., 2014; Fartmann et al., 2021; Habel, Samways, & Schmitt, 2019; Habel, Trusch, et al., 2019).

Here, we analyse species' occupancies (the proportion of sites occupied by a species) of three insect taxa over a 40-year period (1980–2019) in the German federal state of Bavaria and analyse the association of species' occupancy changes with climate- and habitat-related attributes. The three selected insect taxa exemplify different life histories, diets, and habitat preferences, with diurnal butterflies (Lepidoptera, Rhopalocera) representing herbivorous pollinators, grasshoppers (Orthoptera) representing herbivorous/omnivorous insects and dragonflies and damselflies (Odonata, henceforth summarized as dragonflies) representing predatory, semiaquatic insects. These taxa are commonly used as indicators for the health of terrestrial and freshwater ecosystems (Samways et al., 2020; van Swaay & Warren, 2006). Our study region is located in the centre of Europe and contains a wide variety of climatic conditions, as well as habitat and land-use types (Dalelane et al., 2018; Dou et al., 2021). Land cover and use have undergone extensive changes, especially agricultural intensification as well as abandonment, typical of the region (Dou et al., 2021).

In terms of long-term trends, we expected to see differences as well as commonalities among the three insect taxa: across all

taxa, we hypothesized increases of warm-adapted species and decreases of cold-adapted species. Given the findings of Termaat et al. (2019), we predicted that this divergence is particularly strong for dragonflies, which have high dispersal capacity and range-shifting behaviour. Generally, we expected positive mean trends in semi-aquatic dragonflies due to improved habitat quality of freshwater ecosystems in Central Europe, but negative mean trends in butterflies and grasshoppers due to continuing land-use intensification and abandonment in terrestrial ecosystems. We also predicted higher mean occupancies for generalists compared with specialists, as well as stronger negative effects on habitat specialists across taxa. Furthermore, we hypothesized across all taxa a greater decline in habitat specialists and species with small range sizes in Europe due to their lower adaptation capacity, compared with habitat generalists and species with larger ranges. In addition, grasshoppers have a less complex life history compared with butterflies and dragonflies; thus, we hypothesized some differences in their vulnerability to anthropogenic changes. Also, across terrestrial taxa, we expected to find that species using open, agricultural habitats have fared worse than species of closed forest habitats.

2 | MATERIALS AND METHODS

2.1 | Species occurrence data

We obtained species occurrence data for butterflies (Lepidoptera, Rhopalocera, 176 species), grasshoppers (Orthoptera, 78 species), and dragonflies (Odonata, 77 species) from the Bavarian Environment Agency (Bayerisches Landesamt für Umwelt/LfU), covering the German federal state of Bavaria, an area of 70,542 km². Records were mapped to an approximately 5 km × 5 km grid (TK25 quadrants) commonly used in Germany for reporting gridded spatial data, making up a total of 2266 grid cells (sampled grid cells: butterflies 2216—97.8%, grasshoppers 2202—97.2%, dragonflies 2144—94.6%). We focussed on the last 40 years from 1980 to 2019 as the number of samples in this time frame is reasonably high (minimum number of records/minimum number of sampled grid cells per taxon and year: butterflies = 996/105; grasshoppers = 279/40; dragonflies = 357/48) to allow for reliable modelling of all three taxa. Twelve species were excluded from our analysis because all their last records in Bavaria were from before our study period (4 butterfly, 6 grasshopper and 2 dragonfly species). For a full species list, see Supporting Information Tables S1–S5. Most of the database is the result of a semi-systematic and on-going collection of species records initiated in the 1980s (Bräu et al., 2013; Kuhn & Burbach, 1998; Schlumprecht & Waeber, 2003). However, the database of species in Bavaria ('Bayerische Artenschutzkartierung (ASK)', www.lfu.bayern.de/natur/artenschutzkartierung) also includes records of museum specimens and private collections, as well as single observations and records from standardized mapping schemes. Some characteristics of the data set need to be considered in the analysis. First, all records have been validated by experts, allowing us to assume that there are no false presences. Second, non-detections are inconsistently reported across data sources; thus, we used only the presence records in our analysis.

2.2 | Species attribute analysis

We compiled attribute data for our three insect taxa covering a spectrum of species characteristics, which could potentially influence their occupancy changes over time (summarized in Table S7).

To analyse effects of habitat types and habitat specificities, we compiled information on species' habitat preferences. Data were obtained from the atlas of the respective insect taxon (Bräu et al., 2013; Kuhn & Burbach, 1998; Schlumprecht & Waeber, 2003). For butterflies and grasshoppers, we categorized the habitat types into preferring open habitats, forests, more open or more forest habitats, or both habitat types equally. For dragonflies, we categorized them as preferring lentic (standing water bodies), lotic (running waters), more lentic, more lotic, or both habitat types equally. To assign dragonfly species to habitat specialists or generalists, we followed the definition from Willigalla and Fartmann (2012). For butterflies and grasshoppers, we defined species occurring in up to three habitats as specialists and species occurring in four to the maximum number of eleven habitats as generalists. For dragonflies, we defined species occurring in up to two habitats as specialists and species occurring in three to the maximum number of eight habitats as generalists.

We calculated species' climatic niches based on information on their ranges within Europe (cf. Devictor et al., 2012). For butterflies, we used digitized gridded atlas range data from Kudrna et al. (2011); for grasshoppers, we gridded polygon range data from Hochkirch et al. (2016); and for dragonflies, we used gridded atlas data from Kalkman et al. (2018), all to a 5 km × 5 km grid. All range maps were cropped to the smallest common denominator in spatial extent (10°W, 30°E, 35°N and 71°N). Using this information, we calculated the continental range size (km²) per species as the sum of the covered grid cells multiplied by the respective area of each grid cell. Based on the range sizes, we calculated several measures of the species' climate niche position, breadth and upper and lower limits using bioclimatic variables (for more details, see Supporting Information S6). Bioclimatic variables were derived from Euro-Cordex climate data using the function BIOVARS of the R-package DISMO (Hijmans et al., 2020).

We tested for correlations among the different species attribute variables using the Pearson correlation coefficient, calculated with the function COR of the R-package STATS (R Core Team, 2020). We dropped all combinations that resulted in $|r| > 0.7$ (Dormann et al., 2013), leaving six sets of ecologically meaningful attribute combinations with low correlations. We checked for multi-collinearity in these sets of variables using the function CHECK_COLLINEARITY of the R-package PERFORMANCE (Lüdecke et al., 2020). In our analysis, variables with a variance inflation factor lower than three were considered (Tucker et al., 2019; Zuur et al., 2009). Using the results of our occupancy models as response variables, we compared the fit of

general linear mixed-effect models on the attributes with different uncorrelated variable combinations based on Akaike's (AIC; Akaike, 1974) and Bayesian information criterion (BIC; Schwarz, 1978), using the function GLMMTMB of the R-package GLMMTMB (Brooks et al., 2017) for each taxon separately. Models with habitat class, habitat type, continental range size, median of the annual mean temperature of the continental range (median temperature) and the median of the annual precipitation of the continental range (median precipitation) as insect attributes showed lowest correlations and had the lowest AIC; hence, we report these models.

2.3 | Organisation of detection histories

Occupancy models assess the detection probability of a species using information from repeated visits to a site within a so called closure period—the period within a year when species' occupancy is constant (Kéry, 2011; Outhwaite et al., 2018). Therefore, they need a definition of a visit—here described as a unique combination of the 5 km × 5 km grid cell sampled, the date, and the person who has collected the record. For each visit, we defined whether each species was detected (1) or not detected (0), thus providing information on non-detection from our presence-only data. The non-detection information consist both of true absences and false absences where a species has been overlooked. The model assesses whether the non-detection is a true or false absence based on estimated species' detectability, as well as additional information on the sampling effort given as the number of records per year, the number of species observed per visit, and whether a list was a singleton record (i.e. only one species recorded).

To define the closure period, we only used observations reported during the spring and summer months when species are abundant, active and subsequently readily assessed (butterflies: March–October, grasshoppers: May–October, dragonflies: April–October). Some butterfly species (here *Thecla betulae*, *Favonius quercus* and *Satyrium w-album*) are, however, difficult to observe as adults and experts search for their eggs during the winter months. Thus, we modelled them separately using the full years' observations.

We included all species with at least ten observations during our study period. We intentionally used a low number so that we could include rare species in the analysis, which might display different trends, as well as species that vanished from or moved into Bavaria within the study period. In fact, most species had many more observations than this minimum threshold (median observation per species: butterflies = 918, grasshoppers = 830, dragonflies = 1079; lower 5%: butterflies = 24, grasshoppers = 31, dragonflies = 64; upper 95%: butterflies = 14,468, grasshoppers = 10,719, dragonflies = 7780; maximum number of observations: *Pieris napi* = 23,471; *Pseudochorthippus parallelus* = 24,491; *Ischnura elegans* = 15,271 observations). For a summary of the available data per species, see Tables S2–S5, and for a list of species excluded from occupancy modelling from the full data set and reasons for exclusions, see Table S1. We constructed occupancy models for 300 species (163

butterfly, 66 grasshopper and 71 dragonfly species) using a total of 809,845 individual records (452,966 butterfly, 183,292 grasshopper and 173,587 dragonfly observations). The spatial coverage and number of records varied between the years (Figure S13).

2.4 | Occupancy models

Occupancy models are hierarchical models that split the modelling process into a state submodel describing the best estimate of occupancy per site and year, and the observation submodel describing the detection probability of a species at a specific site. Following other studies (Bowler et al., 2021; Outhwaite et al., 2019), the occurrence probability (ψ) is a function of year (t) and site (i) variation, the latter decomposed into ecoregion (97 factor levels) and site (5 km grid). The best estimate of occupancy for each species and site per year is given as $z_{i,t}$, which can be described by a Bernoulli distribution:

$$z_{i,t} \sim Bernoulli\ (\psi_{i,t})$$
$$logit\ (\psi_{i,t}) = year_t + site_i + ecoregion_i$$

The observation submodel models the detection probability (p) for each visit (j) per site and year. The detection probability is assumed to depend on the year, the day of the year as a linear and quadratic term (*yday*, which relates to the effect of species' phenology on detectability), and three estimates of sampling effort. For butterfly species with more than one generation per year (i.e. a complex seasonal pattern that would not be captured by a quadratic effect of *yday*), we excluded the day of the year and instead added a week term (*week*) as a random effect to model changes in detection more flexibly during the year. The estimates of sampling effort include the number of records of the year of the visit (*samplInt*) as a proxy for sampling interest by the environmental agency which we expect to affect sampling efforts on the visit level as well, the number of species reported per visit (logarithmic transformation, log(*nuSpecies*)), and a binary vector for single-species records (*singleList*).

Species with one generation per year:

$$logit(p_{i,t,j}) = \alpha_j + \beta_{yd}yday_j + \beta_{yd2}yday_j^2 + \beta_{sl}samplInt_t$$
$$+ \beta_{nSpec}log\left(nuSpecies_j\right) + \beta_{sL}singleList_j$$

Species with more than one generation per year:

$$logit\ (p_{i,t,j}) = \alpha_j + \beta_w week_j + \beta_{sl}\ samplInt_t$$
$$+ \beta_{nSpec}\ log\left(nuSpecies_j\right) + \beta_{sL}singleList_j$$

Then the observation (y), which is either 1 (observed) or 0 (not observed) for each visit, is described as being conditional on the occupancy ($z_{i,t}$, drawn from a Bernoulli distribution, compare (Kéry & Royle, 2016)):

$$y_{i,t,j} \mid z_{i,t} \sim Bernoulli\ \left(z_{i,t}p_{i,t,j}\right)$$

We based our occupancy models on Outhwaite et al. (2018), using a random walk prior distribution to share information across years for the year effect on the occupancy. For the other parameters, we used vague prior distributions. We fit the occupancy models using JAGS, a program to fit models with Bayesian inference through Markov Chain Monte Carlo simulations for fitting the hierarchical models, using the R-packages GGMCMC and JAGSUI (Fernández-i-Marín, 2016; Kellner, 2021). We used three chains with 20,000 iterations and a burn-in of 10,000. We assessed model convergence using the Gelman-Rubin statistic (Rhat), where the within-chain variance is compared with the between-chain variance (Gelman & Rubin, 1992). Modelled occupancy estimates with Rhat values above or equal 1.1 are considered not convergent (Kéry & Schaub, 2012). We estimated each species' occupancy as the mean proportion of sites occupied by a species in each year, plus the standard deviation across model runs as the uncertainty of this proportion.

All model predictions were checked for plausibility and approved by taxonomic experts for each taxon.

2.5 | Species selection

We applied two criteria to our models to select the species to include in the trend and attribute analysis:

1. We excluded species with bad model quality: mean Rhat ≥ 1.1 and/or mean standard deviation ≥ 0.1 (Kéry & Schaub, 2012).
2. We included species with a minimum occupancy of 0.025 in at least 1 year within our 40-year study period (this corresponds to 55 grid cells for butterflies and grasshoppers and 54 grid cells for dragonflies).

After the filtering process, we continued our analysis with 124 butterfly species, 49 grasshopper species and 63 dragonfly species (minimum number of observations of species included in trend and attribute analysis: butterflies 77, grasshoppers 123, dragonflies 34; see Table S5 for a full species list including number of observations and grid cells with observations, and Tables S2–S4 for lists of species excluded from the analysis).

2.6 | Species trend calculation

We assessed species linear trends for the study period between 1980 and 2019, using Bayesian generalized linear models from the R-package BRMS (Bürkner, 2017), which fits Bayesian models in STAN (Stan Development Team, 2022b) via RSTAN (Stan Development Team, 2022a) for each species. We ran our models with and without including each year's standard deviation of the occupancy estimate as a measure of uncertainty of the response variable (using the mi function), and tested three different priors (default, flat priors, slightly narrower normal (0,10) and narrower normal (0,1) priors for fixed effects). We used 4000 iterations and four chains with a warmup of

2000, a tree depth of 12, and increased the step of the algorithm via adapt_delta to 0.99999. We compared models with different priors for each species and selected those models where model Rhat was closest to 1. All selected species' models show good convergence (Rhat < 1.1). For a comparison of trend estimates between selected models, models without occupancy uncertainty considered, and discarded priors, see Figure S10. We extracted each species' slope, indicating their linear trends across our study period, and the corresponding 95% credible intervals.

2.7 | Attribute analysis using generalized linear mixed-effect models

To analyse the potential effects of insect attributes on the change of distribution over the years, we applied Bayesian generalized linear mixed-effect models, using BRMS (Bürkner, 2017) for each taxon separately. We used the best estimate of annual occupancy (that is, the mean of the posterior distribution) of each modelled species per taxon as response variable in the models. Given that the occupancies were bounded between zero and one, and not normally distributed (see Figure S15), we used models with a beta distribution. Explanatory variables were year, selected attribute variables and their interaction with year. Hence, our models tested whether the trend over time (year effect) was modified by species attributes (year × attribute interaction). We used habitat type and habitat class (generalist or specialist species) as categorical variables. Continuous attribute variables were scaled and centred for each taxon. Species was included as a random effect (intercepts and slopes for year). We used 4000 iterations and four chains, with a warmup of 2000, a tree depth of 12 and increased the step of the algorithm via adapt_delta to 0.99999. We ran our models with and without including each year's standard deviation of the occupancy estimate of each species as a measure of uncertainty of the response variable, and tested three different priors for the fixed effects (default, weakly informative priors, slightly narrower normal(0,10) and narrower normal(0,1) priors for fixed effects). We used the default, weakly informative priors for the other parameters. We compared all models' coefficients additionally with those calculated using classical inference (using the function GLMMTMB of the R-package GLMMTMB (Brooks et al., 2017) weighted by occupancy/occupancy standard deviation), to assess the consistency of our results to alternative model decisions (see Figure S11). We decided on the models with a normal(0,10) prior for fixed effects that included occupancy variability but similar results were obtained for alternative priors. All model coefficients had Rhat < 1.1, indicating reliable model results. We assessed model R^2 using the BAYES_R2 function of the R-package BRMS (Bürkner, 2017; see Table S12), which can be interpreted as variation explained by our models' fixed effects. We report estimates for each of the coefficients, and the corresponding 95% credible intervals. We report those coefficients to have a significant effect on species' trends where the 95% credible intervals are either fully positive or negative.

We calculated estimated marginal means to show the effects over time of those attributes identified as significant for species' trends, using the R-package EMMEANS (Lenth, 2020). Estimated marginal means give the mean response for focal explanatory variables, adjusted for all other explanatory variables' effects in the model. For categorical variables, we compared the categories, such as habitat specialists against generalists, and for continuous variables, we compared lower 5%, median, and upper 95% of each variable. These values correspond to, for example, species preferring cold climates (lower 5%) and those preferring warm climates (upper 95%). Thus, estimated marginal means allow us to compare the effects of assorted species' characteristics, represented by lower, median and upper attribute values, while taking into account the mean effects of all other attributes in our models.

All analyses were conducted using R version 4.0.2. (R Core Team, 2020).

3 | RESULTS

We found widespread variation in species' occupancy trends, estimated as annual change in the proportion of occupied sites, within as well as between insect taxa (Figure 1). Across all taxa, the occupancy of 37% of the species decreased: highest for butterflies (41%, 51 species), and grasshoppers (41%, 20 species) and dragonflies (27%, 17 species). By contrast, 30% of all species increased: highest for dragonflies (52%, 33 species), followed by grasshoppers (27%, 13 species) and butterflies (20%, 25 species) (Figure 2). 33% of the species showed no significant trend (butterflies 39%, 48 species; grasshoppers 33%, 16 species; dragonflies 21%, 13 species). Yearly mean trends were positive for dragonflies (estimate 0.00178, lower credible interval (CI) 0.000704, upper CI 0.00287), while butterfly trends were leaning towards negative (estimate −0.000556, lower CI −0.00126, upper CI 0.000163) and stable for grasshoppers (estimate −0.0000045, lower CI −0.00103, upper CI 0.00103). All results presented are robust and independent of the choice of model priors or whether occupancy uncertainty was included in the models (compare Figures S10 and S11).

The attribute affecting species' occupancy trends with the highest significance across taxa was temperature preference—the higher the preferred temperature, the greater the increase in the proportion of occupied sites over the last 40 years (Figure 3). This temperature effect was similar for all three insect taxa, with the strongest effect on dragonflies and the weakest on butterflies. At the beginning of our study period (1980), species with higher temperature preferences had low occupancies, especially for dragonflies but increased through time (Figure 4a–c). For instance, between 1980 and 2019 dragonflies of mean temperature preference changed in occupancy
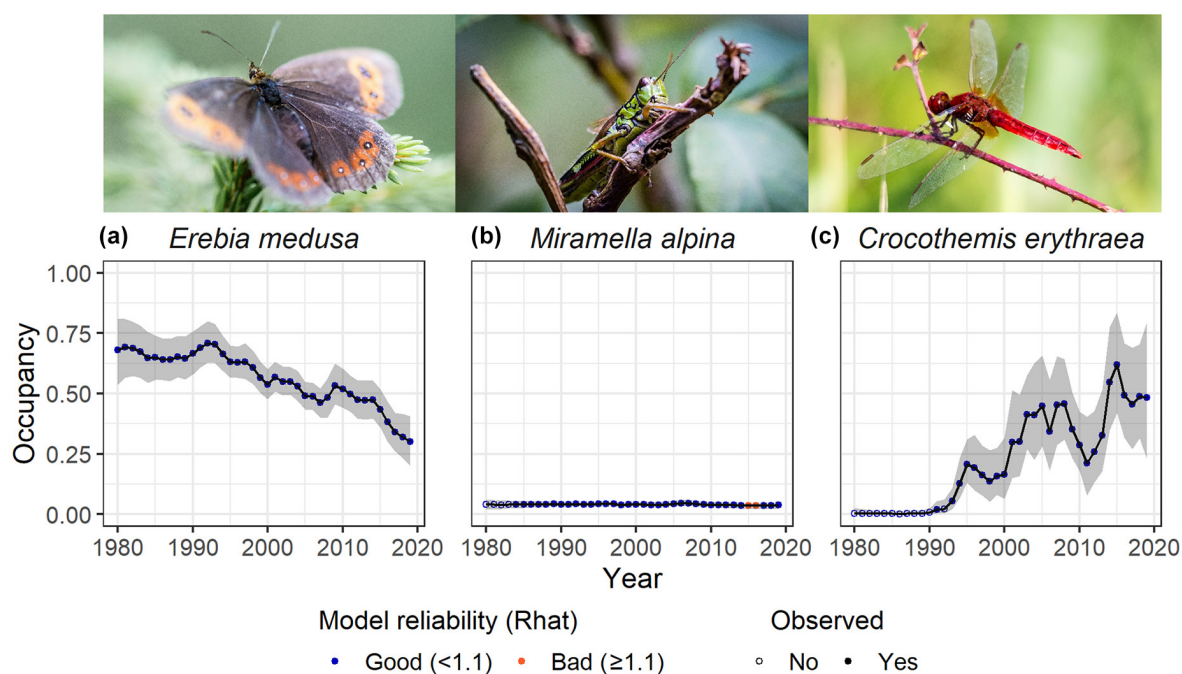

(a) *Erebia medusa*   **(b)** *Miramella alpina*   **(c)** *Crocothemis erythraea*

Model reliability (Rhat)
• Good (<1.1)   • Bad (≥1.1)

Observed
○ No   • Yes

FIGURE 1 Exemplary occupancy model results for an exemplary butterfly (*Erebia medusa*, (a)), grasshopper (*Miramella alpina*, (b)) and dragonfly (*Crocothemis erythraea*, (c)) species. For each species, the trend in the annual proportion of the occupied study area (State of Bavaria, Germany) between the years 1980 to 2019 is shown. Blue points indicate good (Rhat < 1.1) and red points (see panel (b) years 2015 and 2016) indicate inacceptable model convergence (Rhat ≥ 1.1) as calculated with the Gelman-Rubin statistic. Filled points indicate that a species was observed in the respective year, while unfilled points indicate that the species was not observed in the study area and the respective year. Grey ribbons indicate 95% credible intervals. See Figure S14 for a comparison to record data (panels (a)–(f)) and each species' estimated long-term trends derived from generalized linear models (panels (g)–(i)). (Picture credits E. K. E.)
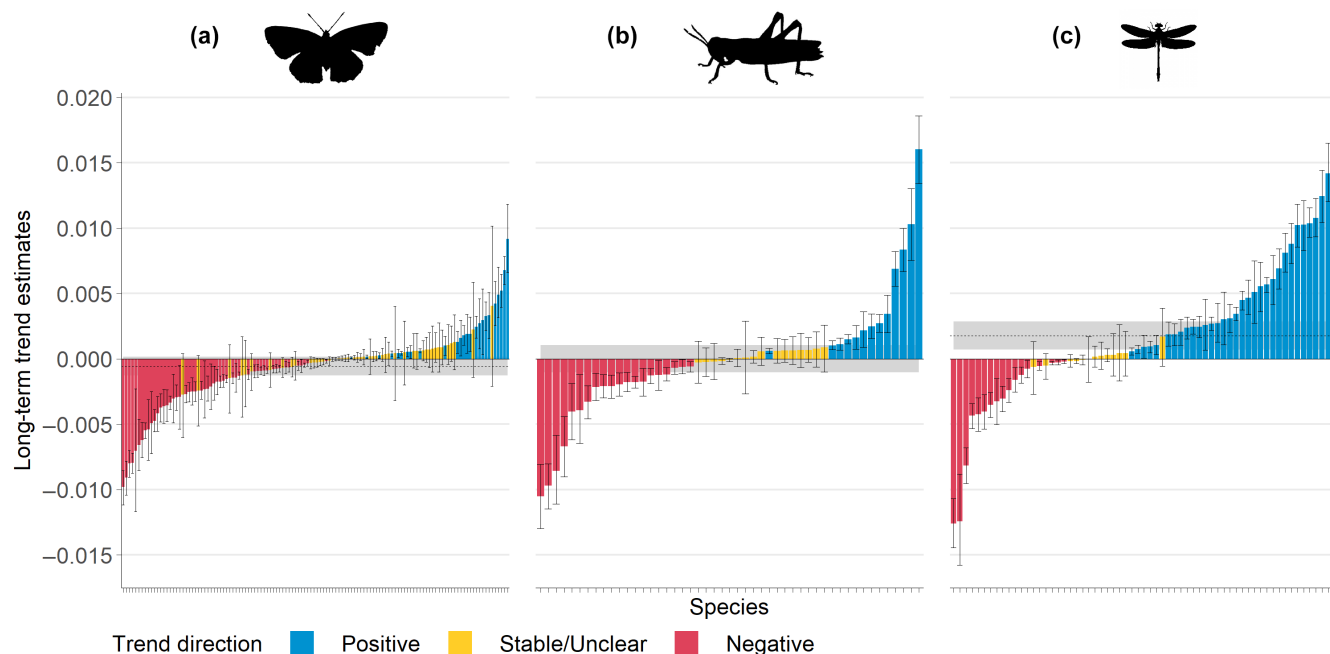
FIGURE 2 Estimated long-term trends in species' distributions. (a) Butterflies, (b) grasshoppers, (c) dragonflies. Each bar represents one species (*x*-axis) ordered by magnitude of their linear trend, blue indicates positive trends, red negative trends, yellow trends are stable or unclear (95% credible intervals positive and negative). Whiskers indicate 95% credible intervals. Long-term trend estimates (y-axis) are calculated as mean annual change in % occupied grid cells, based on Bayesian generalized linear models. Dashed line indicates the taxon mean trend, grey ribbon indicates taxon trend 95% credible interval. See Figure S10 for a comparison of species' trends modelled with different priors or without taking occupancy variation as standard deviation into account
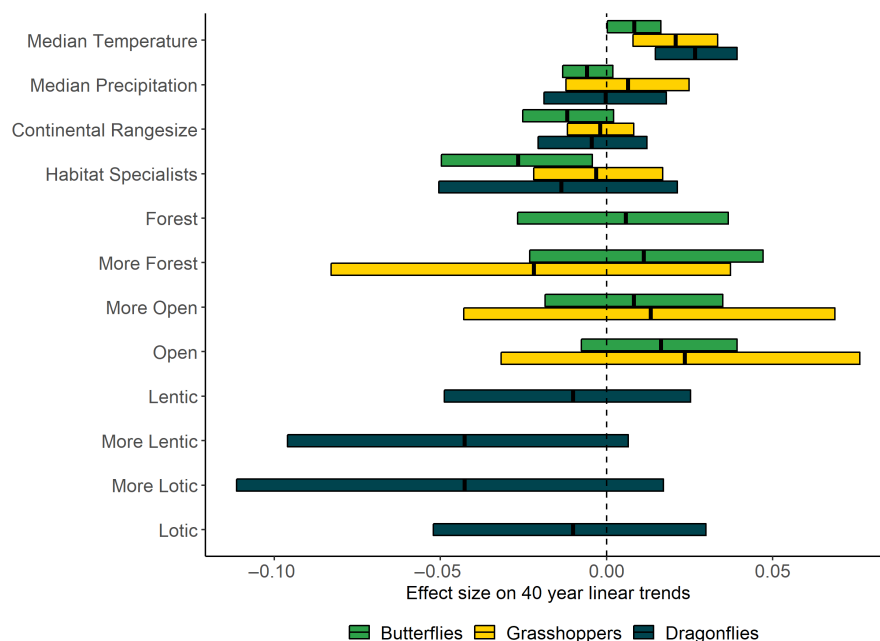

FIGURE 3 Effect of species' attributes on their long-term occupancy trends, in other words, the effect of species attributes over time as untransformed slopes, tested in a Bayesian generalized linear mixed-effect model for each taxon with species as random effect. Medium green is butterflies', light yellow is grasshoppers' and dark blue is dragonflies' effect sizes. The dashed line marks no effect. Shown are the mean effect sizes ± the 95% credible intervals. See Table S8 for plotted values and effects of species' attributes and study year on their occupancy. Continuous variables were scaled to units of their standard deviation. See Table S5 for a list of species included in the analysis

by +5%, whereas species with a 1°C warmer temperature preference increased by 18% (see Table S9 for estimated occupancy changes of each taxon based on environmental preferences). By contrast, species preferring cold temperatures had higher occupancies initially but showed decreasing trends over time (Figure 4a–c). In case of the dragonflies, species with a 1°C colder temperature preference decreased by almost 12%. These trends lead to a convergence of the dominance pattern over time: at the end of the study period, grasshopper species preferring cold temperatures had similar occupancies as those preferring warmer temperatures. Dragonflies showed the same trend, but as warm- and cold-adapted species started with stronger differences in their occupancies, the reversing dominance trend was not as pronounced. Butterflies showed a similar but weaker shift (Figure 4a). Neither precipitation preference nor European range size had a significant effect on species trends over time (Table S8).

Habitat specialization had a negative effect on distribution change for butterflies, but not for the other two taxa (Figure 3). At the beginning of our study period, butterflies specialized to certain habitats had slightly larger distributions than habitat generalists (Figure 4d). Over time, specialist butterfly species decreased their occupancy, while the occupancy of habitat generalists increased. Grasshopper generalists show larger distributions than in specialists, but no significant effect of specialization on their trends (Figure 4e), while dragonfly generalists and specialists neither differ in distribution size, nor trend (Figure 4f). Habitat preferences (open vs forest, lentic vs lotic) had no significant effect on species distribution trends (Figure 3).

4 | DISCUSSION

Our analyses revealed climate change as a key driver of insect distributional changes. Thus, the distribution of warm-adapted species increased, and the distribution of cold-adapted species decreased across all taxa. We also found effects of habitat specialization in
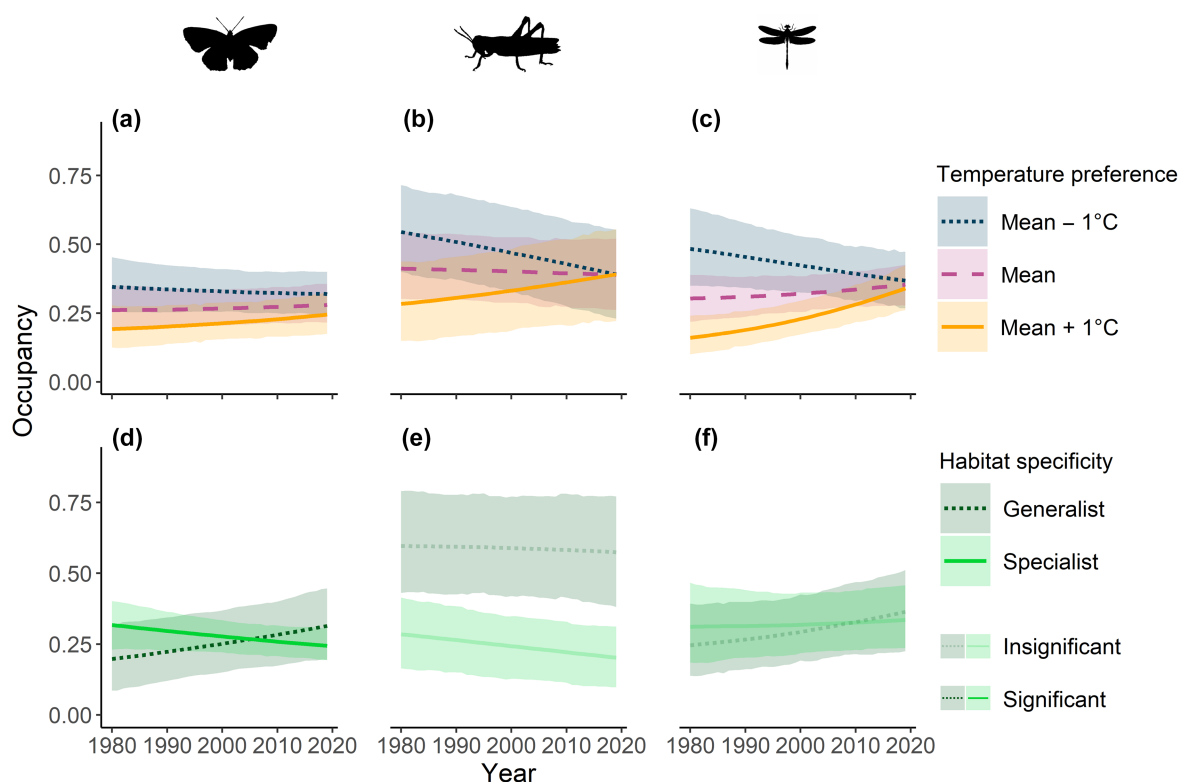

FIGURE 4 Estimated marginal mean effects of temperature preference and habitat specificity on occupancy trends of butterflies (a, d), grasshoppers (b, e) and dragonflies (c, f) over 40 years, fitted using Bayesian generalized linear mixed-effect models. Effect sizes over time of all attributes tested are given in Figure 3 and Table S9 for estimated occupancy changes. Estimated marginal means give the mean response for focal explanatory variables, adjusted for all other explanatory variables' effects in the model. Lines give mean estimates with colour intensity indicating whether the effect is significant, and ribbons indicate 95% credible intervals. Temperature preference (a–c): scaled and centred median annual temperature in species' continental range. We show estimated marginal means for the mean temperature preference across species of each taxon (medium, dashed red), for a temperature preference of 1°C cooler than the taxon mean (dark, dotted blue), and for a temperature preference of 1°C warmer than the taxon mean (light, solid yellow). Mean temperature preference: (a) butterflies 9.5°C (maximum 12.3°C, minimum 3.1°C), (b) grasshoppers 9.2°C (maximum 11.4°C, minimum 7.1°C), (c) dragonflies 9.6°C (maximum 12°C, minimum 6°C). Habitat specialization (d-f): habitat generalists (dark, dotted green) inhabit more habitat types in the study region than habitat specialists (light, solid green). Butterflies (d, significant effect) and grasshoppers (e, insignificant): generalists are species occurring in ≥4 habitat types; dragonflies (f, insignificant): generalist are species occurring in ≥3 habitat types. Results are displayed on the response scale

butterflies, with more specialized species showing stronger decreases in their distribution, while generalists showed increasing trends. However, in contrast to the climate signal, this habitat signal did not occur in grasshoppers or dragonflies, suggesting that climate change has had more widespread and consistent effects across terrestrial and freshwater insect taxa in central Europe.

The annual temperature in our the study region has increased by more than 1°C towards the end of our study period compared with the 1930s (Danneberg et al., 2012; Steinbauer et al., 2016). Our results show that responses to increased temperatures are strongest for dragonflies. More than half of the dragonfly species have significantly increased their distributions since the 1980s, which is likely associated with their relatively high dispersal capacity (Bowler et al., 2021; Grewe et al., 2013) in combination with the improved quality of aquatic habitats (Dahl et al., 2016; Karle-Fendt & Stadelmann, 2013; Termaat et al., 2015). The lack of suitable habitats has been shown to limit species ability to respond to climate warming (Warren et al., 2001). Indeed, similar patterns for dragonflies have been found across Europe in connection with climate change and improved habitat quality (Termaat et al., 2019). Across different insect taxa, temperature increases have been linked to changes in species' abundances across realms (Bowler, Hof, et al., 2017; Pardikes et al., 2015), to changes in insect life cycles (Buckley et al., 2015), and to range shifts (Hickling et al., 2005) as well as phenological changes (Parmesan & Yohe, 2003). Our study, however, reveals that some insect taxa are able to respond quicker than others.

Our findings also revealed differences in the strength of negative effects of habitat specialization on species occupancy trends among the three insect taxa. Occupancies of butterflies that inhabit a small number of habitat types in the study region decreased, while butterfly generalists increased their occupancy. This effect of habitat specialization did not appear in the other two taxa. While 83% of our butterfly species are considered habitat specialists, only 61% of grasshopper and 60% of dragonflies are classified as such. The occurrence of specialized species often depends mostly on habitat quality, followed by habitat area (Löffler & Fartmann, 2017; Poniatowski et al., 2018; Thomas et al., 2011). Increased land-use intensity as well as abandonment leads to a decrease in habitat quality, especially for species of open habitats, and land-use change can lead to a dominance of certain habitats (Dou et al., 2021; Stoate et al., 2009). Therefore, the decrease of butterfly specialists could hint towards a threat associated with land-use, which might affect butterflies more strongly than the other taxa as a larger proportion of species is highly specialized.

Interestingly, despite the importance of habitat specialisation, main habitat type did not significantly affect species trends in our models. Other studies have suggested that grassland butterflies are particularly in decline (Van Swaay et al., 2006). Indicators of land-use intensity, such as pesticide use, which are known to be important drivers of insect trends (Beketov et al., 2013; Ewald et al., 2015), might be more important than land-use *per se*. Hence, the coarseness of our habitat data might have contributed to the inconsistent signal of habitat preference. In addition, the attributes used

are only indirect proxies for encoded drivers and the habitat type is a rough classification. The lack of distinct driver data does not allow us to exclude any land-use parameters as drivers of species' change. In addition, contrary to our expectations, the distribution trends over time were not significantly affected by species' range size across Europe.

Our study highlights the great potential of previously unused data sources to increase the understanding of distribution trends of insects over the past decades. Occupancy models facilitate the analysis of species trends for previous decades where no systematic monitoring data are available and the collected data are highly heterogeneous (Isaac et al., 2014; van Strien et al., 2013). Although purely opportunistic citizen science data might not be suitable to estimate reliable species trends (Kamp et al., 2016), our data have the advantage that professional observers are sent to resample neglected regions by the Bavarian environmental agency (as proposed by Tulloch et al., 2013, see also Figure S13). Additionally, citizen scientists who report observations of insects are often taxon experts themselves, and observations included in our database undergo a review process to ensure their validity.

Overall, we believe that our modelling approach was able to find the balance between the potentially contrasting needs to deliver accurate species-specific occupancy estimates and, at the same time, produce an overview of trends across different insect taxa. In fact, most of the model predictions were in line with expert expectations. In some cases, however, our model results did not match expert expectations, but were included in the analysis. For some butterfly and grasshopper species that are difficult to detect, such as *Favonius quercus*, *Thecla betulae* or *Barbitistes serricauda*, species-specific increase in sampling effort was visible as occupancy peaks in our model results (data not shown). In addition, the strength of the trends for rare species might be less reliable, as they need greater sampling effort to monitor distribution changes (Specht et al., 2017). Additionally, the random walk priors used in our models that generally improve model quality might also lead to more conservative change estimates (Outhwaite et al., 2018). Therefore, some trend estimates might be inaccurate compared to real species trends, however, this should not bias the hypothesis being tested, especially as we included model uncertainty in all our analyses. The identification of such model limitations illustrates the importance of including expert knowledge in data analysis (Outhwaite et al., 2019) and the importance of careful interpretation.

In this study, we focused on changes in distribution and not changes in abundance, which are different aspects to consider when assessing changes in species' status. Species abundance can decrease while at the same time range shifts can lead to an increase in species distribution (Dennis, Morgan, et al., 2019), and when both metrics are correlated, distribution trends tend to underestimate trends in species abundance (Buckley & Freckleton, 2010; Webb et al., 2012, but see Pinkert et al., 2020). However, reliable abundance data across larger regions and for many species are rarely available. Even though our findings show that

heterogeneous occurrence data can be used for reliable trend estimates, this study focuses on three taxa that are rather well documented and amongst the more species-poor insect groups. To fully understand long-term trends in insect diversity and abundance we still need large-scale, standardized, multi-taxon monitoring programs. Special monitoring approaches may be needed for very rare species, which are often neglected in standardized monitoring schemes (Potts et al., 2021).

Efforts to streamline monitoring programs at the European level (Potts et al., 2021) should go hand in hand with necessary and immediate action for insect conservation (Harvey et al., 2020; Samways et al., 2020). Even when regional, national or even European monitoring schemes are implemented, we argue for basing conservation evidence on the data that are already available, especially to assess changes that have already happened. Our study highlights the value of a collaborative approach to biodiversity monitoring and data synthesis, involving taxon experts, citizen scientists and quantitative ecologists to assess species trends (Kühl et al., 2020). Some obvious stressors on insects, such as low aboveground water quality, have been already tackled, in part due to pressure from the public, and the results are visible in the trends found for dragonflies. Other, more complex stressors such as nitrogen deposition and pesticide use are also increasingly being pushed into the focus of the public (Kurze et al., 2018; Nijssen et al., 2017; Sánchez-Bayo, 2021). Examining changes in potential drivers explicitly is an important aspect of future research into insect trends.

CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Bavarian State Agency for the Environment (Bayerisches Landesamt für Umwelt, LfU). Restrictions apply to the availability of these data, which were used under license for this study. Species' annual occupancy estimates and codes for occupancy models and trait analyses are available in Dryad datafiles (https://doi.org/10.5061/dryad.4f4qrfjf5).

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