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Light and Malaise traps tell different stories about the spatial variations in arthropod biomass and method-specific insect abundance

Annika Busse[1] | Claus Bässler[1,2] | Roland Brandl[3] | Nicolas Friess[4] | Hermann Hacker[5] | Lea Heidrich[3,5] | Torben Hilmers[6] | Gisela Merkel-Wallner[7] | Christian Schmid-Egger[8] | Linda Seifert[1] | Jörg Müller[1,5]

[1]Department of Nature Conservation and Research, Bavarian Forest National Park, Grafenau, Germany

[2]Faculty of Biological Sciences, Institute of Ecology, Evolution and Diversity, Department of Conservation Biology, Goethe University Frankfurt, Frankfurt am Main, Germany

[3]Animal Ecology, Department of Ecology, Faculty of Biology, Philipps-University Marburg, Marburg, Germany

[4]Environmental Informatics, Faculty of Geography, Philipps-University Marburg, Marburg, Germany

[5]Ecological Field Station, University of Würzburg, Germany

[6]Chair of Forest Growth and Yield Science, TUM School of Life Sciences, Technical University of Munich, Freising, Germany

[7]Bühläcker 3, Bad Kötzting, Germany

[8]Fischerstr. 1, Berlin, Germany

Correspondence
Annika Busse, Department of Nature Conservation and Research, Bavarian Forest National Park, 94481 Grafenau, Germany.
Email: annika.busse@npv-bw.bayern.de

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Abstract

1. Conclusions reached in meta-analyses of changes in insect communities may be influenced by method-specific sampling biases, which may lead to inappropriate conservation measures.

2. We argue that the contradictory conclusions regarding terrestrial insect biomass, abundance and richness patterns are, at least partly, due to methodological limitations that reflect taxon-specific responses to environmental changes.

3. In this study, light and Malaise traps were simultaneously deployed to sample insects at 52 plots in a temperate forest in Germany along gradients of elevation (>1000 m) and canopy openness (3%–100%). These gradients were used as predictors in models of total arthropod biomass according to the two trapping methods and in models of abundance and richness of three commonly targeted groups: nocturnal moths, sampled using light traps, and hoverflies and bees, collected with Malaise traps.

4. A comparison of the total arthropod biomass obtained with the two methods revealed contrary results along the canopy openness gradient. Biomass in light traps showed a decreasing trend with increasing canopy openness while biomass in Malaise traps increased. The same opposing pattern was found for the abundance of selected taxa.

5. The different patterns describing spatial variation of arthropod communities obtained using light and Malaise traps can be explained by differences in the taxa predominantly collected. Regarding the ongoing debate on insect decline, our results demonstrate that comparing different taxa from different taxon-specific traps is inappropriate. Thus, we recommend that future meta-analyses take into account the sampling methods and taxon-specific responses to environmental changes.

KEYWORDS
canopy openness, elevation, insect decline, sampling method

INTRODUCTION

Insects play a central role in the functioning of ecosystems (Schowalter, 2013) and thus have been used as bioindicators of ecosystem health (Bharti et al., 2016; McGeoch, 2007). A major drawback of studies using insects as bioindicators is that they focus on one or a few taxa and then extrapolate the results to all insect populations, for example, Boyes et al. (2021) extrapolate detrimental effects of light pollution found for caterpillar assemblages to detrimental effects for the entire local insect population in the title of their study differences in environmental conditions and in insect responses to the environment hamper comparisons of insect taxa, with a risk of unwarranted generalisations and suggestions of conservation measures that may do more harm than good (Saunders et al., 2020). While recent meta-analyses of insect decline found no evidence of consistent temporal trends (Crossley et al., 2020; van Klink, Bowler, Gongalsky, Swengel, Gentile, et al., 2020), they were criticised for having based their conclusions on data sets representing diverse taxa and methods (Desquilbet et al., 2020; Welti et al., 2021), which can be attributed to the lack of standardised data available (van Klink, Bowler, Gongalsky, Swengel, & Chase, 2020). Reviews of the literature on insect communities have similarly pointed out that existing studies can be biased in many ways, including a lack of standardised sampling procedures (Cardoso & Leather, 2019; Habel et al., 2019). Moreover, while a wide range of taxa can be collected using sampling methods such as Malaise and sticky traps (Clark & Samways, 1997), regularly the studied hypotheses are specific for one or few of the collected taxa and only

a subset of the sampled insect community is used for further statistical analyses (Muirhead-Thompson, 2012). Method-specific sampling biases such as active versus passive attraction can also affect the number of individuals collected. For example, the effectiveness of attraction-based traps depends on the competing ambient availability of the bait (Didham et al., 2020). Additionally, the duration of trap exposure (Samways et al., 2010) determines whether seasonal community patterns are represented accurately (Niemelä et al., 1990).

There is, as yet, no empirical evidence of opposing trends in insect communities that is based on a direct comparison of different methods employed under the same environmental conditions within a single study. To close this gap, we compared trends in arthropod biomass along two environmental gradients assessed by the two currently most prominent sampling methods used in the long-term terrestrial insect monitoring (Muirhead-Thompson, 2012) (Figure 1): light traps, which use light to attract nocturnal moths (Jonason et al., 2014; Muirhead-Thompson, 2012), and Malaise traps, which mainly capture Diptera (75%) and Hymenoptera (15%) (Karlsson et al., 2020; Matthews & Matthews, 1971). Both were set up along gradients of canopy openness and elevation. The elevational gradient represented macroclimatic changes and the canopy openness gradient microclimatic changes. Both macro- and microclimate are major drivers of insect habitat selection (Pateman et al., 2016; Wallisdevries & van Swaay, 2006) that reflect the climatic stressors acting upon insect populations in the context of human-induced environmental changes (Pilotto et al., 2020; Scaven & Rafferty, 2013; Settele et al., 2008; Wagner, 2020). Total arthropod biomass (hereafter
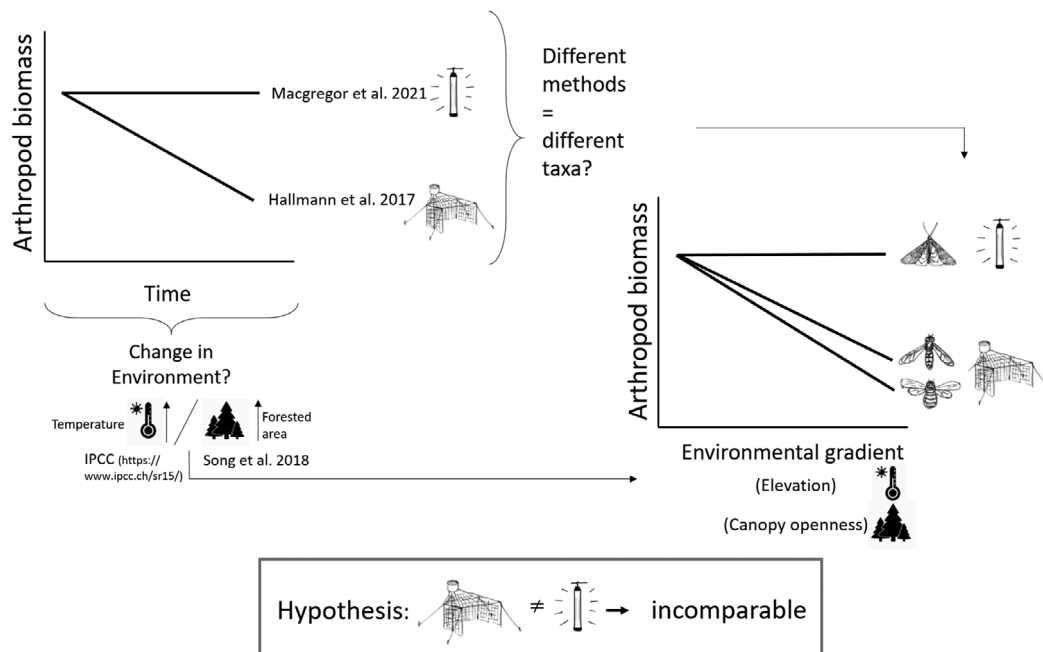

FIGURE 1 Conceptual basis of the study. Studies of the development of insect communities over time have yielded conflicting results. We test the assumption that data obtained using different taxon-specific methods can be directly compared in attempts to draw broad conclusions regarding the trends in insect communities or if taxa may differ in their responses to long-term environmental changes. In our study, insect communities from light and Malaise traps were compared along gradients of elevation (macroclimatic change) and canopy openness (microclimatic change) during spring and summer in 2016.

referred to as biomass) was estimated from each trap type together with abundance and richness of taxonomic groups, selected by method-specific criteria: Lepidoptera (hereafter nocturnal moths), collected in light traps, and Aculeata (bees and wasps, hereafter bees) and Syrphidae (hereafter hoverflies), collected in Malaise traps. These taxa were chosen based on established field practises (Samways et al., 2010; Sheikh et al., 2016).

In the light of the ongoing debate about insect decline, we tested whether the theoretical assumption made in the context of meta-analyses that the biomass, estimated from the two trap types, follows similar patterns along gradients of macro- and microclimate, holds true. Furthermore, we investigated whether the taxonomic groups selected according to the sampling method respond in the same ways to environmental change in terms of abundance and species richness.

METHODS

Study area

The study was conducted in 2016 in the German section of the Bohemian Forest in Europe (S1). The study area is located in the temperate zone and covers an elevational gradient from 297 m to 1368 m a.s.l. The mean annual temperature decreases from 9.0°C at lower elevations to 3.5°C at higher elevations (Bässler et al., 2015). Total annual precipitation along the elevational gradient varies between 900 and 1800 mm (Bässler et al., 2015). The dominant tree species are *Picea abies* L. H. Karst and *Fagus sylvatica* L. (Bässler et al., 2008). The forest structure in this area is strongly influenced by windthrow events and bark beetle outbreaks, which are left unmanaged such that natural forest succession gives rise to plots that cover the entire canopy openness gradient (Hilmers et al., 2018).

Sampling and environment

Sampling took place during spring and summer in 2016 (light trapping: May–August, Malaise trapping: April–September) on 52 plots along elevational and canopy openness gradients (S1). For each plot, canopy openness was assessed once by measuring the gap percent based on single tree measurements with a diameter at breast height >7 cm within an area of 500 m^2 around the plot centre. Tree height was exemplarily measured and then extrapolated via regression referring to diameter at breast height for all other trees on the plot (Pretzsch, 2002). Based on this information, individual canopy length and width were approximated using allometric coefficients (Pretzsch et al., 2015), assuming that the tree canopies were spherical in shape. These data were used to calculate the gap percentage as an estimate of canopy openness within each 500 m^2 plot area. Insects were sampled using light and Malaise traps. One trap of each type was positioned within a radius of
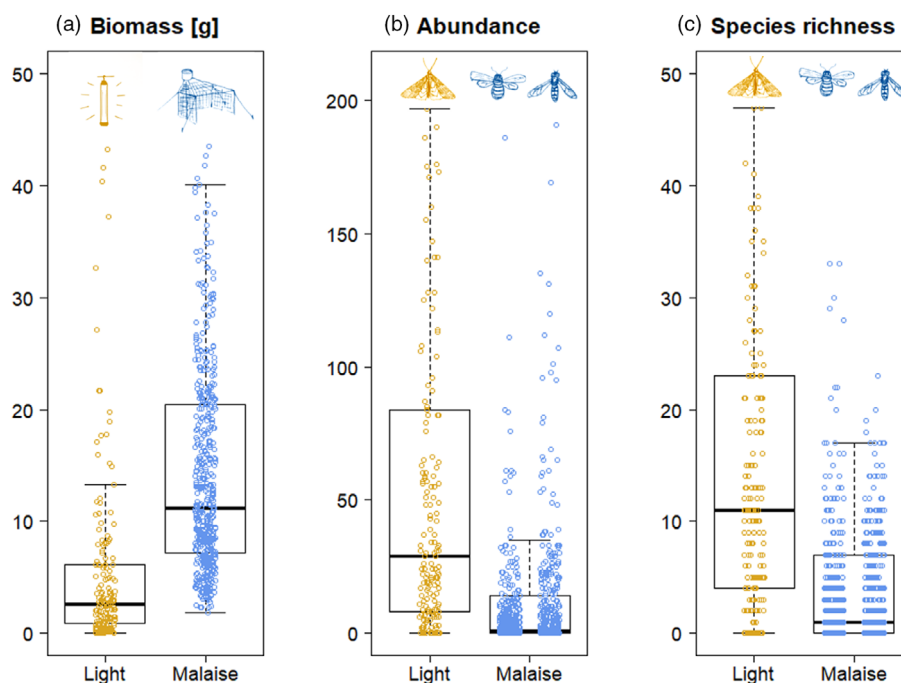

FIGURE 2 Catch results using light and Malaise traps. (a) Biomass (g) data represent the total amount of arthropods. (b) Abundance and (c) species richness were analysed using the most prominent taxa (nocturnal moths: yellow, bees and hoverflies: blue) obtained using light traps (yellow) and Malaise traps (blue). Samples were collected at 52 different sites in the German section of the bohemian Forest during spring and summer in 2016. Insects were collected with light traps up to four times for one night per plot (n_{light} = 189). Malaise traps were emptied twice monthly at each plot with the loss of one sample ($n_{Malaise}$ = 519). The middle line represents median values. The upper and lower lines represent first and third quartile. The lower and upper hinge represent maximum and minimum values excluding suspected outliers. For graphical reasons, extreme outliers are not shown.

8 m around the plot centre. Light traps consisted of super-actinic UV lamps (12 V/15 W) installed over a funnel that guided the insects into a bucket in which chloroform effused. The traps were hung 1.5 m above the ground and were switched on automatically at night via a light sensor (Kemo Electronic M122 'Twilight switch'). Between May and August, light trapping was conducted four times within each plot by installing one light trap per plot for one night. In 13 of the plots, light trapping was done only three times and in one plot only two times due to technical failures (n_{Light} = 189). Nights with a full moon, heavy rain or windy conditions were avoided. Malaise traps consisted of black

mesh (1.7 m × 0.95–1.7 m trap opening) and continuously present sampling bottles filled with 80% ethanol. Bottles were emptied twice per month, with the loss of one sample ($n_{Malaise}$ = 519). To assess the total biomass of flying insects and other arthropods, all catches of the two lethal sampling methods were weighed as fresh weight (g) (after a standardised 5-min drain for Malaise trap catches) prior to sorting. As both light and Malaise traps are biased towards specific taxa, abundance and species richness were only assessed for the taxonomic groups typically sampled by each of the two methods: nocturnal macro moths in the light traps and bees and hoverflies in the Malaise traps.
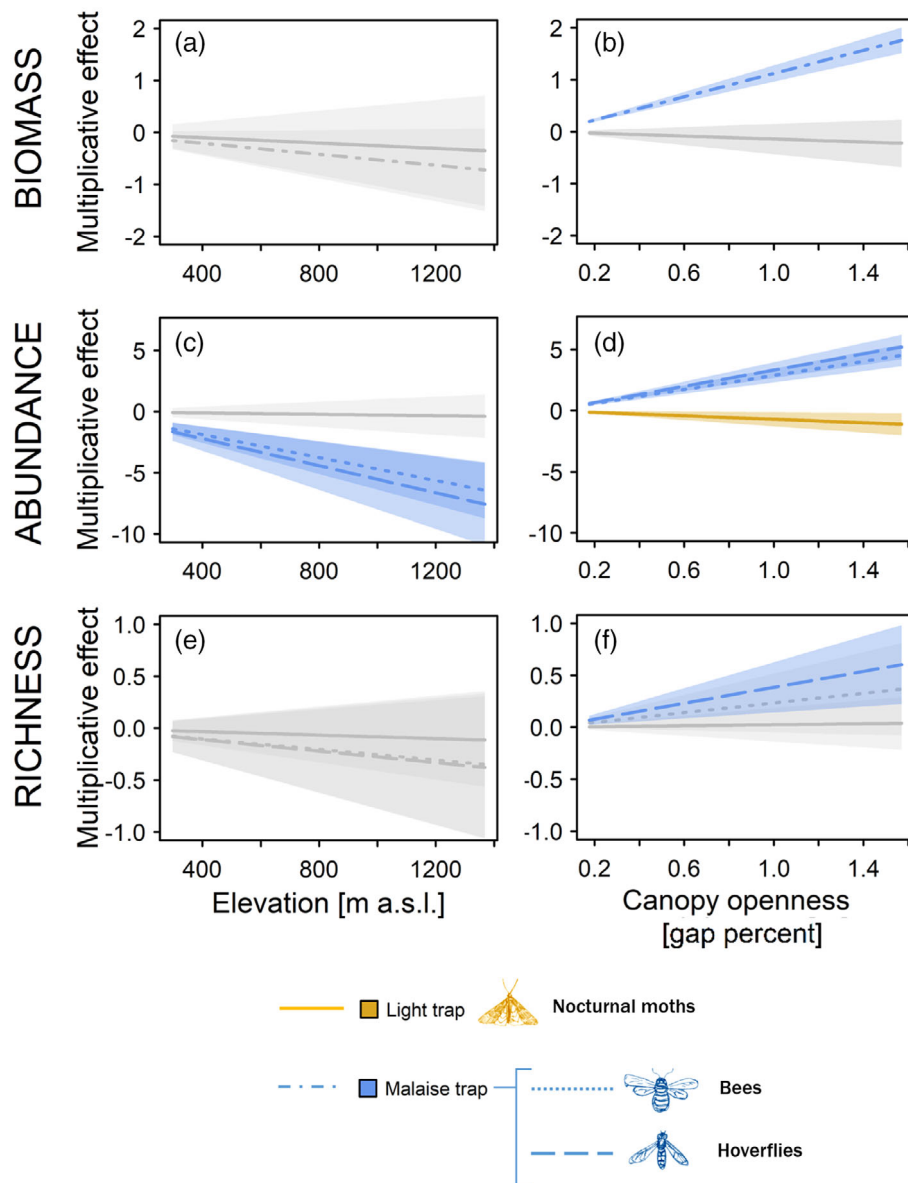

FIGURE 3 Effects of macroclimate (elevation) and microclimate (canopy openness) on the insect taxa sampled using light and Malaise traps. The data were analysed using generalised additive models (GAMs, link = $\log_e$) and then plotted as the multiplicative effect, that is, an exponentiated fit, to enable comparisons of the results. The shaded areas represent the 95% confidence intervals. n_{light} = 189, $n_{Malaise}$ = 519. Elevational range: 297–1368 m a.s.l. canopy openness (as gap percent) range: 3.1%–100%. The right-hand x axis showing canopy openness represents asin(sqrt(gap percent)) as used in the GAMs. Biomass data (Gaussian distribution) represent the total amount of arthropods. Abundance and species richness (negative binomial distribution) were determined based on nocturnal moths from the light traps, and bees and hoverflies from the Malaise traps. Grey: not significant in the GAMs. Light trap – yellow, Malaise trap – blue. nocturnal moths – continuous yellow line, bees – dotted blue line, hoverflies – dashed blue line

All individuals of these taxa were identified to species level by experts (bees: Christian Schmid-Egger, hoverflies: Gisela Merkel-Wallner, nocturnal moths: Hermann Hacker).

Data analysis

A generalised additive model (GAM, link = log$_e$) (Wood, 2017) was applied to determine the relationships between biomass, species richness and abundance and the abiotic factors (i.e. elevation, canopy openness and date). Biomass models were based on total mass of all arthropods sampled, and abundance and species richness models on count data of the selected taxonomic groups described above. Biomass, abundance and species richness, as dependent variables, were analysed separately for each trapping method. Biomass data were modelled using a Gaussian distribution, and abundance and species richness models using a negative binomial distribution. Species richness models included log$_e$-transformed abundance data as the linear main effect to correct for abundance effects (Gotelli & Colwell, 2001). Seasonality and spatial factors were accounted for by entering the date and the coordinates, respectively, into the models. Both variables were incorporated in the models as smooth functions using thin plate regression splines. Smoothing parameters were selected using 'REML' (Wood, 2017). An offset was included in the Malaise trap models to account for differences in the duration of trap exposure. All models were fit according to the model Formula (1):

$$Y \sim s(date) + offset(\log_e(trap\ exposure\ duration)) + elevation \\ + asin(sqrt(canopy\ openness)) + s(x\_coordinate, y\_coordinate) \quad (1)$$

To determine whether the dependent variables showed trap-specific changes along the environmental gradients, additional GAMs were modelled that included trap-environment interactions as independent variables (Formula 2). This was achieved by summing the abundance and species richness of the two taxonomic groups targeted by the Malaise traps (bees and hoverflies) to detect overall differences between the two trapping methods. Another GAM was used to identify significant differences among the trap-specific changes along the environmental gradients (Formula 3). The trap exposure offset was removed from the models to avoid the identification of significant differences based on inherent features of the traps.

$$Y \sim s(date) + trap + trap : elevation + trap : asin(sqrt(canopy\ openness)) \\ + s(x\_coordinate, y\_coordinate) \quad (2)$$

$$Y \sim s(date) + trap + trap^*elevation + trap^*asin(sqrt(canopy\ openness)) \\ + s(x\_coordinate, y\_coordinate) \quad (3)$$

All analyses were done in R version 3.6.1 (R Core Team, 2019), using the 'mgcv' package for GAM analyses.

RESULTS

A total of 189 samples from the light traps and 519 samples from the Malaise traps were analysed. The 722 species that were identified included 404 species of nocturnal moths, 130 species of hoverflies

TABLE 1 Generalised additive model (GAM, link = log$_e$) of trap-specific insect community trends along elevation and canopy openness gradients, with interactions between the trapping method and the environmental gradient

Predictors	Biomass		Abundance		Species richness	
	t value	p value	z value	p value	z value	p value
Intercept	7.846	**<0.001**	7.308	**<0.001**	−4.153	**<0.001**
Log$_e$(Abundance)	NA	NA	NA	NA	39.371	**<0.001**
Light versus Malaise trap	−1.028	0.305	−11.630	**<0.001**	−0.189	0.850
Light trap: Elevation	−1.043	0.297	−4.165	**<0.001**	−1.672	0.095
Malaise trap: Elevation	−2.655	**0.008**	−3.841	**<0.001**	−1.181	0.238
Light trap: Canopy openness	−1.239	0.216	−0.906	0.365	2.155	**0.031**
Malaise trap: Canopy openness	11.723	**<0.001**	9.300	**<0.001**	1.936	0.053

Smooth terms	F value	p value	X^2	p value	X^2	p value
Date	49.111	**<0.001**	329.640	**<0.001**	44.033	**<0.001**
Coordinates	6.494	**<0.001**	37.120	**<0.001**	6.225	0.218

Note: The results reported in the table describe the relationships between trap and environment (trap: environment). Grey shaded areas indicate significant differences between trap–environment relationships (trap * environment), that is, significant differences between the slopes in Figure 3b + d. Biomass data (Gaussian distribution) represent the total mass of all arthropods sampled. Abundance and species richness (negative binomial distribution) were determined based on nocturnal moths from the light traps, and bees and hoverflies from the Malaise traps. Species richness models included log$_e$-transformed abundance data as the linear main effect to correct for abundance effects. Values shown in bold are significant. $n_{light} = 189$, $n_{Malaise} = 519$. Elevational range: 297–1368 m a.s.l. Canopy openness (measured as gap percent) range: 3.1%–100%.
Abbreviation: NA, not applicable.

and 188 species of bees. Mean biomass in light traps ($6.50 \pm$ SE 0.85 g, range: 0.01–78.98 g) was lower than mean biomass in Malaise traps ($14.85 \pm$ SE 0.52 g, range: 1.86–119.99 g) and accordingly cumulative biomass from light traps (1228 g) was lower than from Malaise traps (7708 g) (Figure 2a). The light traps contained 19,877 nocturnal moth individuals and the Malaise traps 2678 bee and 5575 hoverfly individuals. Bees and hoverflies were present almost equally in the Malaise traps in terms of species richness and abundance (Figure 2b + c).

Biomass

Arthropod biomass in light and Malaise traps showed opposing trends along the canopy openness gradient. Biomass in the light traps showed a decreasing trend with increasing canopy openness while it increased in the Malaise traps (Figure 3b, S2). Elevation showed no relationship with biomass in both trapping methods (Figure 3a, S2). Testing trap–environment interactions revealed significantly different
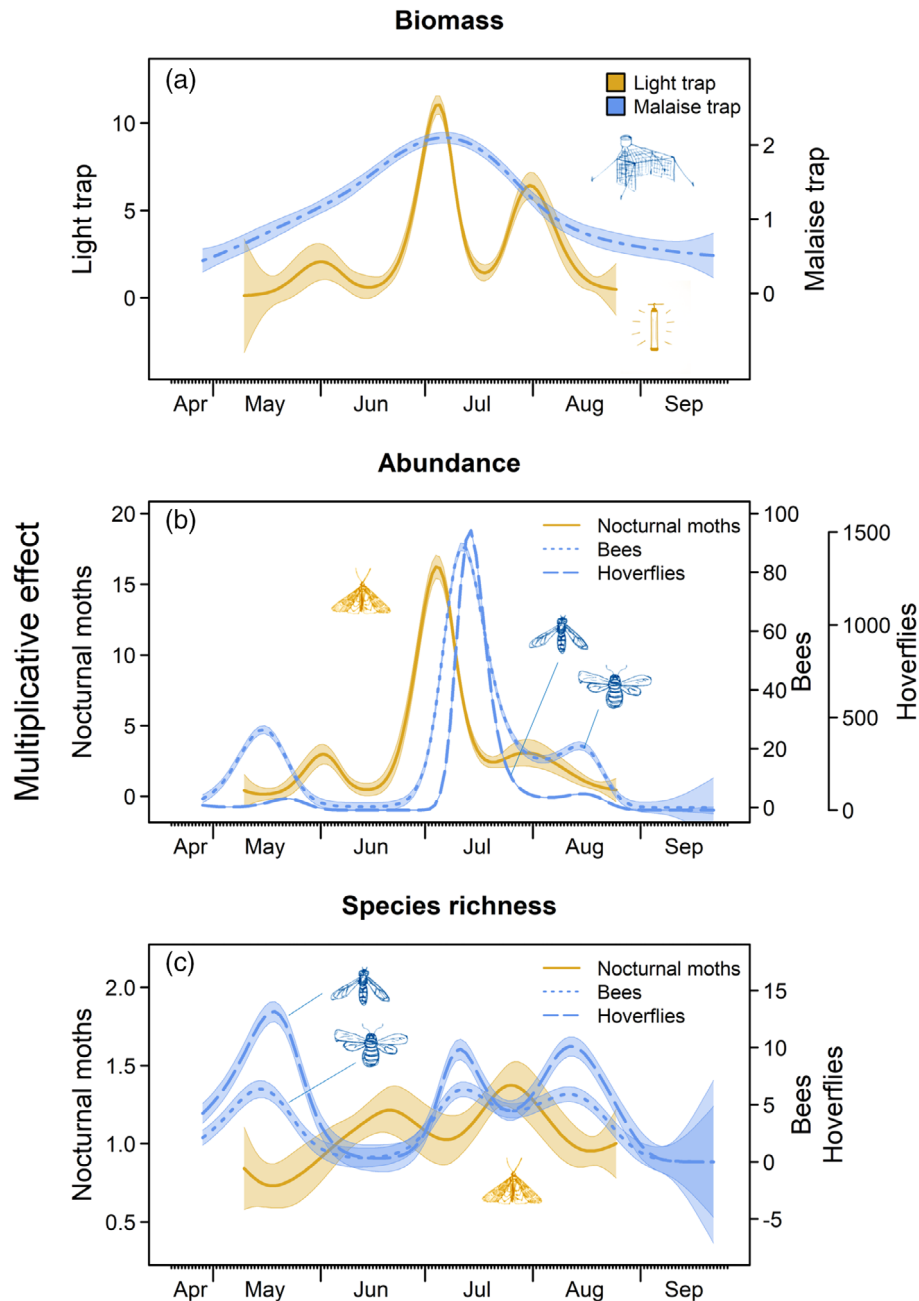

FIGURE 4 Phenology of light and Malaise trap catches. The data were plotted as the multiplicative effect, that is, as an exponentiated fit, to enable comparisons of the results. Shaded areas indicate the 95% confidence intervals. Samples were obtained at 52 different sites in the German section of the Bohemian Forest in 2016. Biomass data represent the total amount of arthropods. Abundance and species richness were determined using nocturnal moths from the light traps and bees and hoverflies from the Malaise traps. $n_{light} = 189$, $n_{Malaise} = 519$. Elevational range: 297–1368 m a.s.l. Canopy openness (measured as gap percent) range: 3.1%–100%. Light trap – yellow, Malaise trap – blue. Nocturnal moths – continuous yellow line, bees – dotted blue line, hoverflies – dashed blue line

trends in biomass estimated from light versus Malaise trap catches along a canopy openness gradient but not along an elevation gradient (Table 1, Figure 3a + b).

The two trapping methods showed distinct seasonal patterns for biomass with different frequencies of seasonal peaks (Figure 4a, S2). Biomass of arthropods sampled with Malaise traps peaked only at the beginning of July, whereas the biomass of light traps catches was characterised by peaks in May/June, the beginning of July and in July/August (Figure 4a).

Abundance and species richness

Nocturnal moths caught by light trapping decreased in abundance with increasing canopy openness but showed no trend along the elevation gradient (Figure 3c + d, S2). Species richness of nocturnal moths was unaffected by both investigated environmental gradients (Figure 3e + f, S2). Bees and hoverflies caught by Malaise trapping decreased in abundance along the elevation gradient and increased in abundance along the canopy openness gradient (Figure 3c + d, S2). Testing trap–environment interactions revealed significantly different trends between the method-specific abundances estimated from light and Malaise trap catches along a canopy openness gradient (Table 1). Differences in species richness were found only for hoverflies along the canopy openness gradient, whose species richness increased with increasing canopy openness (Figure 3f, S2).

The abundance and species richness of all three taxonomic groups generally formed three peaks distributed throughout the season (Figure 4b + c), except in the case of the species richness of nocturnal moths, which formed only two peaks (Figure 4c). Peaks in the abundance and species richness of bees and hoverflies occurred at approximately the same time (Figure 4b + c).

DISCUSSION

In our study, a direct comparison of catches from light and Malaise traps revealed that communities of flying insects show differences in biomass patterns along different environmental gradients. Biomass patterns of the trap catches were similar along the macroclimatic gradient represented by elevation. However, opposing biomass patterns were determined along the microclimatic gradient represented by canopy openness. Specifically, with increasing canopy openness, the arthropod biomass caught in the light traps decreased, whereas it increased in Malaise traps. The same opposing pattern was found for the abundance, but not for species richness, of selected taxa from the two trap types.

Canopy openness gradient

Canopy openness affected the abundance, but not the species richness, of taxa groups sampled in different ways. The abundance data of our study are unsuited for a direct comparison of the two trap types because they represent different taxa with an opposing response along a canopy openness gradient. However, meta-analyses are often based on such inappropriate comparisons and by highlighting the important effect of sampling method on the results of meta-analyses, we hope to contribute to a better understanding and interpretation of insect monitoring data.

Differences in the abundance of taxa groups along an environmental gradient could indicate the absence of a particular habitat preference (open or forested) of bees, hoverflies and nocturnal moths, with differences in the performances of these insects in different habitats. Possible taxon-specific explanations for the opposing abundance trends along the canopy openness gradient include the following.

First, a change in microclimatic variability along the canopy openness gradient could account for the trend in nocturnal moth abundance. Insects are ectotherms such that their activity is regulated by the ambient temperature (Chown et al., 2002). Depending on the habitat type, microclimatic conditions can differ considerably in their temperature range from macroclimatic conditions (Suggitt et al., 2011). In forest habitats, macroclimatic conditions are buffered by the canopy cover (Zellweger et al., 2020) such that night-time temperatures will be warmer and the activity phases of nocturnal moths accordingly longer in areas with a closed canopy than in more open areas (Muirhead-Thompson, 2012). As the Malaise traps were in continuous operation during the study, temperature would not have been a major limiting factor for the catch probability of bees and hoverflies. Some bee and hoverfly species prefer sites with a higher irradiance but others are either unaffected, prefer shaded sites or alternate between open and shaded habitats during the day (Gilbert, 1985; Herrera, 1995; Maier & Waldbauer, 1979). However, both bees and hoverflies strongly depend on flowering plants as a food resource (McCabe et al., 2019), but food availability is more limited under a dense canopy cover (Armentrout & Pieper, 1988). Therefore, the second potential explanation for the abundance trends of these two insect groups along the canopy openness gradient could have involved the availability of food resources, whereas this would not have influenced nocturnal moths, given that the imagoes of many species do not feed and therefore do not depend on flowering plants (Altermatt & Pearse, 2011).

A direct comparison of arthropod biomass collected from the light versus the Malaise traps revealed opposing trends along the canopy openness gradient. This demonstrates that the choice of trapping method needs to be consciously included in a study's design and in the analyses of the data, especially when investigating insect response to environmental changes. The taxa groups predominantly caught by each method can potentially explain these trap-specific differences.

Spatial and temporal trends

The different trends in biomass estimated from Malaise versus light trap catches are consistent with the findings of Hallmann et al. (2017), who found a decline in total flying insect biomass catches as determined from Malaise traps, and Macgregor et al. (2021), who observed no change in mean moth biomass based on light trap catches. Both

studies relied on long-term (≥27 years) data sets obtained through continuous sampling and can therefore be considered to have had sufficient statistical power to detect trends over time (White, 2019). Our spatial results can be compared with the temporal trends reported by Hallmann et al. (2017) and Macgregor et al. (2021), by assuming that the canopy openness gradient, a focus of our study, was influenced by the environmental changes that occurred over the time frames of those two studies. Both were conducted in Europe, where environmental conditions have changed during the last four decades, including a strong increase in growing stock and forested area (Schelhaas et al., 2003; Song et al., 2018) that has increased vegetation density, resulting in warmer microclimatic conditions in forests. Warmer nights favour nocturnal moths and other insect groups (Müller et al., 2012), which could be part of an explanation for the lack of change in mean moth biomass described by Macgregor et al. (2021). Also, forest coverage increased in the 200 m radius surrounding the traps deployed by Hallmann et al. (2017), and the resulting reduction in food resources could contribute to the decrease in bees and hoverflies determined from the Malaise traps in that study.

Additional reasons for the disparity of these two studies could lie in the site-selection. On the one hand, the sampling sites of Hallmann et al. (2017) are all located in protected areas and are therefore subject to a nonrandom site-selection bias (Fournier et al., 2019). On the other hand, many of the sampling sites of Macgregor et al. (2021) are in an urban context and are thus much more susceptible to human impacts.

Representativeness and generalisations

Meta-analyses of insect community trends make use of diverse data sets to draw general conclusions on the health of insect communities (Crossley et al., 2020; Sánchez-Bayo & Wyckhuys, 2020; van Klink, Bowler, Gongalsky, Swengel, Gentile, & Chase, 2020). However, ambiguous results in terms of insect community development have been documented, such as in comparisons of terrestrial and aquatic insect communities (van Klink, Bowler, Gongalsky, Swengel, Gentile, & Chase, 2020). A problem in relying on the data sets from several studies is that their spatial resolution or time span (Habel et al., 2019) as well as the extent of the environmental gradients investigated (van Klink, Bowler, Gongalsky, Swengel, Gentile, & Chase, 2020) may differ. Due to these discrepancies, several literature reviews have expressed caution in generalising results, thereby also highlighting the challenges of insect monitoring (Cardoso & Leather, 2019; Didham et al., 2020; Habel et al., 2019; Montgomery et al., 2020). In our study, potential biases were avoided by parallel trap deployment within the same plots, which allowed a direct comparison of the biomass data.

Light and Malaise traps are standard sampling methods for the most commonly studied insect taxa (Hymenoptera and Diptera: Noriega et al. (2018)) and for the longest continuously studied insect taxon (Lepidoptera: e.g. Macgregor et al. (2021)). This implies a prominent role for sampling method in the ongoing debate on trends in insect biomass (Montgomery et al., 2021). In our study, direct comparisons of the catches obtained with light and Malaise traps demonstrated that insect community responses to environmental changes may be very different depending on the sampling method and the accordingly caught taxa. In contrast, in a meta-analysis, opposing responses may cancel each other out (e.g. Crossley et al. (2020)) and thereby remain undetected, such that threats to insect community health and losses of biomass and individual taxa, including their ecosystem functions, may be obscured. The different patterns of biomass along microclimatic gradients as estimated based on our light versus Malaise trap catches lead us to reject the assumption that, in studies of environmental change, biomass data obtained using different trap types are comparable. Instead, insect trends over time are known to strongly fluctuate, making such data sets very sensitive to minor changes. For example, impacts of software errors by Macgregor et al. (2019) changed the results from a net gain in mean biomass to no change in mean biomass between the first and last decades of monitoring (Macgregor et al., 2021). Therefore, we urge caution in the interpretation of such data and point out that abundance estimates for selected taxa might show varying responses to environmental change. Although our results did not show contrasting trends for method-specific species richness along the examined gradients, this finding should be confirmed in further studies that include a larger number of taxa and trap types as well as additional environmental gradients.

In summary, biomass, abundance and species richness do not provide reliable surrogates of insect community health because their trends may differ along environmental gradients as well as among selected taxa. This makes comparisons of different taxa from different taxon-specific traps inappropriate to draw generalised conclusions. While a recent literature study of hoverflies concluded that large reductions in biomass indicate a declining diversity (Hallmann et al., 2021), this relationship was not found in a study of bees (Vereecken et al., 2021), indicating taxon-specific responses. Earlier studies already showed that one taxon is not representative of another (Pilotto et al., 2020; Wolters et al., 2006), as demonstrated and elaborated upon in our study of bees, hoverflies and nocturnal moths. Future studies aimed at evaluating possible insect decline and its drivers should be designed to allow a better comparability of the data.

Implications for future insect monitoring

Given the variety of insect trapping methods and the differences in the taxa they trap, a low level of data comparability is to be expected not only from Malaise and light traps but also from other methods. In fact, different results have been obtained even for the same taxonomic group when different trapping methods were used, as reported for saproxylic beetles sampled with window and eclector traps versus bark sampling (Alinvi et al., 2007). The success of methods such as window traps depends on the activity of the insects of interest. However, the activity might also depend on the population-density and population sizes can be easily under- or over-estimated (Didham et al., 2020). Differences in detection probability are rarely recorded,

but they would contribute valuable information in comparisons of data sets (Pollock et al., 2002; Southwood & Henderson, 2009). For example, some insects exhibit strong multi-year variability (Büntgen et al., 2009) and should therefore be sampled continuously for decades to distinguish short-term fluctuations from long-term trajectories and to quantify ecological responses to environmental change (Lindenmayer et al., 2012). In our study, the seasonal variation in the catches of the two trap types could not be compared because the Malaise traps were deployed continuously while the light traps were used in single date samplings, such that seasonal peaks may have been missed. Although light trap sampling was carried out only under suitable weather and moon conditions, weather- and moon-dependent differences in moth activity and phototactic response cannot be excluded. Thus, although peaks in the abundance and richness of nocturnal moths were often reached earlier than those of bees and hoverflies in the present study, this might have been an artefact of the discontinuous sampling of the moths as other studies show a pronounced peak in summer for nocturnal moths (Roth et al., 2021).

In addition to the documentation of method- and taxon-specific detection probabilities and the use of continuous sampling, in future studies sampling procedures should be standardised to include the parallel, long-term deployment of trap combinations suitable for the habitat of interest (Missa et al., 2008). For temperate forests, a comprehensive set of standardised trapping methods consists of pitfall, window flight, light and Malaise traps (Nageleisen & Bouget, 2009). Another improvement would be the use of combi traps combining, for example, features of window and Malaise traps (Basset, 1988; Knuff et al., 2019) or, window and pan traps (Duelli et al., 1999) to broaden the range of sampled taxa. Sampled individuals from the relevant taxa should be identified to the species level by qualified taxonomists. Direct or indirect information about the microclimatic conditions for each sampling site, for example, by assessing canopy openness (De Frenne et al., 2013), or nitrogen deposition (Dirnböck et al., 2014) would provide further, essential information. To avoid method biases when handling the already existing diverse data sets, future meta-analyses should separate studies by trapping method and taxa groups and make more detailed analyses before drawing generalised conclusions.

CONCLUSION

Spatial and temporal patterns of insect communities determined using light and Malaise traps are very different, reflecting the differences in the taxa predominantly collected by each trapping method. Despite the importance of insect ecosystem services and the strong environmental constraints that are currently leading to declines in many insect taxa, caution is needed in generalising the results of different studies, as differences in the various trapping methods and in the environmental conditions must be taken into account. Studies using standardised sampling procedures across large temporal and spatial scales are the next step towards a better monitoring of insect communities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1 Supplementary Information