ORIGINAL ARTICLE

Exploring the power of moth samples to reveal community patterns along shallow ecological gradients

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Funding information
University of Vienna, Faculty of Life Sciences; Heinrich Böll Stiftung, Berlin

Associate Editor: Noelline Tsafack

Abstract

1. Analysing the effects of environmental variation on species assemblages is a key topic in community ecology. However, the outcome may strongly depend on the focal species group. Moths have often been used as the target in ecological studies due to their fast response to environmental change. Yet, some moth subgroups might be more sensitive than others to reflect environmental differences, depending on their functional and physiological characteristics.

2. We investigated which moth subsets are especially suitable to mirror responses to subtle variation in vegetation. We analysed the susceptibility of different subsets to local weather conditions and inter-annual fluctuations. Finally, we checked for the importance of including abundance information. We analysed moth communities (392 species, 23.870 individuals) at 60 sites within two Mediterranean forest reserves and investigated relationships between community composition and environment of (1) all moths (with and without taking abundances into account), and of subsets comprising only (2) small-sized species, (3) host-plant specialists, (4) moss, lichen and detritus feeding species, (5) 'microlepidoptera', (6) 'macro-moths' and (7) random subsets of 50, 100 and 200 species.

3. Incidence data performed similarly to abundance data in matrix regression models. Host plant specialists responded especially sensitive to small-scaled variation in vegetation composition. Macro-moth samples in contrast were highly prone to local weather conditions and to inter-annual abundance fluctuations. Accordingly, a focus on host-specialists and micro-moths is the best way to analyse relationships between shallow environmental gradients and insect communities.

KEYWORDS
community composition, differentiation diversity, environmental gradients, moth indicator groups, stochastic factors

INTRODUCTION

Analyses of ecological datasets often have the goal to assess ecosystem quality and how it is affected by different management regimes, structural habitat changes over time, or by surrounding landscape characteristics (Chisté et al., 2016; Luppi et al., 2018; Neff et al., 2019).

The outcome however may depend on the focal species group selected and the diversity measure that has been analysed, with different taxa responding differently to ecosystem change (Hilmers et al., 2018; Müller et al., 2020), and different diversity measures varying in their sensitivity of reflecting local or landscape-scale factors (Gavish et al., 2019; Hillebrand et al., 2018).

For insects, there are plenty of case studies elucidating responses of different insect groups to local and landscape-scale drivers (Burks & Philpott, 2017; Kennedy et al., 2013; Luppi et al., 2018). Here, one insect group that often has shown its great potential to reflect ecosystem properties is moth communities (Kadlec et al., 2018; Mangels et al., 2017; Thorn et al., 2015). Being easy to sample by light trapping, this species-rich group of insects offers an opportunity to obtain fast and with manageable effort a representative shortcut to what happens in an ecosystem. Even though moths are mobile insects, many of them have strong bounds to a special larval food plant or habitat. As a consequence, they have often been found to reflect variation in local plant diversity (Root et al., 2017), management intensity (Mangels et al., 2017), have been analysed along urbanisation gradients (Merckx & van Dyck, 2019), and they provided useful response variables for habitat fragmentation or degradation studies (Alonso-Rodríguez et al., 2017; Merckx et al., 2019; Summerville & Crist, 2003).

Even very small-scaled environmental gradients can be analysed by using moth communities. Our own previous work has shown that moths do not only mirror larger-scale differences but may also reflect very fine nuances in vegetation variation within one focal study area (Uhl et al., 2020; Uhl et al., 2021a). This high sensitivity to even subtle ecological contrasts offers many opportunities for ecologists to study the effects of environmental variation on species-rich biota. Though, the more shallow the gradient, the more likely it is obscured by stochastic factors, such as temperature variation (Jonason et al., 2014; Yela & Holyoak, 1997) or abundance fluctuations of a few dominant species from year to year (Didham et al., 2020; Highland et al., 2013; Spitzer et al., 1984). So, which moth species are particularly suitable to get a robust insight into finely grained ecological gradients? And which species are especially prone to stochastic weather events and inter-annual fluctuations?

The fractions of variation in community datasets explained by vegetation or by weather might vary when looking at different types of ecological data, for example, when focusing on just one functional or taxonomic group, or the decision of working with incidence or abundance data. One basic assumption is that with more species being included, community composition patterns become clearer, resulting in recommendations to always include as many species as possible. Yet, many empirical studies have focused specifically on 'macro-moth' communities (De Smedt et al., 2019; Merckx et al., 2019; Valtonen et al., 2017) or only taken a few Lepidopteran families into account (Heidrich et al., 2021; Moreno et al., 2021), as the identification, especially of micro-moths, is considered difficult and labor-intensive. A solution to include the whole species set without spending too much time on identification work is arising with new methods such as meta-barcoding (Aagaard et al., 2017; Jin et al., 2013). However, barcoded samples do primarily inform about species incidences, while information on abundances is largely lost. This loss in information might have an adverse effect on the outcome and especially abundance-based changes in community composition might be obscured (Hillebrand et al., 2018).

In our present study, we, therefore, elucidate the power of different moth community data (sub)sets to mirror the effect of subtle variation in the structure and composition of the vegetation. Furthermore, we want to explore which functional or phylogenetic groups of moths are particularly prone to react to weather conditions or tend to show large inter-annual abundance fluctuations. Most moth species are herbivores on vascular plants during their larval stages (Potocký et al., 2018), yet a sizeable fraction of species thrives on alternative food sources like dead plant matter, mosses, lichens or fungi (Bodner et al., 2015; Potocký et al., 2018). Accordingly, moth community composition is shaped by the floristic composition as well as structural attributes of the vegetation of their habitats (Uhl et al., 2021b). The relative strength of these relationships might vary between different species groups, depending on larval feeding habits, adult body size or philopatry. So, we address the following hypotheses:

- Using incidence data instead of abundance data leads to a loss in explained variation, as species occurrence and species abundances are both equally important to evaluate community variation along gradients.
- Moth species whose larvae are specialised in one particular vascular food plant taxon are more dependent on the floristic composition at their habitats.
- Moth species with alternative feeding habits (e.g., moss and lichen feeders, detritivores) depend more on forest structure than on plant species composition.
- Small-sized species and especially so-called 'microlepidoptera' tend to be more philopatric and fly over shorter distances (Slade et al., 2013); therefore they are strongly related to local habitat characteristics. As a result, the exclusion of micro-moths from analyses reduces the signature that local habitat attributes leave on insect communities.
- Inter-annual fluctuations in individual numbers contribute to apparent shifts in community composition and are not necessarily the same for different, but neighbouring study areas.

For each of these hypotheses, we use species abundance data collected in two neighbouring forest reserves. By comparing the outcomes between both reserves, we aim to evaluate if the observed patterns within species subsets might indicate general trends, or if the results are strongly dependent on the focal study area.

METHODS

Study sites and field sampling

We performed systematic field surveys of moth assemblages in Mediterranean lowland mixed pine/oak stands, replicated in two coastal forest reserves in north-eastern Italy, near the city of Ravenna. In each of the two reserves, 30 moth sampling sites were selected a priori, regularly distributed across each reserve using a grid system (Uhl, 2020). We sampled each year 10 sites per reserve, summing up to a total of 30 different sites per reserve being surveyed after three years. Because of restrictions in manpower, it was impossible to survey all 30 sites per reserve in one year. Geographical coordinates of

all sampling sites can be seen in the map provided by Uhl et al. (2020). Within either reserve, study sites were situated about 500 m distant from another. Spatial autocorrelation between sites was found to be negligible in previous analyses of the same data set (see Uhl et al., 2021b). Pineta san Vitale (hereafter PsV) covers a total area of about 950 ha, while Pineta di Classe (hereafter PdC) has an area of approximately 900 ha. Both forest reserves are part of the regional park in the Po delta and as such are listed as UNESCO biosphere reserves.

The main vegetation within both reserves is a mix of oak and pine forest, with a dense understory composed of for example *Ligustrum vulgare*, *Crataegus* spec. and *Ruscus aculeatus*. At some places, especially in PsV, soil conditions are humid, supporting riparian forests with tree species like *Fraxinus ornus* and *Populus alba*. Furthermore, there are open grassland and reed areas within the park. However, for our study, we exclusively selected sites in mixed oak and pine woods. Light traps were positioned in a grid pattern across each reserve, at least 100 m away from each other as well as from other habitat types. This study design (Uhl et al., 2020; Uhl et al., 2021b) aimed at covering only the insect communities of the target forest type, depicting shallow ecological gradients within either reserve.

Automated light traps were equipped with two 18 W light tubes (one blacklight and one white blacklight tube), powered by a 12 V dry battery pack. The basic design of the traps followed Axmacher and Fiedler (2004). These low-power light traps predominantly attract moths from a radius of less than 20 m (Truxa & Fiedler, 2012). We sampled moths twice per site, once in early summer (June) and again in late summer (August), with 20 randomly selected sites each sampled in the years 2015, 2016 or 2017, respectively. Sampling was only conducted at favourable conditions, on warm nights without strong wind, heavy rainfall and avoiding full moon periods, as all these factors can have a major influence on moth catch sizes (Yela & Holyoak, 1997). Sampling started at dusk and ended after 6–8 h when the battery was finished. Although this caused some variation in sampling duration, we expected no big effects on sample composition, as most moths are on the wing till midnight and only a few new species can be found later on (Sato et al., 1986). In tropical ecosystems, a considerable fraction of moths are also on the wing after midnight (de Camargo et al., 2016; Moreno et al., 2021; Scherrer et al., 2013). Yet in temperate-zone ecosystems air temperature drops substantially in the course of the night, reducing moth flight activity during most nights steadily after midnight (Adams et al., 1995; Nowinszky et al., 2007; Taylor, 1963; Taylor & Carter, 1961). Directly beside the light trap at breast height, we positioned a data logger (Lascar Electronics, EL-USB-2 RH/TEMP Data Logger) that recorded every two minutes the ambient temperature and air humidity. On the next morning, the sampling containers were emptied and the data loggers retrieved. Moths were then identified to species level, resulting in a species abundance matrix overall of 60 study sites (Uhl et al., 2020). If necessary to firmly establish species identity, a genital dissection was made. For analysing species subsets, we collated information on traits like caterpillar food plants and adult wing span using different faunal monographs (species traits used for our present analyses are given in Table S1, for a complete trait matrix see Uhl et al., 2021c).

Measurements from data loggers were used to calculate the mean temperature and air humidity between 21.00 and 01.00 h in each sampling night (corresponding to the main sampling time and flight time of moths). As insect samples from June and August were pooled for analysis, we also aggregated the temperature data from early summer and summer, resulting in one mean temperature and one mean air humidity value per site.

For vegetation analysis, we randomly selected five 1×1 m^2 plots per site, where all herbs and grasses were identified to species level. Five additional 5×5 m^2 plots per site were chosen to map the shrub vegetation layer. The forest structure was analysed by doing 10 point-centered-quarter-analyses (PCQ) per site. PCQ is a commonly used method to express forest density (in trees ha^{-1}) and forest cover (in m^2 ha^{-1}) overall trees or for single tree species. For this, the distance to the four nearest trees (one in each 'quarter') is measured. Then the diameter at breast height and the species identity of these trees are noted. A detailed protocol is given in Mitchell (2010). Forest density and the mean basal areas of trees (as a proxy for forest age) were used as vegetation structure variables in the following analyses. An overview of all samples that were made per site is given in Figure 1. All vascular plant species per site were summarised within a species-incidence matrix. This matrix was the basis for all further vegetation composition analyses. Additionally, we extracted mean Ellenberg indicator values of humidity and nutrients for all vascular plant species and vascular plant species richness per plot. For an in-depth analysis of the vegetation data see Uhl et al. (2021b).

Data analysis

Data from PsV and PdC were analysed separately as plant and moth species assemblages between the two reserves differed significantly (Uhl et al., 2021a). Information from the plant species lists was aggregated by means of a Principal Coordinates Analysis (hereafter PCoA), calculated using the ape package (Paradis et al., 2004) and based on a Soerensen distance matrix. The results of the PCoA were visualised in an ordination plot. Vascular plant species richness, mean Ellenberg indicator values for soil nutrients and humidity, the cover of oaks, and cover of conifers were overlaid as explanatory vectors, to facilitate an interpretation, of how vegetation changes along axes. The first two PCoA axes were then extracted. They served as numerical representations of floristic composition in the subsequent moth community analyses. Since most moth species are herbivores during their larval stages and often occupy rather narrow feeding niches, we deemed species composition of the local vegetation to be more important for moth community composition than plant species richness per plot. We selected forest density and mean basal area of trees as 'forest structure' factors, and mean temperature and air humidity during the two sampling nights as 'weather variables'. Predictors were tested for normal distribution and (if necessary) transformed. All factors were z-transformed to remove scaling effects. The year of sampling was included as a categorical factor, leading to in total seven predictors per community composition analysis.
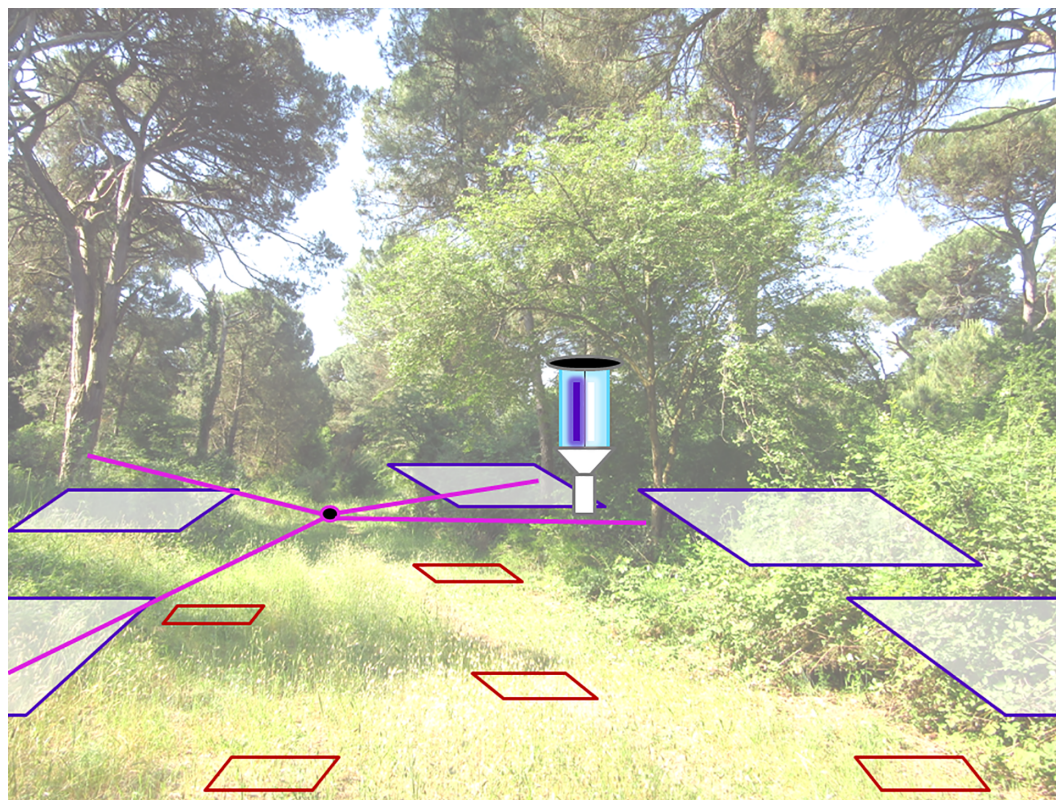
FIGURE 1 Overview over the samples taken per plot. One light trap in the center sampled moths during one night in June and in August, respectively. Five herb layer plots (red squares) and five shrub layer plots (blue squares) were surveyed to assess vascular plant species diversity. For forest structure, 10 point centered quarter analyses (PCQ) were made around each light trap site. In the figure, there is only one PCQ exemplarily shown (violet circle and lines to the nearest four trees)

To check for relationships of our selection of predictors with moth communities, we performed Canonical Analyses of Principal Coordinates (CAP), with the square-root transformed moth counts as a basis and using Bray-Curtis distances. In total, ten CAP analyses per reserve were run: one for all moths including their abundances, one for all moths but only looking at incidences, one for small-sized moths (smaller than 25 mm wingspan, irrespective of their systematic affiliation; hence, also small geometrid moths or small Nolidae were included), one for larval host specialists (species whose larvae feed on hosts in just one plant family), one for moss, lichen and detritus feeders combined, one for the Macrolepidoptera (Drepanidae, Geometroidea, Noctuoidea, Lasiocampidae and Bombycoidea sensu Regier et al., 2013 but also including Cossidae and Hepialidae), and one for 'micro-moths' (including Pyraloidea, but excluding all species belonging to the Macrolepidoptera families). We tested for significant influences of the predictors by using PERMANOVA tests with 999 permutations. Additionally, we took random subsets comprising 200, 100 and 50 insect species, using the 'sample' routine in the basic package of the R environment. These subsets were subjected to additional CAP analyses and PERMANOVA testing. For each subset size, this procedure of random subsampling, CAP and PERMANOVA testing was replicated 1000 times, to obtain a mean R^2 for random data subsets with fixed species richness. This was done to check for the mere effect of species number on explained variation. Subsampling,

CAP and PERMANOVA were performed within the vegan package (Oksanen et al., 2018). Finally, to assess if individual moth species showed up predominantly in certain years, thus indicating larger population fluctuations, indicator species were characterised for each year using the indval function of the labdsv package (Roberts, 2016). All statistical analyses were performed in the R workspace (R core Team, 2021). The R script and all raw data are available in Appendix S1.

RESULTS

We found 23.870 moths belonging to 392 species (32 families) in the two forest reserves. In PsV, moth species richness was slightly higher (340 species, of which 81 only occurred in this reserve), compared to PdC (311 species, with 52 species exclusive for PdC). Structural characters of the forests also differed slightly between the two reserves, with PsV forest stands being on average less dense (fewer trees per ha) and consisting of bigger trees. Temperature and air humidity during sampling nights were consistent throughout the two reserves (Table 1).

Even though all light-trapping sites had been selected from the same habitat type (viz. mixed pine/oak forest), the analysis of their vascular plant species lists revealed a substantial spread in reduced

TABLE 1 Structural forest parameters and weather conditions at light traps during moth sampling nights in PsV and PdC

	PsV	PdC
Forest density (trees ha^{-1})	308.3 ± 121.1	345.0 ± 103.0
Basal area (m^2 ha^{-1})	897.5 ± 357.4	755.4 ± 238.4
Air temperature (°C)	20.3 ± 1.5	19.7 ± 1.4
Air humidity (%)	80.4 ± 4.4	78.7 ± 5.2

ordination space (Figure S1). Overall, the first two eigenvalues of the PCoA together captured 32.2% of the variation in plant species composition in PsV and 31.5% in PdC.

Looking at the entire moth communities, relationships with the same set of environmental descriptors differed remarkably between the two pine forest reserves (Figure 2). Moreover, the regression models achieved consistently higher explanatory power in PdC rather than PsV (Table S2). Only moth assemblages from PdC were significantly shaped by local vegetation composition and structure. Here, 10.9% of the variation in insect community composition could be explained by floristic composition, while another 10.4% were related to forest structure. In PsV, in contrast, we found only one statistically significant relationship between full moth communities and vegetation, although floristic composition (9.3%) and forest structure (8.1%) together also accounted for about 17.4% of the variation. Night temperatures and air humidity were by far the most important correlates of apparent community composition, explaining up to 12.8% of the variation in PsV moth assemblages and even 15.5% in PdC. About 10% of the variation in species composition was accounted for through inter-annual fluctuations between moth assemblages in PdC, whereas in PsV this contribution was weaker (7.3%) and not statistically significant. So, inter-annual fluctuations were responsible for

apparent shifts in community composition but were not equally important in both study areas.

When only incidence data were used, the outcome of matrix regressions did not change substantially (explained variation by vegetation; PsV: incidence 17.30% vs. abundance 17.44%; PdC: incidence 21.53% vs. abundance 21.30%). Therefore, apparently, no ecological information got lost in our case when excluding abundance information. Vegetation composition in PsV turned into a significant predictor of moth community composition and compositional differences explained by weather became less pronounced in PdC (Table S2). Hence, stochastic factors (e.g., weather and year) had less effect on incidence data, compared to abundance data.

Looking at the random species selections, larger subsets were able to explain slightly more variation than smaller subsets. However, explained variation differed only by 1–2 percentage points, when comparing for example, 50-species subsets with 200-species subsets (Figures 3 and 4). Randomly drawn species subsets were not consistently inferior in reflecting environmental variation, as compared to subsets defined through taxonomy or by ecological traits.

The performance of functionally or taxonomically defined species subsets with regard to the proportion of variation in moth assemblages to be explained through habitat characters were more or less stable, yet generally lower in PsV (30%–39%) than in PdC (43%–53%) (Figure 3). Larval host specialists (PsV: 160 species in 6163 individuals; PdC: 152 species in 4466 individuals) performed quite well in both reserves (Figure 3). The specialist subsets performed better than all random selections, indicating that the suitability to detect environmental variation is shaped by functional characteristics and not only an effect of the included species number. Here, floristic composition explained up to 16% of the variation (in PdC; PsV: 11.1%, Figure 4), and was always included as a significant predictor in regression models. Forest structure, in contrast, turned out to be important only
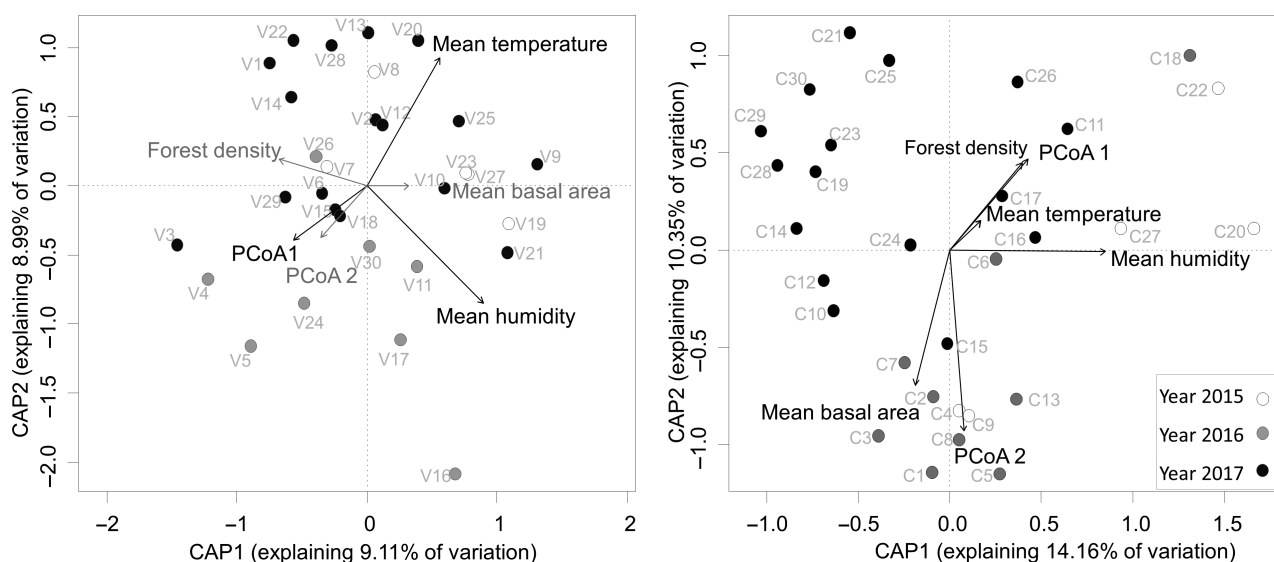
FIGURE 2 Canonical analysis of principal coordinates for PsV (left) and PdC (right) of the full moth assemblages, based on bray-Curtis distances (from square-root-transformed abundance data). Significant explanatory factors are shown as black arrows, factors that were not significant are in grey. Shading indicates the year of light-trap sampling
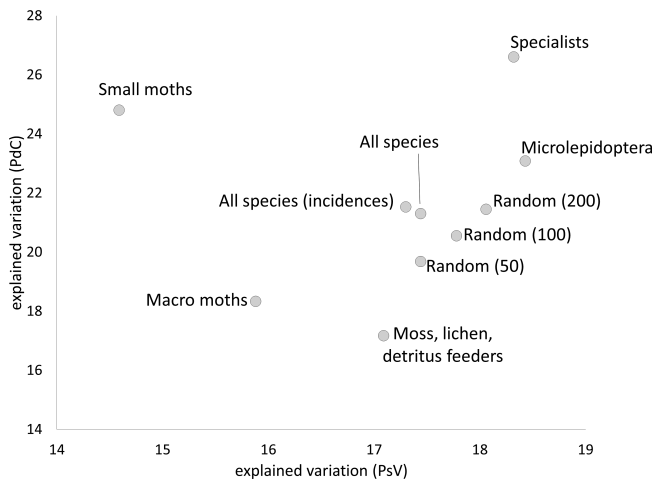
FIGURE 3 Percentage of explained variation by vegetation characteristics in PsV (*x*-Axis) and PdC (*y*-Axis). Shown is the performance of the different moth subgroups

temperatures and humidity became even more important, compared to other moth subsets or the whole community. Here, 14.8 (in PsV) to 18.6% of the variation in the species composition of moth samples could be explained by weather conditions alone. Even random samples of similar catch sizes (viz. the random subset composed of 50 species) performed better than this functional group.

By concentrating only on smaller-sized species (PsV: 187 species in 9857 individuals; PdC: 178 species in 7069 individuals), with wing spans below 25 mm, the relative importance of the various predictors likewise stayed more or less unaffected, compared to the whole species set. However, in PsV matrix regressions only explained 30% of the variation in insect community composition, which was the lowest value among all analysed subgroups (Figure 4). In PdC in contrast, small-sized species performed better than the whole dataset, with 47% of the variation being explained by the included predictors. So, the small-species-subset was the only one with strongly varying explanatory power, when looking at the two study areas, as it performed better than most other species subsets in PdC, but worse than any other species set in PsV (Figure 3).

By partitioning the data set into 'macro- and microlepidoptera', nearly all formerly observed significant patterns got lost within the macrolepidoptera subgroup (PsV: 181 species in 4449 individuals, PdC: 165 species in 4038 individuals). Additionally, year-wise fluctuations explained up to 15% of the total variation within macrolepidoptera, indicating strong inter-annual fluctuations to be prominent
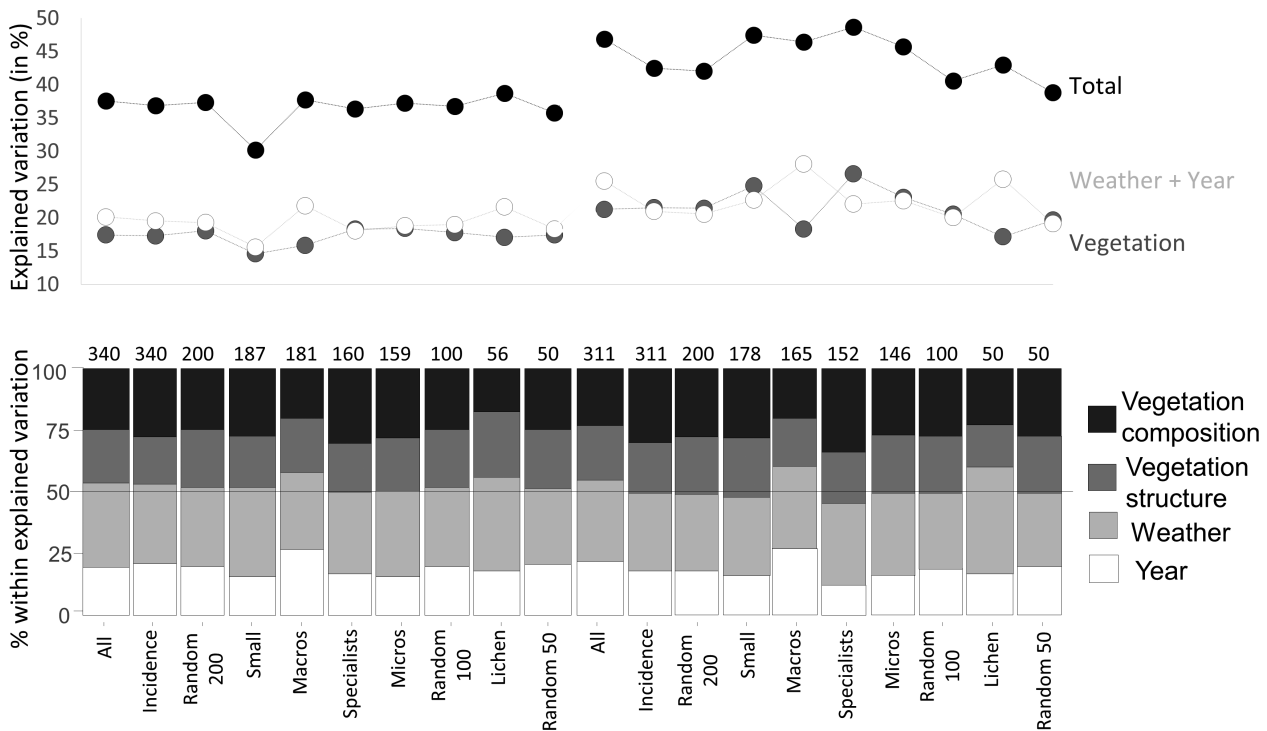
for host specialists in PdC, but not in PsV. The strong correlation between specialists and their food plants, therefore, was reflected by the increased importance of floristic composition. In contrast, for moss, lichen and detritus feeders (PsV: 56 species in 2158 individuals; PdC: 50 species in 2825 individuals) neither vegetation composition nor forest structure turned out as a determinant factor. Indeed, night

FIGURE 4 Explained variation in matrix regression models relating moth assemblages to small-scaled environmental variation in PsV (left) and PdC (right). Given are also the species numbers per subset (black numbers above the bar chart) and the proportions of explained variation by sampling year, weather, vegetation structure, and vegetation composition. The larger the proportion of explained variation by vegetation components, the more are insect species subsets suitable as targets in small-scaled gradient analyses and the less are they prone to stochastic fluctuations due to weather and inter-annual abundance variation

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TABLE 2 Indicator moth species for different sampling years in PsV and PdC and their indicator values as derived by the 'indval' function

	Indicator species PsV		Indicator species PdC	
Year 2015	Athetis hospes	0.66	Spodoptera exigua	0.78
	Chiasmia clathrata	0.66	Ethmia terminella	0.60
	Spodoptera exigua	0.62	Ancylis selenana	0.58
	Isturgia arenacearia	0.51	Ancylis apicella	0.58
	Dichomeris derasella	0.50	Deltote pygarga	0.55
	Schrankia costaestrigalis	0.42	Gypsonoma aceriana	0.53
			Acronicta rumicis	0.47
Year 2016	Noctua pronuba	0.54	Trachonitis cristella	0.48
	Plutella xylostella	0.47	Nomophila noctuella	0.46
Year 2017	Eilema depressa	0.63	Chrysoteuchia culmella	0.78
	Yponomeuta cagnagella	0.55	Cyclophora puppilaria	0.56
	Sciota rhenella	0.46	Eudonia mercurella	0.55
	Chrysocrambus linetella	0.41	Scoparia basistrigalis	0.52
			Idaea aversata	0.50
			Peribatodes rhomboidaria	0.48

Note: Shown in the table are only those species with an indicator value >0.4 and with a probability of >0.05 to show up preferentially in one year.

within this group (Figure 4). In both reserves, the macrolepidoptera subgroup performed worse than most of the other subgroups, and also worse than the random selections (Figure 3). For microlepidoptera (PsV: 159 species, 9198 individuals, PdC: 146 species in 6185 individuals), in contrast, most correlations with vegetation composition and forest structure were still observable. Overall, the microlepidoptera – together with host-plant specialists – showed the strongest relationship to the finely grained vegetation gradients inside the two nature reserves (Figure 3) and always performed better than random species selections.

The analysis of year-wise indicator species revealed a small set of species that mainly occurred in just one of the three sampling years. Of these, only the agricultural crop pest *Spodoptera exigua* was very abundant in 2015 in both reserves simultaneously, while all the other annual indicator species related to one of the three sampling years differed between PsV and PdC (Table 2). Another agricultural pest species was *Plutella xylostella*, which showed up as very abundant species in 2016, yet only in PsV. Both of these pest species, as well as the indicators *Athetis hospes*, *Nomophila noctuella* and *Cyclophora puppilaria* are known as long-distance migrants (Fu et al., 2014; Jiang et al., 2010; Pedgley et al., 1995; Sparks et al., 2007). In 2017, especially lichen, moss and detritus feeders showed up as indicator species (*Eilema depressa*, *Eudonia mercurella*, *Scoparia basistrigalis*, *Idaea aversata*). Otherwise, the identity of these 'indicators' did not reveal any clear pattern. Species of dry open grassland (*Chiasmia clathrata*,

Isturgia arenacearia) were found in the list besides wetland (*Schrankia costaestrigalis*) or woodland moths (*Sciota rhenella*, *Peribatodes rhomboidaria*).

DISCUSSION

How did different subsets of moth communities perform, when they were used to analyse relationships with environmental variation? First of all, our findings were more or less consistent among the two reserves, indicating that our findings on the suitability of different subsets to detect responses to small-scaled shallow environmental gradients can likely be generalised. Nevertheless, more studies also including other regions and habitat types are needed. Local site factors explained between 14% and 26% of the variation in the species composition of the analysed moth datasets. Including weather effects like temperature and air humidity further increased explained variation up to 53%. The remaining unexplained variation can partly be attributed to landscape-scale factors, which are known to affect local moth assemblages (Uhl et al., 2021c). Altogether, contrary to expectation, the various analysed subsets did not show substantial differences in their explanatory power, even though they varied substantially in the number of species and individuals considered. Rather, the outcome was remarkably stable throughout all focal species groups. However, some subsets performed slightly better, which might give hints to a targeted selection of focal groups in future studies, when not 'all' moths can be evaluated, for example, due to limitations in available manpower.

Notably, we found no differences in the performance between abundance data and incidence data. In contrast, incidence data seemed to be less prone to weather fluctuations and therefore more likely reflect the subtle differences in habitat structure. Similar patterns were already observed in previous studies (Brehm & Fiedler, 2004). In their work, they found abundance-based analyses to be dependent on the sample size, with small sample sizes – such as is the case for our study – being prone to weather fluctuations. As a result, it is advisable to obtain more than one nightly sample from a location, as with samples pooled over multiple nights temperature effects on light-trap samples should become ever smaller. Doing so, abundance data can give valuable additional information on the community composition patterns (Brehm & Fiedler, 2004; Hillebrand et al., 2018). However, the array of sites to be surveyed or the manpower available might often constrain the number of nightly replications feasible per site. Consequently, we assume that with small sample sizes, the use of incidence data might be a solution to avoid strong temperature effects. When only incidence data are needed, it is sufficient to identify each species once per sample, which can spare a lot of time on identification work, especially when dealing with species complexes that are only distinguishable by genitalia dissection or by other complex methods. Nowadays, meta-barcoding data are often used to obtain a species incidence matrix.

When looking at the random species selections, taking more species into account had remarkably small effects on the outcome of

matrix regressions. Using 200 instead of 50 species did not substantially ameliorate the proportion of explained variation in the dataset. So, small subsets of species can be as informative as large subsets. This outcome is consistent with previous findings, stating that massive structural redundancies can be observed in moth communities, which means that a small fraction of species can be as informative for species composition studies as a large dataset (Truxa & Fiedler, 2016). Additionally, randomly drawn samples did not perform consistently worse than functional or taxonomic subsets. Therefore, we assume that already within the 50 species subset, the functional trait space is sufficiently reflected. Though consisting of a small fraction of the whole community, such subsets might hence give an adequate picture of the community composition patterns. As a consequence, it might not always be necessary to identify each of the caught moths down to species level. In contrast, it might be sufficient to identify species best as possible but discard for example, highly damaged individuals when identification is no longer possible by external characteristics. Doing so, the time and cost-intensive identification work might be reduced by orders of magnitude. Nevertheless, identification work should not be too focused on species that are easy to identify, as for example, small but ecologically informative species (e.g., small sized host-plant specialists) might then become underrepresented.

In fact, a focus on only one special taxonomic or functional group can have severe effects on the outcome. For example, host plant specialists were especially suitable for detecting relationships with subtle variation in vegetation. Focusing on specialised species with restricted feeding habits, we found the strongest correlations with vegetation composition, which confirms our fourth hypothesis. They performed better when compared to the random selections of similar species richness and therefore, seem especially suitable for gradient analyses. Additionally, specialised species often are considered K-strategists, with lower fecundity per female, lower abundance variation between generations, and therefore lower susceptibility of stochastic population fluctuation (Spitzer et al., 1984). As a consequence, however, they might also be very prone to vegetation changes for example, due to forest management or climate change. In fact, specialised species showed stronger population declines than generalists in recent decades (Roth et al., 2021; Wagner et al., 2021). They react sensitively to land-use intensification (Mangels et al., 2017), landscape simplification (Gámez-Virués et al., 2015) and climatic changes (Thomsen et al., 2016). Zooming into the community composition of specialised species therefore can give a particular insight into biodiversity threats, as these species are likely to react most sensitively.

We expected also small-sized species to perform quite well in explaining small-scaled differences. Small-sized species tend to show higher larval host specificity and were found to have less stochastic variation in population sizes in previous studies (Gaston, 1988). However, for this subset of species, our analyses did not render a consistent outcome. In PdC, compositional differences in small-sized species were to a large part explainable by variation in vegetation characteristics. In PsV, in contrast, small moth species had the lowest explanatory

power. We attribute these reserve-specific results to differences between the two study areas. In PsV, the landscape composition surrounding the reserve is more diverse, resulting in a stronger influence of landscape characteristics on PsV moth communities (Uhl et al., 2021c). The effect of these landscape-scale factors might be the reason for small species performing relatively poorly in PsV, compared to PdC. Small-species, therefore, might be especially valuable for community composition studies, however, they do not only reflect vegetation differences but can also be more strongly constrained by landscape composition around the target habitat. We, therefore, discard our hypothesis that small-sized species are mostly governed by local habitat characteristics. Though, we emphasise giving attention to small-sized species also in future studies to check for their possibly enhanced sensitivity to reflect environmental gradients.

The classification of small-sized species included all species with a wingspan below 25 mm, for example, also small geometrid and noctuid moths. The microlepidoptera subsample, in contrast, was only considering taxonomic families not belonging to the macroheterocera, irrespective of their wingspan. Many microlepidoptera have strong bounds to their hostplants and only fly very short distances (Gaston et al., 1992; Menken et al., 2010). Their suitability to mirror environmental gradients was already shown in previous studies (Uhl et al., 2016). When excluding the so-called microlepidoptera and only using macro-moth species, the influence of year-wise abundance fluctuations and weather conditions became much more pronounced. With about 21%–28% of the variation explained by these stochastic factors, macro-moths in our samples seemed to be much more influenced by temperature, air humidity and abundance fluctuations. The same was observed for the group of moss, lichen and detritus feeders, correlating always highly significantly with temperature and air humidity variation. This might be an effect of temperature-dependent flight-to-light behaviour, with more moths flying actively around at warmer temperatures and being more likely to settle down immediately when temperatures decrease (Wölfling et al., 2016). However, the flight-to-light behaviour of micro-moths so far was not analysed which makes a clear assumption on behavioural differences between macro-and micro-moths to date impossible. Finally, macro-moths, as well as moss, lichen and detritus feeders, seem less useful to analyse shallow environmental gradients. They performed even worse than random selections of similar size, indicating that the inclusion of microlepidopteran communities is crucial when finely nuanced gradients are to be analysed. Metabarcoding here can help to reduce time- and cost-intensive identification work. By applying combined techniques, for example, only using some legs of the insects for metabarcoding and keeping the specimens (Hao et al., 2020), even abundance data may be retained for later analyses.

Having finally a look at the indicator species of the different sampling years, we found quite different species sets, characterising the samples of PsV and PdC in the years 2015, 2016, and 2017, respectively. Only *Spodoptera exigua* showed up as an annual indicator shared between both reserves in 2015. This suggests that in 2015 a population high of this agricultural pest species occurred in the entire landscape around the two reserves, affecting the community

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composition throughout the study region. In contrast, all other species indicative for particular sampling years were reserve specific, which indicates that species-specific abundance peaks did not occur in the entire region. This observation renders analyses based on samples of just one-year prone to artefacts, as one species might be over-abundant only at one site in one year. However, this does not necessarily mean that this species cannot be very abundant at the other site the next year. Long-distance migrants seem especially prone to interannual fluctuations. Therefore excluding such species from analyses might help to get a more clear picture of the local community composition and reduce stochastic fluctuations.

CONCLUSION

Our analyses revealed that moth communities can reflect subtle variation in vegetation within the same forest habitat type. The use of incidence tables did not reduce the power of analyses. On top, the incidence-based analysis was even less prone to the influences of weather on the composition of community samples. Therefore incidence tables can be used for analyses of shallow environmental gradients, especially when only small sample sizes are available. However, the inclusion of abundance data is suggested, when there is a sufficiently high amount of sample replicates, reducing the effect of weather on sample composition. Doing so, valuable information on community composition dynamics can be gained, apart from the mere presence or absence of a species (Hillebrand et al., 2018).

Especially host specialists mirrored the local vegetation composition and were therefore suitable indicators for local environmental variation. Also, microlepidoptera performed quite well in that regard. Yet, this high sensitivity for such fine-nuanced differences underlines also their threat by anthropogenic actions (Roth et al., 2021; Wagner et al., 2021). Macro-moths in contrast showed strong correlations to local weather conditions and also were the most affected by interannual abundance fluctuations. Therefore, the analysis of macro-moth communities might not be as efficient to detect the small-scaled environmental variation. We thus recommend that microlepidopterans should always be included in moth community studies, especially when finely grained shallow ecological gradients are to be analysed.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Britta Uhl and Mirko Wölfling sampled the data in the field. Mirko Wölfling organised permissions and field trips. Britta Uhl made the statistical analysis and wrote the manuscript. Konrad Fiedler was the supervisor of the project, helped elaborate the study design, gave advice on statistical analysis and helped editing the manuscript.

DATA AVAILABILITY STATEMENT
All data that supports the findings of the study are available in the supplementary material. Any further information can always be requested from the corresponding author via email.

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SUPPORTING INFORMATION

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

Figure S1. PCoA ordinations of PsV (left) and PdC (right) plant communities at the 30 light-trap sites each. Vectors indicate some of the vegetation variables which were significantly related to the first two PCoA axes.

Table S1. Species trait matrix.

Table S2. Variation (in %) in moth assemblage composition explained by various predictors, following permutation tests (999 permutations) based on CAP-ordinations.

Appendix S1. Supporting Information.