## ORIGINAL ARTICLE
### Editors' Choice

# Moth communities are shaped by season, weather, elevation, and landscape composition

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[Correction added on 21 July 2025, after first online publication: The copyright line was changed.]

## Abstract

1. Insect community records are strongly influenced by the timing of sampling (e.g. season, weather) and the location of sampling (e.g. elevation, land use). However, we still poorly understand how the combination of these factors affects communities of insects such as moths.

2. We analysed a vast moth community dataset from Switzerland, collected by a single expert over a period of 50 years, containing data on 2.8 million moth individuals (1045 species) and covering the entire annual cycle. We used regression models to relate moth community characteristics (total abundance, species richness, biomass) to season, weather, elevation, and land use (landscape composition).

3. Total abundance, species richness, and biomass showed a clear bimodal seasonal cycle with peaks in early spring and in summer. The different peaks reflected peaks of moth species with different overwintering stages, for example the spring peak was driven by species overwintering as pupae or adults. Moth abundance, richness, and biomass also increased with increasing temperatures at the time of sampling and increased further when precipitation events occurred around warm sampling nights. We also found increases along the elevational gradient and with increasing forest cover.

4. We show how land use, elevation and weather shape moth communities, and that overall community characteristics such as total abundance have distinct peaks across the season. It is therefore important that studies of spatio-temporal changes in moth communities take into account all these factors, such as the under-sampling of early-season communities that often occurs in sampling campaigns.

**KEYWORDS**
community, elevation, forest, insects, land use, Lepidoptera, moths, phenology, season, weather

## INTRODUCTION

Ecological studies of insect communities often rely on samples collected using standardised sampling methods such as trapping. In addition to the choice of sampling method (e.g. Busse et al., 2022), both the timing of sampling, for example, related to seasonal factors and weather conditions, and the location of sampling, for example, related to land use and elevation, can strongly influence the communities that are recorded. To date, the combined effect of timing and location of sampling on insect community characteristics has mostly been addressed in spatially or temporally restricted studies. Analyses based on datasets covering large temporal and spatial scales are therefore needed to improve our understanding of the simultaneous contribution of the different sampling factors to community records. Moths,

which are typically sampled at night using light traps (Jonason et al., 2014), are a highly diverse group of insects and are distributed over large temporal and spatial gradients (New, 2004). This makes them an ideal case to study how insect communities vary with the timing and location of sampling.

Regarding the timing of sampling, the seasonality of insect communities is a critical issue that is often not sufficiently taken into account. In temperate regions, insect communities follow distinct seasonal cycles (Mellard et al., 2019). Thus, the timing of sampling strongly influences the recorded community. When samples are pooled across seasons, which is almost always the case, this can lead to biased conclusions, for example, if phenological shifts are not taken into account (Didham et al., 2020). For moth communities, it is known from previous studies with a limited spatio-temporal scale or taxonomic focus that abundance and species richness show multiple peaks throughout the year (Busse et al., 2022; Hickinbotham et al., 2024; Jonason et al., 2014; Roth et al., 2021), reflecting the different overwintering strategies of moths. A comprehensive analysis of peaks in abundance, richness or biomass across the entire year and covering the whole moth community is, to our knowledge, currently lacking, partly due to the lack of robust data on moth communities throughout the year.

Abiotic conditions at the time of sampling, especially those related to weather conditions, are closely related to the number of insects sampled. Thus, if, for example, weather is neglected in ecological studies, biased conclusions may be drawn (Didham et al., 2020). At foremost, temperature at the time of sampling has been repeatedly found to be positively related to moth abundance, richness or biomass (Beck et al., 2010; Butler et al., 1999; Jonason et al., 2014; Knop et al., 2018; Williams, 1940, 1961; Yela & Holyoak, 1997). The relationship between moth numbers and precipitation, which can be highly variable between sampling events, is less clear. Many studies have found no clear relationship between moth abundance, richness or biomass and precipitation (Beck et al., 2010; Jonason et al., 2014; Williams, 1940; Yela & Holyoak, 1997), while others have found evidence of negative relationships (Butler et al., 1999; Holyoak et al., 1997). At the same time, field observations have repeatedly reported higher flight activity of moths on warm summer nights in the vicinity of a thunderstorm or with light rain (e.g. Wymann et al., 2015). Such observations would imply an interactive effect between temperature and precipitation, which to our knowledge has not been empirically tested. A quantification of the combined effects of temperature and precipitation, including their interaction, is still missing and requires a dataset with a large temporal and spatial extent and samples taken under different weather conditions.

The location of sampling in ecological studies is crucial because insect communities in general, and moth communities in particular, vary along different spatial gradients, such as elevational gradients or land-use gradients (e.g. Dolson & Kharouba, 2024; Uhler et al., 2021). Many biotic and abiotic factors change with elevation, resulting in gradual changes in the characteristics of ecological communities. Species richness, for example, often follows an unimodal pattern with a mid-elevation peak (Dolson & Kharouba, 2024; Rahbek, 2005).

Large-scale studies of moth communities along elevational gradients are rare, but existing evidence also points to a mid-elevation peak in species richness (Beck et al., 2017). With respect to land-use gradients, the composition of the landscape surrounding a sampling location is often clearly related to the insect communities sampled. For months, the proportion of forest has previously been found to be positively related to their abundance and species richness (e.g. Fuentes-Montemayor et al., 2012, 2022; Kühne et al., 2022), probably because forests provide habitat and food for a diversity of species (e.g. Uhl et al., 2021). For agricultural areas, a high proportion of grassland is usually positively associated with moth community characteristics, while a high proportion of cropland is often detrimental (Fox, 2013). With regard to urbanisation, different underlying processes may be associated with moth community characteristics (cf. Fox, 2013). Although urban areas can provide a large amount and diversity of habitats and food resources (Hall et al., 2017), many anthropogenic pressures increase with urbanisation. For example, light pollution has been shown to negatively affect moth communities (van Grunsven et al., 2020). Thus, moth abundance and richness are often negatively associated with urbanisation (Merckx & Dyck, 2019; Sanetra et al., 2024), as is often the case for insect communities in general (e.g. Uhler et al., 2021). How moth communities vary with elevation and landscape composition over large spatial scales, and in combination with season and weather, is not yet well resolved, but is crucial for understanding patterns in ecological datasets and for planning future sampling campaigns.

In this study, we analysed a vast moth dataset collected with light traps by a single expert over 50 years and across all seasons and under various weather conditions in Switzerland, spanning a large elevational gradient. Based on the abundance, species richness, and estimated biomass of macro-moths from this dataset of exceptional spatial and temporal extent, we addressed the following research questions:

Q1 How do recorded moth abundance, richness, and biomass change with season? How are these patterns influenced by the overwintering stage of the different species (egg, larva, pupa, adult)?

Q2 How do recorded moth abundance, richness, and biomass vary with weather conditions (temperature, precipitation, and their interaction)?

Q3 How do recorded moth abundance, richness, and biomass vary along an elevation gradient?

Q4 How does landscape composition relate to recorded moth abundance, richness, and biomass?

We had the following hypotheses:

> **H1.** Seasonal patterns of moth abundance, richness, and biomass follow a multimodal distribution, with distinct peaks associated with peaks of species with different overwintering stages. Adult overwintering species appear first in the year, followed by species overwintering as pupae, species overwintering as larvae, and finally species overwintering as eggs (cf. Uhl et al., 2022).

**H2.** Nights with higher temperatures have higher recorded moth abundance, richness, and biomass. Nights with higher precipitation also have higher moth abundance, richness, and biomass, but only when temperature is high (interactive effect).

**H3.** Moth abundance, richness, and biomass show an unimodal pattern along elevation, with a peak at intermediate elevation.

**H4.** On the one hand, moth abundance, richness, and biomass are higher when there is higher cover of forest and grassland in the landscape. On the other hand, these community characteristics are lower when there is a higher cover of cropland and sealed areas (i.e. urbanised areas).

## MATERIALS AND METHODS

### Moths dataset

The data were collected with light traps over a 50-year period by one of the main experts of the group in Switzerland, Dr. Ladislaus Rezbanyai-Reser (ZOBODAT, 2014–2025), with the aim of describing macro-moth communities (including abundance distribution and phenology) at different sites (cf. Rezbanyai-Reser, 2018). The dataset, hosted by *info fauna* (The Swiss Topic Center on Fauna), contains data on macro-moth abundance at the species level (Table S1.1 in Supporting Information). Light trap samples are used to characterise local moth communities (Truxa & Fiedler, 2013). All attracted moths were collected and killed with a sampling fluid (mostly chloroform). Light traps were operated in two different ways (Figure S1.1): Fixed traps, which were installed for a long period of time (usually several months) and emptied daily by L. Rezbanyai-Reser and helpers during the whole period of their activity, and manual traps, which were installed only on single selected nights and were active for only a few hours (sampling duration from 1 to 13 h). For fixed traps, there was a commonly used trap model ('type 1', used in 154 site–year combinations) and a less commonly used trap model ('type 2', used in 10 site–year combinations) (Figure S1.1). The number of traps installed at a site and the lamps used varied between sampling procedures, sites, and years, but were constant per site within each sampling year. The number of traps varied from one trap up to four simultaneously active traps at a single site (Figure S1.2), but we used pooled data from all active traps per sampling location to avoid bias between traps. Throughout the 50 sampling years, three different lamp types have been used interchangeably for trapping (all mercury lamps with similar light spectra): 150–160 W mercury mixed-light lamps (150–160 W HWL), 80 W mercury mixed-light lamps (80 W HWL), and 125 W mercury vapour lamps (125 W HQL) (Figure S1.3). Where multiple traps were active, multiple lamp types may have been used, resulting in a combined category 150–160 W HWL/125 W HQL.

The dataset includes data from 171 sites spread across Switzerland (Figure S1.4), with distances between sampling sites ranging from 36 m to 334 km (mean pairwise distance 104 km). The sampling sites cover an elevational gradient between 193 m asl. and 2454 m asl. (Figure S1.4) and 49 sampling years (1972–2021; no samples in 2019), resulting in 663 unique site and year combinations. A total of 37,461 nights were monitored, capturing 2,814,187 individuals of 1045 nocturnal macro-moth species (diurnal species captured accidentally were excluded from analyses) (Table S1.1). Some sites with manual traps were in close proximity to each other and usually operated simultaneously on the same nights (34 site groups including 94 sites, with distances between simultaneously active sites ranging from 38 m to 6.1 km). We still treated these sites as separate sites but accounted for their grouping in the statistical models. We also accounted for the possibility of reduced sampling efficiency (i.e. when simultaneously operating a nearby site) by including an additional variable in our models (see below). For fixed traps, we assumed that stretches of 10 nights or more without a single record were due to trap inactivity (e.g. due to malfunction) and we excluded them from the analyses (1614 nights, leaving 35,847 nights). Fixed traps were active on average 194 nights per site and year (range: 5–362 nights), with July 24 being the mean sampling day of the year (range of means: February 3–August 28); manual traps were active on average 8 nights per site and year (range: 1–71 nights), with July 16 being the mean sampling day of the year (range of means: February 3–November 11) (Figure S1.5).

### Weather data

To test how weather conditions during sampling affected moth abundance, richness, and biomass, we determined the temperature and precipitation for each sampling event. We used gridded daily temperature and precipitation data (1.25-degree minute grid; approx. 2.3 × 1.6 km) provided by MeteoSwiss (https://www.meteoswiss.admin.ch) and used the values of the closest grid cell. The mean temperature and total precipitation of the two sampling days enclosing the sampling night were used (2-day average/total).

### Landscape composition

We determined the landscape composition at the study sites based on aerial photo interpretation for the whole of Switzerland in four time steps (1979–1985, 1990–1998, 2004–2009, 2012–2019), in which each hectare square (100 × 100 m) on a grid was assigned a categorical land-use and land-cover value ('Arealstatistik', Bundesamt für Statistik, 2021). We determined the cover of four broad land-use types (forest, grassland, cropland, sealed areas (i.e. paved areas, buildings)) (Table S1.2) in a 500 m radius around the plots. Starting from the centre point of the hectare square of the grid containing the study site, we included all hectare squares whose centre point was within the 500 m radius of this focal point (81-hectare squares). We chose

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the 500 m radius because it covers the dispersal distances of many moth species and is a relevant scale for the different land-use types that were involved (Fuentes-Montemayor et al., 2011). We assigned these land-use covers to the average year of the aerial photos. For sampling years that fell between the four land-use observation times, we linearly interpolated land-use covers from the land-use covers of the two adjacent times (assuming a gradual change in land-use cover composition). For sampling years before the first year with available land-use data (~1982) or after the last year with available land-use data (~2015), we used the proportions of the nearest year, following a conservative scenario of no change. We used the land-use covers per year (1972–2021) and sampling sites as explanatory variables in the regression models (see below).

## Statistical analyses

We used R version 4.2.0 (R Core Team, 2022) for all statistical analyses. Codes are available from the online repository deposited at Zenodo https://doi.org/10.5281/zenodo.14439274 (Neff, 2025).

For each sampling night, we calculated three community characteristics: total abundance (sum of individuals of all species), species richness, and total biomass. To account for differences in sample coverage, we determined species richness corrected for sample coverage with the package 'iNEXT' (Hsieh et al., 2024). We estimated total biomass from species-level dry mass, which we determined from forewing length with an allometric equation of the form 'ln(mass) $\sim$ ln (forewing length) $\times$ taxonomic family' (Kinsella et al., 2020). We compiled species-level wingspan data, which are more readily available than forewing-length data, from Jonko (2002–2024) ($n = 981$) and supplemented them with data from other sources (Fibiger, 1990; Potocký et al., 2018; Ronkay et al., 2001) ($n = 12$). Based on data from a subset of study species (Cook et al., 2022), we determined a linear relationship between forewing length and wingspan, which we used to estimate forewing length for all study species. Finally, we used these data to estimate species dry mass. For species where forewing length could not be retrieved ($n = 13$), we estimated dry mass from congeneric species.

The three community characteristics were our response variables in Bayesian regression models. We used a zero-inflated negative binomial response distribution for abundance (log link) and a hurdle gamma distribution for richness and biomass (log link), which yielded high agreement between posterior predictive and empirical data distributions (Figure S1.6). We fitted one global model per response variable, including a set of predictor variables covering all study hypotheses and correcting for sampling specifics. In all models, we standardised continuous predictor variables to mean 0 and standard deviation 1 prior to analyses. We used sum-to-zero contrasts for nominal factor variables.

All models included a spline-based smoothing term for the day of the year to quantify seasonal patterns (H1), linear terms for weather parameters of the night of sampling (temperature, precipitation, and their interaction) (H2), a spline-based smoothing term for the

elevation of the study site (mean elevation over a one-hectare square containing the study site) (H3), linear terms for the four land cover variables (proportions of forest, grassland, cropland, sealed areas) (H4), and a set of linear terms and random intercepts to correct for sampling specifics (see below). Although the dataset would allow an analysis of long-term temporal trends in moth community characteristics, the focus of this study was on the relationships between moth community characteristics and the timing and location of sampling, so we did not include sampling year as a fixed factor in the analyses but accounted for it in the random structure. To further examine how seasonal patterns are influenced by species with different overwintering strategies (H1), we divided the dataset by overwintering stage (egg, larva, pupa, adult) and fitted the same models to these subsets of data. We report only the results related to the season for these subset models, as only these were part of our study hypotheses. We collected data on overwintering stages from several trait collections (Cook et al., 2022; Mangels et al., 2017; Potocký et al., 2018) and supplemented them with data from additional moth trait databases (Jonko, 2002–2024; Ziegler, 2005–2024).

To account for the sampling design, all models included a set of additional fixed and random factors. The fixed effects were trap type (fixed type 1, fixed type 2, or manual), lamp type (four-level nominal factor), number of traps (four-level ordinal factor), a two-level nominal factor indicating whether the site has been sampled the previous night to account for persisting attraction of light traps, and a two-level nominal factor indicating whether multiple nearby sites were operated simultaneously. We also added a spline-based smoothing term to account for sampling duration. Data on sampling duration were only available for 2 800 of the 4 024 manual sampling nights. For nights with missing data on sampling duration, we assumed an average sampling duration. We chose a smoothing term rather than a linear effect because we expected moth activity to change over the course of a night (e.g. Ma & Ma, 2013). The random structure consisted of the site ID ($n = 171$), the combination of the site ID and year ($n = 663$), a factor to account for sampling night, where nearby sites operating on the same night are grouped together ($n = 34,390$), and a spatio-temporal grouping factor of study sites to account for variability between regions and years ($n = 249$). We defined the spatio-temporal grouping factor so that all sites in a given year that were less than 20 km apart were grouped together. In this way, nearby sites were grouped together, but the grouping did not cross major biogeographic barriers such as high mountain ranges. We report the results for fixed and random factors related to sampling design in Table S1.3 and Figure S1.7.

We used Bayesian models to analyse the data. We built the basic structure of all models using 'brms' (Bürkner et al., 2023) with standard calls for generalised linear models, and then manually adapted the underlying Stan code for more flexibility. We ran the final models through 'rstan' (Guo et al., 2023) (4 Markov chain Monte Carlo chains of 2000 iterations each, including 1000 warm-up iterations). Priors followed the default settings of the 'brms' package representing weakly informative priors (details available in the online code repository). We evaluated model results based on posterior distributions of

model predictions. All codes used to fit the models and extract model predictions are available from the online repository (Neff, 2025).

We used the mean and 95% symmetric credible intervals (CIs) based on the 2.5% and 97.5% quantiles to summarise the posterior distributions. To check whether the four chains mixed well, we calculated Rhat statistics for estimates of intercepts, fixed-effect slopes and spline coefficients (smoothing terms) using the package 'rstan' (Guo et al., 2023). All values of all final models met the standard threshold of 1.1. While the random structure of our models accounted for the spatial arrangement of samples, we additionally checked for spatial autocorrelation in model residuals using variograms generated with the 'fields' package (Nychka et al., 2024). The variograms showed no evidence of spatial autocorrelation (Figure S1.8).

# RESULTS

## Season and weather

All three moth community characteristics (abundance, richness, biomass) showed a clear seasonal pattern with two distinct peaks (Figure 1). The first peak, which was slightly lower (abundance, biomass) than the second peak or only evident as a plateau (richness), occurred at the end of March (maximum on March 24 for abundance and biomass). The second peak was reached in mid-July (July 13 for abundance and biomass, July 9 for richness) and for abundance and biomass was followed by a plateau peaking again in mid-August (August 10 for abundance, August 12 for biomass). The individual peaks were reflected in subsets of the dataset defined by the overwintering stages of the species (Figure 1). At the time of the first peak, we observed a peak in the species overwintering as pupae and in the few species overwintering as adults. At the time of the second peak, species overwintering as larvae had a coinciding peak. Also, all community characteristics of species overwintering as pupae had a second peak at this time, which was however clearly lower than the first peak for abundance and biomass. Species overwintering as eggs, which are rarer than those overwintering as larvae or pupae, peaked late in the year (between October 17 and November 4). Around the same time, the decline in the overall community characteristics was slightly mitigated.

With respect to weather conditions, we observed a clear and strong increase in all community characteristics with increasing sampling night temperatures (Figure 1, Table S1.3). An increase in sampling night temperature by 50% of its range (corresponding to an increase of 17.2°C) was associated with an increase of abundance by a factor of 9.81 (95% CI: 9.10–10.60), of richness by a factor of 6.07 (95% CI: 5.73–6.45), and of biomass by a factor of 5.16 (95% CI: 4.80–5.55) (Table 1). For a 5°C increase in temperature, the factors are 1.94 (95% CI: 1.90–1.99; abundance), 1.69 (95% CI: 1.66–1.72; richness), and 1.61 (95% CI: 1.58–1.65; biomass). The relationship with precipitation on the 2 days containing the sampling night was weaker and dependent on temperature, as evidenced by an interactive effect of temperature and precipitation (Figure 1, Table S1.3). At

the maximum temperature (27.7°C), a 50% increase in precipitation (corresponding to 140 mm) had a predicted increase in abundance by a factor of 1.78 (95% CI: 1.28–2.47), in richness by a factor of 1.30 (95% CI: 0.99–1.70), and in biomass by a factor of 1.67 (95% CI: 1.19–2.34). These factors decreased to 1.11 (95% CI: 1.01–1.23; abundance), 0.99 (95% CI: 0.92–1.08; richness), and 1.19 (95% CI: 1.08–1.31; biomass) at the median temperature (12.5°C), and to 0.62 (95% CI: 0.40–0.96; abundance), 0.70 (95% CI: 0.51–0.99; richness), and 0.78 (95% CI: 0.52–1.16; biomass) at the minimum temperature (−6.7°C).

## Elevation and landscape composition

All three community characteristics increased with elevation, with nearly linear increases for abundance and biomass (Figure 2, Table S1.3). An increase in elevation by 50% of its range (corresponding to an increase of 1130 m) was associated with an increase of abundance by a factor of 3.39 (95% CI: 2.55–4.52) and of biomass by a factor of 3.56 (95% CI: 2.69–4.72) (Table 1). For richness, the increase at lower elevations reached a plateau at about 1250 m asl (Figure 2). For abundance and biomass, such a plateau was only indicated after about 2000 m asl (Figure 2).

Regarding the effects of the landscape variables (Figure 3, Table S1.3), there was strong evidence that community characteristics were higher when surrounding forest cover was high. When forest cover within 500 m of the plot was higher by 50% of its range (corresponding to an approx. proportion of 0.5), abundance was higher by a factor of 1.91 (95% CI: 1.46–2.52), richness by a factor of 1.41 (95% CI: 1.16–1.69), and biomass by a factor of 1.72 (95% CI: 1.33–2.28) (Table 1). There was also a tendency for all community characteristics to be higher with an increasing proportion of sealed areas in the plot surroundings. When the cover of sealed areas (paved areas, buildings) was higher by 50% of its range (corresponding to a proportion of 0.16), abundance was estimated to be higher by a factor of 1.27 (95% CI: 1.00–1.66), richness by a factor of 1.14 (95% CI: 0.97–1.36), and biomass by a factor of 1.25 (95% CI: 0.97–1.61) (Table 1).

# DISCUSSION

We expected the seasonal pattern of moth community characteristics to follow a multimodal distribution due to distinct peaks of species with different overwintering stages (H1), which our results confirmed. When moth community characteristics were related to the day of the year, two distinct peaks were evident: one in early spring and one in summer. The spring peak was associated with high numbers of species overwintering as pupae or adults, while the summer peak was associated with species overwintering as larvae or pupae. In autumn, egg-overwintering species peaked, which was also evident in the seasonal pattern of the total community as a clear plateau. As such, the three peaks correspond well with recent results on a smaller set of moth species (Hickinbotham et al., 2024). While the summer peak is
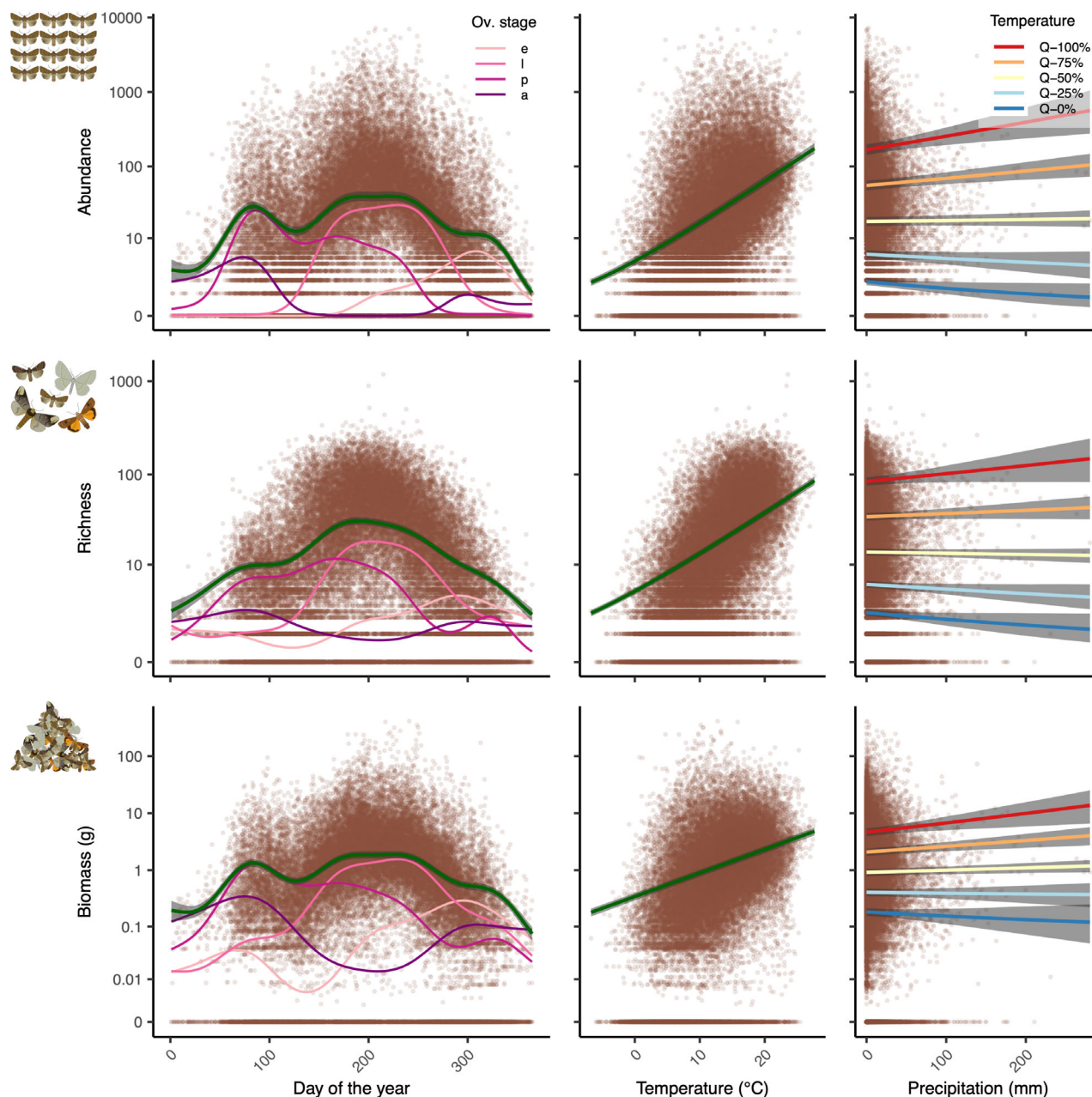
**FIGURE 1** Conditional effects of different model covariates related to season (day of the year) and weather during sampling. For the season, conditional effects from models run on subgroups defined by the overwintering stage (e: Egg; l: Larva; p: Pupa; a: Adult) are shown alongside the conditional effects from the full model. For weather, the main effect of temperature and the combined effect of temperature and precipitation (including their interaction) are shown. To show the interaction, predictions for different quartiles of the temperature range are included (top right legend). The y axis shows (predicted) abundance, richness or biomass per sampling night. Lines show point estimates; shaded areas are 95% credible intervals. The underlying points show data per sampling night ($n = 35,847$). Note that the y axes are on the log scale (after adding the minimum non-zero value to all values). Detailed model results are presented in Table S1.3.

consistent with results from several previous studies (Busse et al., 2022; Jonason et al., 2014; Roth et al., 2021), there is at best some indication of the spring peak in these studies, as sampling only started around this time. Starting sampling campaigns too late in the year may result in systematic under-sampling of species groups that overwinter as pupae or adults. Similarly, the late autumn peak for species overwintering as eggs shows that ending sampling campaigns too

early in the year results in an under-sampling of this group. As the overwintering stage has regularly been linked to species' vulnerability to global change drivers such as climate change or land-use intensification (Forsman et al., 2016; Keret et al., 2020; Mangels et al., 2017; Mattila et al., 2006, 2008), limited sampling within the season may lead to biased conclusions. Furthermore, the observed spring peak was rather narrow. If species phenologies shift within years due to

**TABLE 1** Model predictions of the change in moth abundance, richness, and biomass (g) when a variable is increased by 50% of its range of occurring values (indicated in the '50% step' column). Numbers are factors by which the response variable changes. Point estimates (Est.) and 95% credible intervals (CI) are given. Grey shading indicates variables for which the 95% CI does not include 1.

| Variable | 50% step | Abundance | | | Richness | | | Biomass | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Est. | Lower 95% CI | Upper 95% CI | Est. | Lower 95% CI | Upper 95% CI | Est. | Lower 95% CI | Upper 95% CI |
| Temperature[a] | 17.2°C | 9.81 | 9.10 | 10.60 | 6.07 | 5.73 | 6.45 | 5.16 | 4.80 | 5.55 |
| Elevation[b] | 1130 m | 3.39 | 2.55 | 4.52 | – | – | – | 3.56 | 2.69 | 4.72 |
| Prop. forests | 0.494 | 1.91 | 1.46 | 2.52 | 1.41 | 1.16 | 1.69 | 1.72 | 1.33 | 2.28 |
| Prop. grasslands | 0.488 | 0.99 | 0.71 | 1.34 | 0.95 | 0.78 | 1.17 | 1.00 | 0.73 | 1.36 |
| Prop. croplands | 0.443 | 0.99 | 0.69 | 1.46 | 0.90 | 0.70 | 1.12 | 0.99 | 0.69 | 1.41 |
| Prop. sealed area | 0.162 | 1.27 | 1.00 | 1.66 | 1.14 | 0.97 | 1.36 | 1.25 | 0.97 | 1.61 |

[a]The main effect of temperature clearly exceeds the interactive temperature–precipitation effect and is therefore reported here. For precipitation, the main effect is strongly overlaid by the interactive effect, so it is not reported here.

[b]Term is included as a smoothing term. Because the prediction is close to linear for abundance and biomass, change factors still harbour useful information. The values are the means across 100 different 50% ranges.
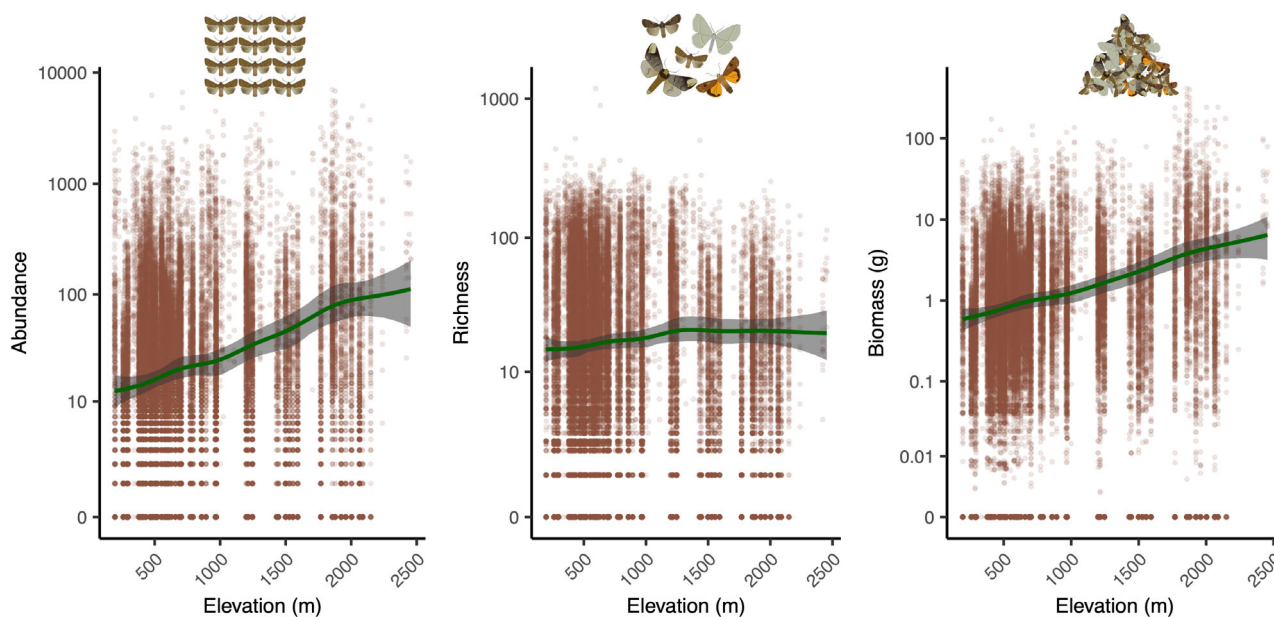


**FIGURE 2** Conditional effects of elevation of the sampling location on moth abundance, richness, and biomass. The y axis shows (predicted) abundance, richness or biomass per sampling night. Point estimates are in green, shaded areas show 95% credible intervals. The underlying points show data per sampling night (n = 35,847). Note that the y axes are on the log scale (after adding the minimum non-zero value to all values). Detailed model results are presented in Table S1.3.

climate change (Duchenne et al., 2020), while sampling schemes are not adapted to these shifts, false conclusions about temporal trends may be drawn (Didham et al., 2020).

We expected higher moth abundance, richness, and biomass on nights with higher temperatures (H2), which was strongly supported by our results. All moth community characteristics increased with increasing temperature, which is consistent with previous findings (Beck et al., 2010; Butler et al., 1999; Jonason et al., 2014; Knop et al., 2018; Yela & Holyoak, 1997) and reflects an increase in moth activity with increasing temperature. The magnitude of the effect was estimated to be a 50%–100% increase in community characteristics for a temperature increase of only 5°C (while correcting for elevation and season),

which is substantial and needs to be considered when analysing datasets covering nights with fluctuating temperatures. In addition, we found the expected interactive effect between temperature and precipitation, with precipitation having a positive effect on sampling numbers on warm nights only (H2). While field observations have repeatedly suggested such an effect (e.g. Wymann et al., 2015), it has, to our knowledge, not been rigorously tested before. It is important to note that we quantified precipitation over the 2 days surrounding the sampling night, so precipitation events did not necessarily coincide with sampling events. Our results suggest that moths prefer warm nights with high humidity, resulting in higher sampling numbers (van Langevelde et al., 2011; Williams, 1940). While temperature was the
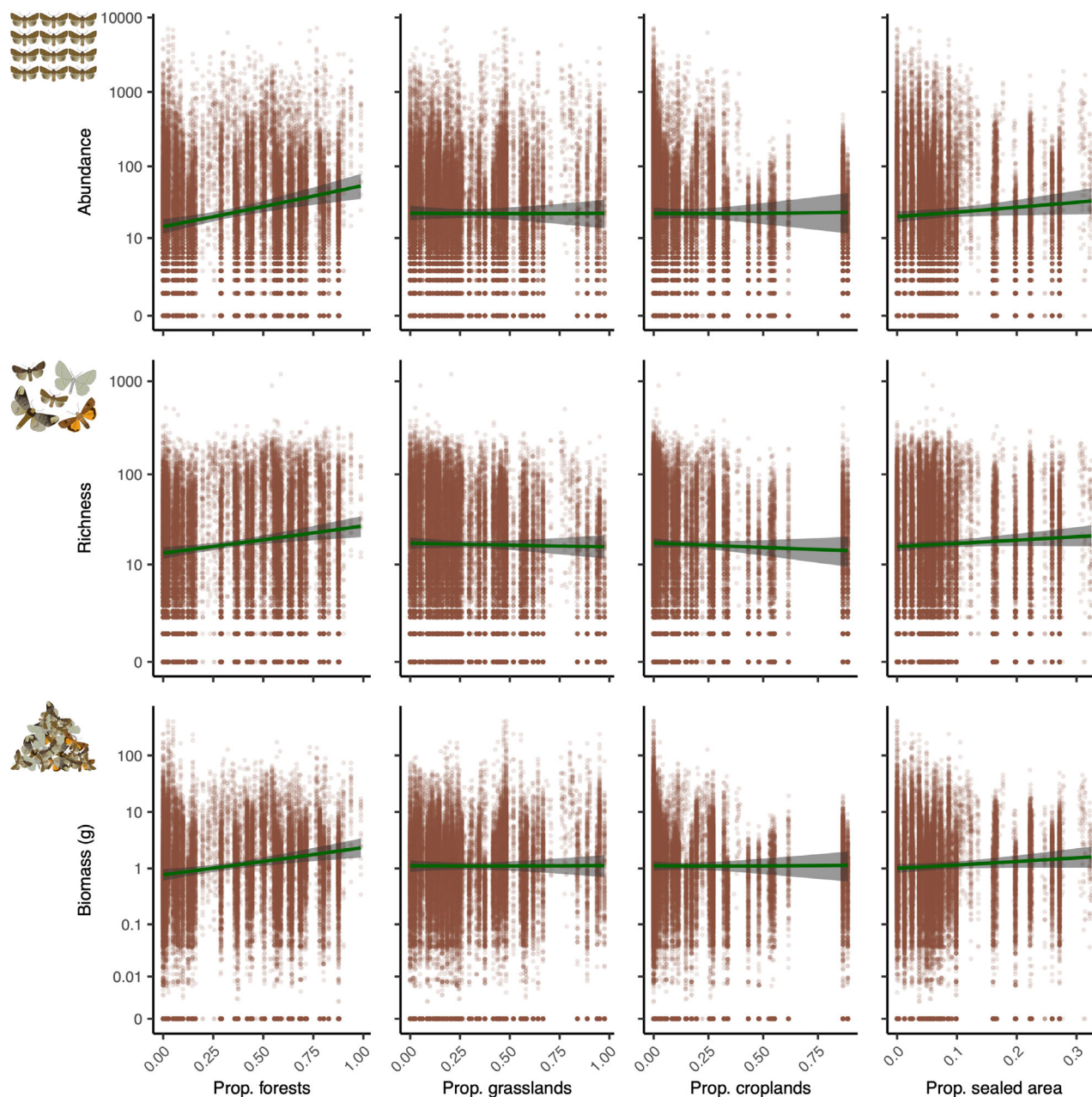
**FIGURE 3** Conditional effects of different landscape variables on moth abundance, richness, and biomass. Landscape variables are the cover of different land-use types (forest, grassland, cropland, sealed area) within a 500 m radius around the study site. The y axis shows (predicted) abundance, richness or biomass per sampling night. Point estimates are in green, shaded areas show 95% credible intervals. The underlying points show data per sampling night ($n = 35{,}847$). Note that the y axes are on the log scale (after adding the minimum non-zero value to all values). Detailed model results are presented in Table S1.3.

main weather parameter driving moth numbers, we were able to show that precipitation can amplify the temperature effect.

Based on previous results on species richness patterns along elevation for different insect groups (Dolson & Kharouba, 2024; Rahbek, 2005) as well as for moths (Beck et al., 2017), we expected an unimodal pattern of moth community characteristics along elevation, peaking at intermediate elevation (H3). Our results only partially supported this hypothesis. We found a clear increase in abundance and biomass along the studied elevational gradient, levelling off at about 2000 m asl. As our dataset included a few sites above 2000 m

asl and none above 2500 m asl, the observed pattern indicates an unimodal pattern with a peak at about 2000 m asl. At the same time, the increase in richness already levelled off at about 1250 m asl, but also no decrease in richness was found at higher elevations. Thus, our results may indicate a peak in moth community characteristics somewhere between 1250 and 2000 m asl. This would be consistent with previous data on moths in the Alps, which indicate an unimodal peak, whose position depends on the season but moves as high as 1800 m asl (Beck et al., 2010), and with data from several other arthropod groups in the Alps (Fontana et al., 2020). The underlying drivers of

such an unimodal pattern could be manifold (Beck et al., 2017; Hodkinson, 2005; McCoy, 1990). For the gradient studied, land-use-related pressures, as well as light pollution, are lower in the less densely populated areas at higher elevations (Becker et al., 2007), which could at least partly explain some of the observed increase in moth community characteristics with elevation.

We expected moth community characteristics to be positively associated with cover of forest and grassland in the landscapes surrounding the sampling locations, and negatively associated with cover of cropland and sealed areas (i.e. urbanised areas) (H4). Indeed, we found strong positive relationships of all moth community characteristics with forest cover. More moths were present when forest cover was high, highlighting the importance of forests in maintaining high moth abundance and richness (Fuentes-Montemayor et al., 2012, 2022; Kühne et al., 2022). While we did not find support for the hypotheses related to agricultural land (grassland, cropland), there was some evidence of a positive effect of a higher cover of sealed areas, that is of urbanised areas, which clearly contradicts our hypothesis. Urbanised areas may provide additional floral resources for moth communities (Hall et al., 2017), which could explain this positive relationship. Further research is needed to understand why the potentially negative effect of higher light pollution (van Grunsven et al., 2020) was not evident in these urbanised landscapes. Clearly, our results show that promoting forest elements in the landscape mosaic is an important measure to support diverse and abundant moth communities (cf. Fuentes-Montemayor et al., 2022).

Based on a moth community dataset of unusually large spatial and temporal extent, we were able to evaluate the relationships between different moth community characteristics and the timing (season, weather) and location (elevation, landscape composition) of sampling. The bimodal seasonal pattern, with two distinct peaks in all community characteristics (abundance, richness, biomass), will help to better evaluate and understand the results of smaller-scale studies, plan future sampling campaigns and target conservation efforts. We also provide a robust estimate of the positive effect of night-time temperatures on sampling numbers and show that precipitation at high temperatures can further increase the number of moths recorded. The increase in moth numbers along the elevational gradient studied highlights the importance of high-elevation habitats for the conservation of moth diversity. At the same time, lower numbers of moth individuals and species at low elevations may be related to multiple anthropogenic pressures, such as intensive land use and light pollution, which are more prevalent at lower elevations. We also confirmed the positive relationship between moth community characteristics and forest cover. In addition to reducing anthropogenic pressures such as light pollution, preserving and promoting forests and other woody elements, particularly in low-elevation landscapes, may be key to maintaining diverse and abundant moth communities in a changing world.

## AUTHOR CONTRIBUTIONS

**Felix Neff:** Conceptualization; investigation; writing – original draft; writing – review and editing; software; data curation; visualization; methodology. **Yannick Chittaro:** Data curation; writing – review and editing; validation; resources. **Fränzi Korner-Nievergelt:** Conceptualization; writing – review and editing; methodology. **Glenn Litsios:** Writing – review and editing; data curation; resources. **Emmanuel Rey:** Data curation; writing – review and editing; resources. **Eva Knop:** Conceptualization; supervision; methodology; writing – review and editing; project administration.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The raw moth record data are hosted by info fauna and protected by a code of conduct but can be obtained from info fauna on request if in accordance with this code of conduct (https://www.infospecies.ch/de/daten). Moth record data with coarser spatial resolution and with a unique identifier for the sampling location and sampling details necessary to reproduce the models are available from the GBIF database https://doi.org/10.15468/dl.gcagva (GBIF.org, 2024). The weather data are under restricted access but can be obtained directly from MeteoSwiss (https://www.meteoswiss.admin.ch). Other data and codes needed to reproduce the analyses are available from Zenodo https://doi.org/10.5281/zenodo.14439274 (Neff, 2025).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1.** Supporting Information.