#### Bimodal seasonal activity of moths and elevation, weather and land use as

#### drivers of their diversity

3	Authors:	Felix Neff <sup>1</sup> , Yannick Chittaro <sup>2</sup> , Fränzi Korner-Nievergelt <sup>3</sup> , Glenn Litsios <sup>2</sup> ,
4		Emmanuel Rey <sup>2</sup> , Eva Knop <sup>1,4</sup>
5		1: Agroecology and Environment, Agroscope, Reckenholzstrasse 191, 8046
6		Zurich, Switzerland
7		2: info fauna, Avenue de Bellevaux 51, 2000 Neuchâtel, Switzerland
8		3: Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland
9		4: Department of Evolutionary Biology and Environmental Studies, University
10		of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
11	Correspondir	ng author:
12	Felix Neff, m	nail@felixneff.ch
13	ORCIDs: Fel	lix Neff 0000-0001-7266-2589, Yannick Chittaro 0000-0003-0236-5110, Fränzi
14	Korner-Niev	ergelt 0000-0001-9081-3563, Glenn Litsios 0009-0000-0712-0337, Emmanuel
15	Rey 0000-00	03-0026-7007, Eva Knop 0000-0001-9402-2216
16		

#### 17 ABSTRACT

18 Moths are an important part of terrestrial insect diversity and contribute substantially to eco-19 system functioning. Yet, how their activity varies with the season and how different biotic 20 and abiotic factors (elevation, weather, land use) are simultaneously linked to moth commu-21 nity characteristics are still poorly understood.

We analysed a vast moth community dataset from Switzerland collected by a single expert across 50 years containing data of 2.8 Mio moth individuals (1,045 species), covering the whole yearly cycle. Using regression models, we related moth community characteristics (total abundance, species richness, biomass) to season, elevation, weather and land use (landscape composition).

Moth community characteristics showed a clear bimodal seasonal cycle with an activity peak in early spring and one in summer. The different peaks could be clearly linked to moth species with different overwintering stages, i.e. the spring peak was driven by species overwintering as pupae or adults. Along the elevational gradient, we found increases of all moth community characteristics, levelling of at around 2000 m asl. Also, moth activity increased significantly with increasing temperatures and was higher in landscapes with higher proportions of forests.

Based on a moth dataset of unseen extent, we present a well resolved seasonal activity pattern and quantify the role of elevation, landscape composition (forests) and weather (temperature) in driving moth community characteristics. These results will help to better understand variation in moth activity across different temporal and spatial scales and to design targeted conservation efforts, e.g. in lower elevation sites.

#### **39 INTRODUCTION**

40 Moths make up the largest share of the species-rich insect group of lepidopterans, but have 41 been receiving less research interest compared to the popular butterflies (New, 2004). This is 42 despite their important role in ecosystems such as pollinators (Knop et al., 2017; Walton et 43 al., 2020) or food source for bats (Vaughan, 1997) and birds (Evans et al., 2024). Moth com-44 munities cover species with various ecological strategies, resulting in community changes 45 along biotic and abiotic gradients. Also, moths are susceptible to various global change driv-46 ers such land use intensification (Mangels et al., 2017), climate change (Hunter et al., 2014) 47 or light pollution (Knop et al., 2017; van Grunsven et al., 2020). The latter is related to their 48 nocturnal activity and their attraction to artificial light sources, which allows to quantify and 49 characterise activity of nocturnal moths using light trap sampling (Jonason et al., 2014). Yet, 50 how moth activity varies over the season and which parameters drive their abundance, spe-51 cies richness and biomass is still poorly understood. Here, we studied how these moth com-52 munity characteristics change over the course of the year and how they are related to different biotic and abiotic drivers (elevation, weather, land use). 53

54 In temperate regions, insects have distinct seasonal cycles, but these cycles have been insuffi-55 ciently quantified because observational studies, including studies on moths, often have tem-56 porally limited sampling schemes. Consequently, often a unimodal activity pattern is as-57 sumed, with one single activity peak of adults during the vegetative period, similar to diel ac-58 tivity peaks. However, recent evidence on different insect groups indicates that neither diel 59 (Knop et al., 2023; Xu et al., 2021; Zoller et al., 2020) nor seasonal activity (Mellard et al., 60 2019) show unimodal patterns by default. In the case of moths, it is also highly unlikely that 61 there is only a single activity peak of adults during the vegetative period, given their high 62 species richness and their different overwintering strategies, with species overwintering as

63 egg, larvae, pupae, and adults. However, except for a few studies that analysed the intra-an-64 nual variability of moth activity over part of the seasonal cycle (Busse et al., 2022; Jonason et 65 al., 2014; Roth et al., 2021) and indicate variability in activity peaks, a comprehensive analy-66 sis of moth activity peaks over the entire year is missing so far, most likely due to the lack of 67 suitable data. Insufficient understanding of intra-annual variation of insect communities is 68 problematic (Montgomery et al., 2021), as important population changes of species due to 69 global change might be missed, namely of those active early or late in the season, resulting in 70 biased conclusions on susceptibility of moth communities to global change and its conse-71 quences for the provision of ecosystem services.

72 Besides changes in moth community characteristics across the season, moth communities are 73 driven by various biotic and abiotic factors. These factors might vary spatially between sam-74 pling sites, but also temporally between days of sampling. For example, the proportion of 75 suitable habitats in a landscape surrounding a sampling site (e.g. forests) is often positively 76 linked to moth abundance and species richness (e.g. Kühne et al., 2022). Also, it has been 77 found that elevation is a driver of moth communities, with highest richness at mid-elevation 78 sites (Beck et al., 2017). Furthermore, weather conditions (temperature, precipitation) are 79 crucial factors linked to moth activity, which vary on a daily basis and result in more individ-80 uals and species of moths being caught during nights in which temperature is higher (Beck et 81 al., 2010; Jonason et al., 2014; Knop et al., 2018). However, large-scale studies on how moth 82 communities are driven by these abiotic and biotic factors are still rare, and their relative im-83 portance is so far not well resolved. Better knowledge on the most important drivers of moth 84 community characteristics is however crucial to design specific and efficient conservation 85 measures.

In this study, we analyzed a vast dataset collected by a single expert across 50 years and
throughout the seasons in Switzerland, spreading across a large elevational gradient. Based

88	on macro-moth abundance, species richness and estimated biomass from this dataset, we ad-
89	dressed the following research questions:

90	1. How do moth abundance, richness and biomass change with seasons? How are these
91	patterns influenced by species with different overwintering stages (egg, larva, pupa,
92	adult)?
93	2. How do moth abundance, richness and biomass vary with weather conditions (tempera-
94	ture, precipitation)?
95	3. How do moth abundance, richness and biomass change along an elevation gradient?
96	4. How does landscape composition relate to moth abundance, richness and biomass?

#### 98 **Methods**

#### 99 Moths dataset

100 The data were collected with light traps across a 50-year timespan by one of the main experts 101 of the group in Switzerland, Dr. Ladislaus Rezbanyai-Reser (ZOBODAT, 2014-2023), with 102 the purpose to describe the macro-moth communities (including abundance distribution and 103 phenology) at different sites (cf. Rezbanyai-Reser, 2018b). The dataset, which is hosted by 104 info fauna (The Swiss Topic Center on Fauna), contains species-level abundance data of 105 macro-moths (Table S1.1 in Supporting Information). The light trap samples allow character-106 isation of local nocturnal moth communities (Truxa & Fiedler, 2013). All attracted moths 107 were collected and killed with a sampling fluid (mostly chloroform). Light traps were oper-108 ated in two different ways (Fig. S1.1): Fixed traps, which were installed for a long period 109 (mostly several months) and emptied daily over the whole period in which they were active, 110 and manual traps, which were installed only in single selected nights and which were only active for some hours (sampling duration of 1-13 hours). For fixed trapping, there was a com-111 112 monly used trap model ("type 1", used in 154 site-year combinations) and a more rarely used 113 trap model ("type 2", used in 10 site-year combinations). The number of traps installed at a 114 site and the lamps used differed between sampling procedures, sites, and years. The number 115 of traps varied from one trap up to four simultaneously active traps at a single site (Fig. S1.2), 116 but moth data were only available for the pooled samples of all active traps. Three lamp types can be distinguished, which were used differently often: 150-160W mercury mixed-light 117 118 lamps (150–160W HWL), 80W mercury mixed-light lamps (80W HWL) and 125W mercury 119 vapour lamps (125W HQL) (Fig. S1.3). When several traps were active, several lamp types might have been used, resulting in a joint category 150–160W HWL/125W HQL. 120

121 The dataset holds data from 171 sites spread across an elevational gradient between 193m asl. 122 and 2454m asl. in Switzerland (Fig. S1.4) and from 49 years (1972-2021; no samples in 123 2019), entailing 663 unique site and year combinations. A total of 37,461 nights were moni-124 tored, in which 2,814,187 individuals of 1,045 nocturnal macro-moth species (Table S1.1) 125 were caught (day active species that were accidentally collected were excluded from anal-126 yses). Some sites with manual traps were in proximity and normally ran simultaneously in the 127 same nights (34 site groups including 94 sites, distances between simultaneously active sites 128 ranging from 38m to 6.1km). These sites were still treated as separate sites, but their group-129 ing was accounted for in the statistical models. For fixed traps, we assumed that stretches of 130 10 or more nights without a single record were due to inactivity of a trap (e.g., due to mis-131 functioning) and we excluded them from analyses (1614 nights, leaving 35,847 nights). Fixed 132 traps were on average active for 194 nights per year (range: 5–362 nights) with July 24 being 133 the mean sampling day of the year (range: Feb 3 – Aug 28); manual traps in a site were on 134 average active for 8 nights per year (range: 1-71 nights) with July 16 being the mean sam-135 pling day of the year (range: Feb 3 – Nov 11) (Fig. S1.5). To test how weather conditions 136 during sampling affect moth activity and thus sampling numbers, we determined the tempera-137 ture and precipitation for each sampling night. We used gridded daily temperature and pre-138 cipitation data (1.25 degree minute grid; approx. 2.3 km × 1.6 km) provided by MeteoSwiss 139 (https://www.meteoswiss.admin.ch) and used the values of the closest grid cell. Mean tem-140 perature and total precipitation of the two sampling days enclosing the sampling night were 141 used (2 days average/total).

# 142 Landscape composition

Landscape composition at the study sites was determined based on aerial photo interpretation
for the whole of Switzerland at four time steps (1979–1985, 1990–1998, 2004–2009, 2012–

145 2019), which attributed each hectare a categorical land-use and land-cover value ("Are-146 alstatistik", Bundesamt für Statistik, 2021). We determined the cover of four broad land-use 147 types (forests, grasslands, croplands, sealed area) (Table S1.2) in the surroundings of the 148 study plots. For forest and grassland cover, we expected positive relations to moth commu-149 nity characteristics, as they may provide valuable habitats (Archaux et al., 2018). For 150 cropland cover, we expected negative relations to community characteristics as the barely 151 provide habitats and might even be detrimental e.g. due to higher amounts pesticide being 152 present (Archaux et al., 2018; Brühl et al., 2021). Cover of sealed area was used as a proxy of 153 urbanisation, for which we might expect negative effects e.g. due to light pollution (van 154 Grunsven et al., 2020), but could also envision positive relations e.g. due to availability of 155 more diverse food plants (Hall et al., 2017). The cover of these land-use types was deter-156 mined in a 500m radius around the plots. Starting from the centre point of the hectare of the 157 study site, we included hectares, whose centre point was within the 500m radius of the focal 158 centre point (81ha). The 500m radius was chosen as it covers dispersal distances of many 159 moth species and is a relevant scale for the different land-use types that were involved 160 (Fuentes-Montemayor et al., 2011). Furthermore, it limits spatial autocorrelation among 161 study sites. These land-use covers were attributed to the average year of the aerial photos that 162 were included. For years that fell between the four observation time points, land-use covers 163 were interpolated linearly from the land-use covers in the two adjacent time points. For sampling years prior to the first year with land-use data available (~1982) or after the last year 164 165 with land-use data available (~2015), proportions of the closest year were used, following a 166 conservative scenario of no change.

#### 167 Statistical analyses

168 All statistical analyses were performed in R version 4.2.0 (R Core Team, 2022). All code

169 used for analyses is available from the online repository located at

170 https://github.com/nefff1/moths-CH-Reser.

For each sampling night, we determined three community characteristics: total abundance
(sum of individuals across all species), species richness (number of species), and total bio-

173 mass. Total biomass was estimated from species-level dry mass, which was determined from

174 forewing length through allometric equations (Kinsella et al., 2020). Species-level wingspan

175 data, which are more readily available than forewing-length data, were assembled from Jonko

176 (2002-2022) (n = 981) and completed with data from other sources (Fibiger, 1990; Potocký

177 et al., 2018; Ronkay et al., 2001) (n = 12). Based on data for a subset of study species (Cook

178 et al., 2022), a linear relation between forewing length and wingspan was determined and

179 used to estimate forewing length for all study species. These data were finally used to esti-

180 mate species dry mass. For species where forewing length could not be retrieved (n = 13), dry 181 mass was estimated from congeneric species.

182 The three community characteristics were used as response variables in the regression mod-183 els. We used a zero-inflated negative binomial response distribution for abundance and rich-184 ness (log link) and a hurdle gamma distribution for biomass (log link), which yielded high 185 agreements between posterior predictive and empirical data distributions (Fig. S1.6). All 186 models included a smoothing term for the day of the year to quantify seasonal patterns, a smoothing term for the elevation of the study site (mean elevation of the study site measured 187 188 at a hectare) as well as linear terms for weather parameters for the sampling night (tempera-189 ture and precipitation). To check how the seasonal patterns are influenced by species with 190 different overwintering strategies, we divided the dataset by overwintering stage (egg, larva,

pupa, adult) and ran the same models for these data subsets. Overwintering stages were gathered from several trait collections (Cook et al., 2022; Mangels et al., 2017; Potocký et al.,
2018) and completed based on additional moth trait databases (Jonko, 2002–2022; Ziegler,
2005–2022). To analyse the relation of abundance, richness, and biomass to landscape composition, we included cover of the different land-use types (forest, grassland, cropland, sealed
area) as predictor variables.

197 Furthermore, all models had a set of fixed and random factors to account for the sampling de-198 sign. Fixed effects were trap type (fixed type 1, fixed type 2, or manual), lamp type (four 199 nominal factor levels), number of traps (ordinal factor with four levels) and a two-level nomi-200 nal factor denoting whether the site was sampled in the previous night to account for persist-201 ing attraction of light traps. Additionally, there was a smoothing term accounting for the sam-202 pling duration, which was only included for manual traps and if data on sampling duration 203 was available (2800 out of 4024 manual sampling nights). We chose a smoothing term over a 204 linear effect as we expected moth activity to be changing over the course of a night (e.g. Ma 205 & Ma, 2013). The random structure was composed of the site ID (n = 171), the site ID and 206 year combination (n = 663), a factor accounting for the sampling night, where proximate sites 207 operated in the same night are grouped together (n = 34,390), and a spatio-temporal grouping 208 factor of study sites to account for among-region and year variability (n = 249). The latter 209 was defined such that all sites in a year that were within 20km of each other were grouped. In 210 all models, continuous predictor variables were standardised to mean 0 and standard devia-211 tion 1 prior to analyses. Sum-to-zero contrasts were used for nominal factor variables. 212 The basic structure of all models was built through 'brms' (Bürkner et al., 2022) and then 213 manually adapted to meet the specific requirements (covariate for sampling duration only in-214 cluded if data was available) by directly changing the underlying Stan code of the model. The 215 final models were run through 'rstan' (Guo et al., 2022) (4 Markov chain Monte Carlo chains

216	with 2000 iterations each, including 1000 warm-up iterations). Priors followed standard set-
217	tings of the 'brms' package representing weakly informative priors (details available in the
218	online repository for the code). Model results were evaluated based on posterior distributions
219	of model predictions.
220	We used the mean and 95% symmetric credible intervals (CIs) based on 2.5% and 97.5%
221	quantiles to summarise posterior distributions. To check whether the four chains mixed well,

222 we calculated Rhat statistics for estimates of intercepts, fixed effect slopes and spline coeffi-

cients (smoothing terms) through the package 'rstan' (Guo et al., 2022). The standard thresh-223

224 old of 1.1 was met by all values of all final models.

#### 225 **Results**

#### 226 Seasonal patterns in moth community characteristics

227 All three community characteristics showed a clear seasonal pattern with two distinct peaks 228 (Fig. 1). The first peak, which was clearly lower (richness) or slightly lower (abundance, bio-229 mass) than the second peak, was at the end of March (March 24 for all community character-230 istics). The second peak was mid-July (July 12 for abundance and biomass, July 8 for rich-231 ness) and for abundance and biomass was followed by a plateau peaking again mid-August 232 (August 10 for abundance, August 12 for biomass). The single peaks could be reconstructed 233 for subsets of the dataset defined by species overwintering stages (Fig. 1). At the same time 234 as the first peak, there was a peak of species overwintering as pupa and of the few species 235 overwintering as adults. At the time of the second peak, species overwintering as larva had a 236 coinciding peak. Also, all community characteristics of species overwintering as pupa had a 237 second peak at this time, which however was for abundance and biomass clearly lower than the first peak. Species overwintering in the egg stage, which tend to be rarer than those over-238 239 wintering as larva or pupa, had their peak late in the year (between October 22 and November 240 3). Around the same time, the decline of overall community characteristics was slightly miti-241 gated.

#### 242 Sampling night specifics and moth community characteristics

Several sampling night specifics were related to the three investigated community characteristics (abundance, richness, biomass) (Fig. 1, Fig. S1.7, Table S1.3). With respect to weather conditions, there was a clear and strong increase of all community characteristics with increasing temperatures of the sampling night (Fig. 1, Table S1.3). An increase of sampling night temperature by 50% of its range (corresponding to a rise of 17.2°C) was related to an increase of abundance by a factor 9.68 (95%-CI: 8.98–10.47), of richness by a factor 6.44

249 (95%-CI: 6.16–6.74), and of biomass by a factor 5.14 (95%-CI: 4.77–5.55) (Table 1). For an

increase of temperature by 5°C, this corresponds to the factors 1.94 (95%-CI: 1.89–1.98);

abundance), 1.72 (95%-CI: 1.70–1.74); richness), and 1.61 (95%-CI: 1.57–1.65); biomass).

252 There was also evidence for slight increases in community characteristics with increasing

precipitation in the sampling night (factor 1.12 [95%-CI: 1.02–1.24] for abundance, 1.03

254 [95%-CI: 0.97–1.1] for richness, and 1.19 [95%-CI: 1.07–1.31] for biomass with an increase

of 50% of the range, corresponding to 140mm) (Table 1).

256 For other night- and sampling-specific covariates, which were included to correct for data

257 specificities, we found particularly strong relations of community characteristics to trap type,

sampling history (i.e. whether there was sampling in the previous night), and to sampling du-

ration (Fig. S1.7, Table S1.3). While there was no clear difference between the two fixed trap

types, samples from manual traps were estimated to have a factor 6.54 (95%-CI: 4.68–9.3)

higher abundance compared to fixed traps of type 1, a factor 3.14 (95%-CI: 2.51–3.97) higher

richness, and a factor 5.07 (95%-CI: 3.56–7.21) higher biomass. If there was no sampling

taking place at a location in the previous night, samples were estimated to have a factor 0.81

264 (95%-CI: 0.71–0.92) lower abundance, a factor 0.88 (95%-CI: 0.81–0.96) lower richness, and

a factor 0.77 (95%-CI: 0.68–0.87) lower biomass. With increasing sampling duration, there

266 were increases in all community characteristics (Fig. S1.7). This increase was not linear, but

there was a first peak with a following plateau reached after approx. 7 hours of sampling

268 (flattening of the curve already after approx. 5 hours).

### 269 Elevation and landscape composition

270 All three community metrics increased with elevation, with the increase being close-to linear

271 (Fig. 1, Table S1.3). An increase of elevation by 50% of its range (corresponding to a rise of

1130m) was related to an increase of abundance by a factor 3.33 (95%-CI: 2.49–4.44), of

273	richness by a factor 1.38 (95%-CI: 1.13–1.67), and of biomass by a factor 3.54 (95%-CI:
274	2.68–4.67) (Table 1). For all three community characteristics and particularly for richness, a
275	peak with a following plateau or decrease was evident after reaching an elevation of around
276	2000 m asl (Fig. 1).
277	For the effects of the landscape variables (Fig. 2, Table S1.3), there was strong evidence for
278	community characteristics to be higher if cover of forests in the surrounding was high . If for-
279	est cover within a radius of 500m around the plot was higher by 50% of its range (corre-
280	sponding to an approx. proportion of 0.5), abundance was higher by a factor 1.93 (95%-CI:
281	1.45–2.53), richness by a factor 1.49 (95%-CI: 1.22–1.81), and biomass by a factor 1.72
282	(95%-CI: 1.30–2.29) (Table 1). There was also a tendency for all community characteristics
283	to be higher with increasing proportion of sealed area in the plot surrounding. If sealed area
284	was by 50% of its range higher (corresponding to a proportion of 0.16), abundance was esti-
285	mated to be higher by a factor 1.26 (95%-CI: 0.97–1.64), richness by a factor 1.16 (95%-CI:

286 0.98–1.39), and biomass by a factor 1.26 (95%-CI: 0.98–1.61) (Table 1).

#### 287 **DISCUSSION**

288 When relating moth community characteristics to the day of the year (question 1), a clear sea-289 sonal pattern was evident, with a peak in early spring and one in summer. The distinct pattern 290 could clearly be related to the life cycles of moth groups distinguished by overwintering 291 stage. The spring peak was related to high activity of species overwintering as adults and pu-292 pae, the summer peak to species overwintering as pupae or larvae. In fall, egg-overwintering 293 species were peaking, which was also evident from the seasonal pattern of the overall com-294 munity. While the observed summer peak matches findings from previous studies (Busse et al., 2022; Jonason et al., 2014; Roth et al., 2021), there is at best some indication for the 295 296 spring peak in these studies because sampling activity only started around that time. Starting 297 sampling campaigns too late within the year result in systematic under-sampling of species 298 groups that overwinter as pupae or adults. As overwintering stage has regularly been related 299 to species' susceptibility to global change drivers such as climate change or land-use intensi-300 fication (Forsman et al., 2016; Keret et al., 2020; Mangels et al., 2017; Mattila et al., 2006, 301 2008), restricted sampling within the season can lead to biased conclusions. Furthermore, the 302 observed spring peak was rather narrow. If species phenologies are shifting within years due 303 to climate change (Duchenne et al., 2020), while sampling schemes are not adapted to these 304 shifts, wrong conclusions about temporal trends might be drawn (Didham et al., 2020). 305 There was a strong signal of the weather conditions of the sampling night on all moth com-

munity characteristics (questions 2). Particularly strong relations were found to the temperature of the sampling night, which is in line with previous findings (Beck et al., 2010; Jonason et al., 2014; Knop et al., 2018) and reflects increases in moth activity with increasing temperature. The effect size was estimated to an increase of community characteristics by 50–100% for a temperature increase of only 5°C (while correcting for elevation and season), which is

311 considerable and needs to be accounted for when analyzing datasets covering nights with312 fluctuating temperatures.

313 Unimodal patterns of species richness along elevational gradients with a mid-elevation peak 314 are common for many species groups (Rahbek, 2005). Large-scale analyses are rare for 315 moths, but mid-elevation peaks seem to be common (Beck et al., 2017). For moths in the 316 Alps, one study based on a spatially and temporally restricted dataset reports an unimodal peak, whose position depends on the season but moves as high as 1800 m asl (Beck et al., 317 318 2010). Here, we show an increase of all community characteristics - particularly strong for 319 abundance and biomass – along the studied elevational gradient, which levels of at around 320 2000 m asl (question 3). Because the studied dataset covers few sites above 2000 m asl and 321 none above 2500 m asl, the observed pattern indicates a unimodal pattern in all community 322 characteristics with a peak at around 2000 m asl. Although the peak is comparably high up 323 the elevational gradient, the pattern corresponds well with previous data on moths (Beck et 324 al., 2010) and with data from several other arthropod groups from the Alps (Fontana et al., 325 2020). The underlying drivers of this pattern might be manifold (Beck et al., 2017; Hodkin-326 son, 2005; McCoy, 1990). For the studied gradient, land-use related pressures as well as light 327 pollution are largely decreasing with elevation, which might be driving at least some of the 328 observed increase with elevation.

With relation to landscape composition (question 4), we found strongest relations of moth community characteristics to the cover of forests. There were more moths present if cover of forests was high, highlighting their importance for sustaining high moth abundance and richness (Fuentes-Montemayor et al., 2012; Kühne et al., 2022). Furthermore, there was indication for a positive effect of a higher cover of sealed area, i.e. of urban areas. As for other pollinator groups, urban areas may present additional floral resources for moth communities (Hall et al., 2017), which might explain this positive relation. Why the potentially negative

effect of higher light pollution (van Grunsven et al., 2020) in these urbanized landscapes was
not evident needs further investigation, though. Promoting forest elements across the landscape mosaic is imminent to support diverse and abundant moth communities.

339 Based on a moth community dataset of unseen extent, we could evaluate the relations of dif-340 ferent biotic and abiotic factors to moth community characteristics. The bimodal seasonal 341 pattern with two distinct peaks in all community metrics (abundance, richness, biomass) is in 342 this fine resolution new to research and will help to better evaluate and understand results 343 from studies on smaller scales, to plan future sampling campaigns, and to target conservation 344 efforts more effectively. Nightly temperatures are a very important driver of moth numbers, 345 with even small increases having profound effects on all community characteristics. All moth 346 characteristics increased along the investigated elevational gradient, highlighting the im-347 portance of high-elevation habitats for conserving moth diversity. At the same time, lower 348 numbers of moth individuals and species at lower elevations might be related to the multitude 349 of anthropogenic pressures such as intensive land use and light pollution, which are more 350 prevalent at lower altitudes. Furthermore, there was a positive relation of moth community 351 characteristics to forest cover. Besides reducing anthropogenic pressures such as light pollu-352 tion, preserving and promoting woodlands, particularly in low-elevation landscapes, might be 353 key to promote diverse and abundant moth communities in a changing world.

#### REFERENCES 354

359

360

355	Archaux, F., Lorel, C., &	Villemey, A.	(2018). Landscape	drivers of butterfly	and burnet
-----	---------------------------	--------------	-------------------	----------------------	------------

moth diversity in lowland rural areas. Landscape Ecology, 33(10), 1725–1739. 356

357 https://doi.org/10.1007/s10980-018-0697-x

358 Beck, J., Altermatt, F., Hagmann, R., & Lang, S. (2010). Seasonality in the altitude-diversity

pattern of Alpine moths. Basic and Applied Ecology, 11(8), 714–722.

https://doi.org/10.1016/j.baae.2010.08.009

- 361 Beck, J., McCain, C. M., Axmacher, J. C., Ashton, L. A., Bärtschi, F., Brehm, G., Choi, S.-
- 362 W., Cizek, O., Colwell, R. K., Fiedler, K., Francois, C. L., Highland, S., Holloway, J.
- 363 D., Intachat, J., Kadlec, T., Kitching, R. L., Maunsell, S. C., Merckx, T., Nakamura,
- A., ... Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse 364
- 365 insect taxon: A global meta-study on geometrid moths. Global Ecology and Biogeo-

366 graphy, 26(4), 412–424. https://doi.org/10.1111/geb.12548

- 367 Brühl, C. A., Bakanov, N., Köthe, S., Eichler, L., Sorg, M., Hörren, T., Mühlethaler, R.,
- 368 Meinel, G., & Lehmann, G. U. C. (2021). Direct pesticide exposure of insects in na-
- 369 ture conservation areas in Germany. Scientific Reports, 11(1), 24144.
- 370 https://doi.org/10.1038/s41598-021-03366-w
- 371 Bundesamt für Statistik. (2021). Die Bodennutzung in der Schweiz. Resultate der Arealstatis-372 tik 2018 (Statistik Der Schweiz). BFS.
- 373 Bürkner, P.-C., Gabry, J., Weber, S., Johnson, A., Modrák, M., Badr, H. S., Weber, F., Ben-
- 374 Shachar, M. S., & Rabel, H. (2022). Bayesian Regression Models using "Stan". R
- 375 package version 2.17.0. [Computer software]. https://cran.r-project.org/web/packa-

ges/brms/brms.pdf 376

377	Busse, A., Bässler, C., Brandl, R., Friess, N., Hacker, H., Heidrich, L., Hilmers, T., Merkel-
378	Wallner, G., Schmid-Egger, C., Seifert, L., & Müller, J. (2022). Light and Malaise
379	traps tell different stories about the spatial variations in arthropod biomass and
380	method-specific insect abundance. Insect Conservation and Diversity, 15(6), 655-
381	665. https://doi.org/10.1111/icad.12592
382	Cook, P. M., Tordoff, G. M., Davis, T. M., Parsons, M. S., Dennis, E. B., Fox, R., Botham,
383	M. S., & Bourn, N. A. D. (2022). Traits data for the butterflies and macro-moths of
384	Great Britain and Ireland. Ecology, 103(5), e3670. https://doi.org/10.1002/ecy.3670
385	Didham, R. K., Basset, Y., Collins, C. M., Leather, S. R., Littlewood, N. A., Menz, M. H. M.,
386	Müller, J., Packer, L., Saunders, M. E., Schönrogge, K., Stewart, A. J. A., Yanoviak,
387	S. P., & Hassall, C. (2020). Interpreting insect declines: Seven challenges and a way
388	forward. Insect Conservation and Diversity, 13(2), 103–114.
389	https://doi.org/10.1111/icad.12408
390	Duchenne, F., Thébault, E., Michez, D., Elias, M., Drake, M., Persson, M., Rousseau-Piot, J.
391	S., Pollet, M., Vanormelingen, P., & Fontaine, C. (2020). Phenological shifts alter the
392	seasonal structure of pollinator assemblages in Europe. Nature Ecology & Evolution,
393	4(1), Article 1. https://doi.org/10.1038/s41559-019-1062-4
394	Evans, L. C., Burgess, M. D., Potts, S. G., Kunin, W. E., & Oliver, T. H. (2024). Population
395	links between an insectivorous bird and moths disentangled through national-scale
396	monitoring data. Ecology Letters, 27(1), e14362. https://doi.org/10.1111/ele.14362
397	Fibiger, M. (Ed.). (1990). Noctuidae Europaeae. Volume 1. Noctuinae I. Entomological
398	Press.

399	Fontana, V., Guariento, E., Hilpold, A., Niedrist, G., Steinwandter, M., Spitale, D., Nascim-
400	bene, J., Tappeiner, U., & Seeber, J. (2020). Species richness and beta diversity pat-
401	terns of multiple taxa along an elevational gradient in pastured grasslands in the Euro-
402	pean Alps. Scientific Reports, 10(1), Article 1. https://doi.org/10.1038/s41598-020-
403	69569-9
404	Forsman, A., Betzholtz, PE., & Franzén, M. (2016). Faster poleward range shifts in moths
405	with more variable colour patterns. Scientific Reports, 6(1), Article 1.
406	https://doi.org/10.1038/srep36265
407	Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J. M., & Park, K. J. (2012). Fac-
408	tors influencing moth assemblages in woodland fragments on farmland: Implications
409	for woodland management and creation schemes. Biological Conservation, 153, 265-
410	275. https://doi.org/10.1016/j.biocon.2012.04.019
411	Fuentes-Montemayor, E., Goulson, D., & Park, K. J. (2011). The effectiveness of agri-envi-
412	ronment schemes for the conservation of farmland moths: Assessing the importance
413	of a landscape-scale management approach. Journal of Applied Ecology, 48(3), 532-
414	542. https://doi.org/10.1111/j.1365-2664.2010.01927.x
415	Guo, J., Gabry, J., Goodrich, B., Weber, S., Lee, D., Sakredja, K., Martin, M., Trustees of
416	Columbia University, Sklyar, O., The R Core Team, Oehlschlaegel-Akiyoshi, J.,
417	Maddock, J., Bristow, P., Agrawal, N., Kormanyos, C., & Steve, B. (2022). Rstan: R
418	interface to Stan. R package version 2.21.7 (2.21.7) [Computer software].
419	Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.
420	S., Baldock, K. C. R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley,
421	M. E., Jackson, J. I., Langellotto, G., Lowenstein, D., Minor, E. S., Philpott, S. M.,

422	Potts, S. G., Threlfall, C. G. (2017). The city as a refuge for insect pollinators.
423	Conservation Biology, 31(1), 24–29. https://doi.org/10.1111/cobi.12840
424	Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and commu-
425	nity responses to altitude. Biological Reviews, 80(3), 489-513.
426	https://doi.org/10.1017/S1464793105006767
427	Hunter, M. D., Kozlov, M. V., Itämies, J., Pulliainen, E., Bäck, J., Kyrö, EM., & Niemelä,
428	P. (2014). Current temporal trends in moth abundance are counter to predicted effects
429	of climate change in an assemblage of subarctic forest moths. Global Change Biol-
430	ogy, 20(6), 1723–1737. https://doi.org/10.1111/gcb.12529
431	Jonason, D., Franzén, M., & Ranius, T. (2014). Surveying moths using light traps: Effects of
432	weather and time of year. PLOS ONE, 9(3), e92453. https://doi.org/10.1371/jour-
433	nal.pone.0092453
434	Jonko, C. (2002–2022). Lepidoptera Mundi. https://lepidoptera.eu/
435	Keret, N. M., Mutanen, M. J., Orell, M. I., Itämies, J. H., & Välimäki, P. M. (2020). Climate
436	change-driven elevational changes among boreal nocturnal moths. Oecologia, 192(4),
437	1085–1098. https://doi.org/10.1007/s00442-020-04632-w
438	Kinsella, R. S., Thomas, C. D., Crawford, T. J., Hill, J. K., Mayhew, P. J., & Macgregor, C. J.
439	(2020). Unlocking the potential of historical abundance datasets to study biomass
440	change in flying insects. Ecology and Evolution, 10(15), 8394-8404.
441	https://doi.org/10.1002/ece3.6546
442	Knop, E., Gerpe, C., Ryser, R., Hofmann, F., Menz, M. H. M., Trösch, S., Ursenbacher, S.,
443	Zoller, L., & Fontaine, C. (2018). Rush hours in flower visitors over a day-night cy-
444	cle. Insect Conservation and Diversity, 11(3), 267–275.
445	https://doi.org/10.1111/icad.12277
	21

446	Knop, E., Grimm, M. L., Korner-Nievergelt, F., Schmid, B., & Liechti, F. (2023). Patterns of
447	high-flying insect abundance are shaped by landscape type and abiotic conditions.
448	Scientific Reports, 13(1), 15114. https://doi.org/10.1038/s41598-023-42212-z
449	Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light
450	at night as a new threat to pollination. Nature, 548(7666), 206–209.
451	https://doi.org/10.1038/nature23288
452	Kühne, I., Arlettaz, R., & Humbert, JY. (2022). Landscape woody features, local manage-
453	ment and vegetation composition shape moth communities in extensively managed
454	grasslands. Insect Conservation and Diversity, 15(6), 739–751.
455	https://doi.org/10.1111/icad.12600
456	Ma, G., & Ma, CS. (2013). Differences in the nocturnal flight activity of insect pests and
457	beneficial predatory insects recorded by light traps: Possible use of a beneficial-
458	friendly trapping strategy for controlling insect pests. European Journal of Entomol-
459	ogy, 109(3), 395-401. https://doi.org/10.14411/eje.2012.051
460	Mangels, J., Fiedler, K., Schneider, F. D., & Blüthgen, N. (2017). Diversity and trait compo-
461	sition of moths respond to land-use intensification in grasslands: Generalists replace
462	specialists. Biodiversity and Conservation, 26(14), 3385-3405.
463	https://doi.org/10.1007/s10531-017-1411-z
464	Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J. S., & Päivinen, J. (2006). Ecological deter-
465	minants of distribution decline and risk of extinction in moths. Conservation Biology,
466	20(4), 1161–1168. https://doi.org/10.1111/j.1523-1739.2006.00404.x
467	Mattila, N., Kotiaho, J. S., Kaitala, V., & Komonen, A. (2008). The use of ecological traits in
468	extinction risk assessments: A case study on geometrid moths. Biological Conserva-
469	tion, 141(9), 2322-2328. https://doi.org/10.1016/j.biocon.2008.06.024

- 470 McCoy, E. D. (1990). The distribution of insects along elevational gradients. *Oikos*, 58(3),
- 471 313. https://doi.org/10.2307/3545222
- Mellard, J. P., Audoye, P., & Loreau, M. (2019). Seasonal patterns in species diversity across
  biomes. *Ecology*, *100*(4), e02627. https://doi.org/10.1002/ecy.2627
- 474 Montgomery, G. A., Belitz, M. W., Guralnick, R. P., & Tingley, M. W. (2021). Standards
- 475 and best practices for monitoring and benchmarking insects. *Frontiers in Ecology and*476 *Evolution*, *8*, 579193. https://doi.org/10.3389/fevo.2020.579193
- 477 New, T. R. (2004). Moths (Insecta: Lepidoptera) and conservation: Background and perspec478 tive. *Journal of Insect Conservation*, *8*, 79–94.
- 479 Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., & Konvička, M. (2018). Life-history
- 480 traits of Central European moths: Gradients of variation and their association with rar-
- 481 ity and threats. *Insect Conservation and Diversity*, *11*(5), 493–505.
- 482 https://doi.org/10.1111/icad.12291
- 483 R Core Team. (2022). R: A language and environment for statistical computing [Computer
- 484 software]. R Foundation for Statistical Computing.
- Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness
  patterns. *Ecology Letters*, 8(2), 224–239. https://doi.org/10.1111/j.1461-
- 487 0248.2004.00701.x
- 488 Rezbanyai-Reser, L. (2014). Zur Nachtgrossfalterfauna von drei Lebensraumkomplexen im
- 489 Kanton Waadt, Westschweiz. Rochers de Naye, 1970m in den Alpen, sowie Chalet
- de la Dôle, 1430m und La Barillette, 1450m im Jura (Lepidoptera: "Macrohe-
- 491 terocera"). Lepidopterologische Mitteilungen Aus Luzern, 14, 1–96.
- 492 Rezbanyai-Reser, L. (2018a). *Lebenswerk.* 22, 1–102.

493	Rezbanyai-Reser, L. (2018b). Vollständige Literaturliste "Rézbányai" bzw. "Rezbanyai-Re-
494	ser" 1968-2018 (Lepidoptera und andere Insekten). Lepidopterologische Mitteilungen
495	Aus Luzern, 22, 1–56.

- 496 Ronkay, L., Yela Garcia, J. L., & Hreblay, M. (2001). *Noctuidae Europaeae. Volume 5. Had-*497 *eninae II.* Entomological Press.
- 498 Roth, N., Hacker, H. H., Heidrich, L., Friess, N., García-Barros, E., Habel, J. C., Thorn, S., &
- 499 Müller, J. (2021). Host specificity and species colouration mediate the regional de-
- 500 cline of nocturnal moths in central European forests. *Ecography*, 44(6), 941–952.
- 501 https://doi.org/10.1111/ecog.05522
- 502 Truxa, C., & Fiedler, K. (2013). Attraction to light—From how far do moths (Lepidoptera)
- return to weak artificial sources of light? *European Journal of Entomology*, *109*(1),
  77–84. https://doi.org/10.14411/eje.2012.010
- 505 van Grunsven, R. H. A., van Deijk, J. R., Donners, M., Berendse, F., Visser, M. E., Veenen-
- 506 daal, E., & Spoelstra, K. (2020). Experimental light at night has a negative long-term
- 507 impact on macro-moth populations. *Current Biology*, *30*(12), R694–R695.
- 508 https://doi.org/10.1016/j.cub.2020.04.083
- 509 Vaughan, N. (1997). The diets of British bats (Chiroptera). *Mammal Review*, 27(2), 77–94.
  510 https://doi.org/10.1111/j.1365-2907.1997.tb00373.x
- 511 Walton, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2020). Nocturnal pollinators
- strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Bi- ology Letters*, *16*(5), 20190877. https://doi.org/10.1098/rsbl.2019.0877
- 514 Xu, X., Ren, Z.-X., Trunschke, J., Kuppler, J., Zhao, Y.-H., Knop, E., & Wang, H. (2021).
- 515 Bimodal activity of diurnal flower visitation at high elevation. *Ecology and Evolution*,
- 516 *11*(19), 13487–13500. https://doi.org/10.1002/ece3.8074

- 517 Ziegler, H. (2005–2022). Butterflies & Moths of Palaearctic Regions. https://euroleps.ch
- 518 ZOBODAT. (2014–2023). Dr. Ladislaus Rezbanyai-Reser (auch Rezbanyai).
- 519 https://www.zobodat.at/personen.php?id=1004
- 520 Zoller, L., Bennett, J. M., & Knight, T. M. (2020). Diel-scale temporal dynamics in the abun-
- 521 dance and composition of pollinators in the Arctic summer. *Scientific Reports*, 10(1),
- 522 21187. https://doi.org/10.1038/s41598-020-78165-w

#### 524 DATA ACCESSIBILITY STATEMENT

525 The raw moths records data is hosted by info fauna and protected by a code of conduct, but

526 might be obtained from info fauna upon request when in accordance with this code of con-

527 duct. Moths records data at coarser spatial resolution and with unique identifier for the sam-

528 pling location and sampling details necessary to reproduce the models will be made available

529 through the GBIF database. The weather data are under restricted access but might be directly

530 obtained from MeteoSwiss (https://www.meteoswiss.admin.ch). Other data and codes neces-

sary to reproduce the analyses are available from the GitHub repository located at

532 https://github.com/nefff1/moths-CH-Reser.

533

## 534 ACKNOWLEDGMENTS

We are grateful to Dr. L. Rezbanyai-Reser for his tireless effort in collecting the moth community data and for providing us with the data for theses analyses. We are thankful to the various helpers that support the field data collection over the many years, in particular to E. Schäffer. We are grateful to E. Leonetti, F. Claude, M.-L. Fetic for digitalization of handwritten data and Y. Gonseth for having initiated this project. We thank the INSECT project consortium for valuable input on earlier versions of these analyses.

- 541 542 Table 1 Model predictions on the change in moth abundance, richness, and biomass (g), if a variable is in-
- creased by 50% of its range of occurring values (indicated in the '50% step' column). Numbers are factors by
- 543 544 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.

		Abundance		Richness			Biomass (g)			
Variable	50% step	Est.	Lower 95%-Cl	Upper 95%-Cl	Est.	Lower 95%-Cl	Upper 95%-Cl	Est.	Lower 95%-Cl	Upper 95%-Cl
Elevation <sup>1</sup>	1130 m	3.33	2.49	4.44	1.38	1.13	1.67	3.54	2.68	4.67
Precipitation	140 mm	1.12	1.02	1.24	1.03	0.97	1.10	1.19	1.07	1.31
Temperature	17.2 °C	9.68	8.98	10.47	6.44	6.16	6.74	5.14	4.77	5.55
Prop. forests	0.494	1.93	1.45	2.53	1.49	1.22	1.81	1.72	1.3	2.29
Prop. grasslands	0.488	1.01	0.73	1.39	0.93	0.74	1.14	0.99	0.74	1.36
Prop. croplands	0.443	1.00	0.69	1.43	0.89	0.69	1.15	0.99	0.69	1.42
Prop. sealed area	0.162	1.26	0.97	1.64	1.16	0.98	1.39	1.26	0.98	1.61

545 546 <sup>1</sup>Term included as a smoothing term. Because the prediction is close to linear, change factors still harbour useful

information. The values are the means across 100 different 50% ranges.



548Fig. 1 Conditional effects of different model covariates (elevation, precipitation and temperature of sampling549night, day of the year) 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.551Underlying points show data per sampling night (n = 35,847). For day of the year, conditional effects from models run on subgroups defined by hibernation stage (e: egg; 1: larva; p: pupa; a: adult) are shown along the conditional effects from the full model. Note that the y axes are on log scale (after adding the minimal non-zero value to all values). Effects of other covariates are shown in Fig. S1.7. Detailed model results in Table S1.3.





**Fig. 2** Conditional effects of different landscape variables on moth abundance, richness, and biomass. Landscape variables are the covers of different land-use types (forests, grasslands, croplands, sealed area) within a radius of 500m 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. Underlying points show data per sampling night (n = 35,847). Note that the *y* axes are on log scale (after adding the minimal non-zero value to all values). Detailed model results in Table S1.3.

# SUPPORTING INFORMATION: Appendix S1

Superfamily	Family	Species					
	Brahmaeidae	Lemonia taraxaci					
	Endromidae	Endromis versicolora					
Bombycoidea	Saturniidae	Aglia tau, Saturnia pavonia, S. pavoniella, S. pyri					
	Sphingidae	Acherontia atropos, Agrius convolvuli, Deilephila elpenor, D. porcellus, Hyles euphorbiae, H. gallii, H. livornica, H. vespertilio, Laothoe populi, Mimas tiliae, Proserpinus proserpina, Smerinthus ocellata, Sphinx ligustri, S. pinastri					
Cossoidea	Cossidae	Cossus cossus, Phragmataecia castaneae, Zeuzera pyrina					
Drepanoidea	Drepanidae	Achlya flavicornis, Cilix glaucata, Cymatophorina diluta, Drepana curvatula, D. falcataria, Falcaria lacertinaria, Habrosyne pyritoides, Ochropacha duplaris, Polyploca ridens, Sabra harpagula, Tethea ocularis, T. or, Tetheella fluctuosa, Thyatira batis, Watsonalla binaria, W. cultraria, W. uncinula					
Geometroidea	Geometridae	Abraxas grossulariata, A. sylvata, Acasis appensata, A. viretata, Adactylotis contaminaria, Aethalura punctulata, Agriopis aurantiaria, A. bajaria, A. leucophaearia, A. marginaria, Alcis deversata, A. jubata, A. repandata, Aleucis distinctata, Alsophia aceriaria, A. aescalaria, Angerona prunaria, Anticlea derivata, Anticolinx sparsata, Apeira syringaria, Aplocera plagiata, A. praeformata, Apocheima hispidaria, Arichanna melanaria, Ascotis selenaria, As- pitates gilvaria, Asthena albutata, A. anseraria, Biston betularia, B. strataria, Bupatus spinaria, Cabera exanthe- mata. C. pusaria, Campaea margaritaria, Camptogramma bilineata, C. scrigturata, Carsia soronitat, Catarlo- cus, C. obscurata, C. pulata, C. variegata, Chesias legatella, C. rufata, Chiasmia clathrata, Chiorissa cloraria, C. viridata, Chloroclysta miata, C. siterata, Chioroclysis v-ata, Cidaria fulvata, Oleora cinctaria, Oleorodes li- chenaria, C. contotata, C. pencinatria, C. turbata, C. punctaria, C. yuppilaria, C. sulabicvellaria, C. abiopunc- tata, C. anularia, C. linearia, C. pendularia, C. porata, C. puncitaria, C. quercimontaria, C. ruficili- aria, C. suppunctaria, Deileptenia ribeata, Dysstroma cirtrata, D. truncata, Earophila badiata, Ecliptopera capitata, E. silaceata, Ectropis crepuscularia, Electrophaes corylata, Elophos caelibaria, E. operaria, Ematurga atomaria, E. silaceata, Ectropis crepuscularia, Electrophaes corylata, Elophos caelibaria, E. operaria, Entephria cae- siata, E. cyanata, E. flavicinctata, E. infusitaria, E. enobilaria, E. polibotophora sabinata, Epione penadaria, E. vespertaria, Epirnhoe alternata, E. galiata, E. molluginata, E. rivata, E. tristata, E. ervanata, E. testata, E. euphysi biangulata, E. rounstata, E. ingapata, E. cauchiata, E. centaureata, E. enoputata, E. Promata, E. testata, E. euphysi biangulata, E. rounstata, E. usignata, E. europatata, E. populata, E. privata, E. estra- versaria, E. gernelitata, E. gueneata, E. haworthiata, E. enoputata, E. envalaria, E. etra- versaria, E. gernelitata, E. gueneata, E.					

 Table S1.1 Overview of all moth species recorded with family and superfamily attribution.

		incanata, S. marginepunctata, S. nigropunctata, S. ornata, S. rubiginata, S. submutata, S. subpunctaria, S. ter- nata, S. umbelaria, S. virgulata, Scotopteryx angularia, S. bipunctaria, S. chenopodiata, S. luridata, S. moeniata, S. mucronata, S. octodurensis, S. vicinaria, Selenia dentaria, S. lunularia, S. tetralunaria, Selidosema brun- nearia, S. plumaria, Siona lineata, Spargania luctuata, Stegania cararia, S. trimaculata, Synopsia sociaria, Teph- ronia sepiaria, Thalera fimbrialis, Thera britannica, T. cembrae, T. cognata, T. cupressata, T. juniperata, T. obe- liscata, T. variata, T. vetustata, Theria primaria, T. rupicapraria, Thetidia smaragdaria, Timandra comae, Trichop- teryx carpinata, T. polycommata, Triphosa dubitata, T. sabaudiata, T. tauteli, Venusia blomeri, V. cambrica, Xant- horhoe biriviata, X. decoloraria, X. designata, X. ferrugata, X. fluctuata, X. incursata, X. montanata, X. quadrifasi- ata, X. spadicearia, Yezognophos dilucidaria, Y. serotinaria, Y. vittaria						
Hepialoidea	Hepialidae	Bazoryctra ganna, Hepialus humuli, Korscheltellus fusconebulosa, K. lupulina, Phymatopus hecta, Triodia syl vina Cosmotriche lobulina, Dendrolimus pini, Friogaster arbusculae, E. catax, E. lanestris, Futbrix potatoria, Gastri						
Lasiocampoidea	Lasiocampidae	Cosmotriche lobulina, Dendrolimus pini, Eriogaster arbusculae, E. catax, E. lanestris, Euthrix potatoria, Gastro pacha quercifolia, Lasiocampa quercus, L. trifolii, Macrothylacia rubi, Malacosoma alpicola, M. castrensis, M. neustria, Odonestis pruni, Phyllodesma tremulifolia, Poecilocampa alpina, P. populi, Trichiura crataegi						
	Erebidae	Arctia caja, A. flavia, A. matronula, A. testudinaria, A. villica, Arctornis I-nigrum, Atolmis rubricollis, Autophila dilu- cida, Callimorpha dominula, Calliteara pudibunda, Calyptra thalictri, Catephia alchymista, Catocala coniuncta, C. dilecta, C. electa, C. elocata, C. fraxini, C. fulminea, C. nupta, C. nymphaea, C. nymphagoga, C. promissa, C. puerpera, C. sponsa, Chelis simplonica, Colobochyla salicalis, Coscinia cribraria, Cybosia mesomella, Diacrisia purpurata, D. sannio, Diaphora mendica, D. sordida, Dysgonia algira, Eilema caniola, E. cereola, E. complana, E. depressa, E. griseola, E. lurideola, E. lutarella, E. palliatella, E. pseudocomplana, E. pygmaeola, E. sororcula, Epatolmis luctifera, Eublemma ostrina, E. parva, E. polygramma, E. purpurina, Euplagia quadripunctaria, Euproctis chrysorrhoea, Grammodes stolida, Gynaephora fascelina, Herminia grisealis, H. tarsicrinalis, H. tar- sipennalis, H. tenuialis, Hypena crassalis, H. lividalis, H. obesalis, H. obsitalis, H. proboscidalis, H. rostralis, Hypenodes humidalis, Hyphantria cunea, Idia calvaria, Laspeyria flexula, Leucoma salicis, Lithosia quadra, Lyge- phila craccae, L. lusoria, L. pastinum, L. viciae, Lymantria dispar, L. monacha, Macrochilo cribrumalis, Meta- chrostis dardouini, Mitochrista miniata, Minucia lunaris, Nudaria mundana, Ocneria rubea, Ocnogyna parasita, Orgyia antiqua, O. recens, Paidia rica, Paracolax tristalis, Parascotia fuliginaria, Pechipogo strigilata, Pelosia muscerda, P. obtusa, Phragmatobia fuliginosa, Phytometra viridaria, Polypogon gryphalis, P. plumigeralis, P. tentacularia, Rivula sericealis, Schrankia costaestrigalis, S. taenialis, Scoliopteryx libatrix, Setina irrorella, Sphrageidus similis, Spilarctia lutea, Spilosoma lubricipeda, S. urticae, Thumatha senex, Trisateles emortualis, Tyria jacobaeae, Watsonarctia deserta, Zanclognatha lunalis, Z. zelleralis						
	Euteliidae	Eutelia adulatrix						
Noctuoidea	Noctuidae	Abrostola agnorista, A. asclepiadis, A. tripartita, A. triplasia, Acontia trabealis, Acosmetia caliginosa, Acronicta aceris, A. alni, A. auricoma, A. cuspis, A. euphorbiae, A. leporina, A. megacephala, A. menyanthidis, A. psi, A. rumicis, A. strigosa, A. tridens, Actebia multifida, A. praecox, Actinotia polyodon, Aedia funesta, A. leucomelas, Agrochola helvola, A. laevis, A. litura, A. lota, A. lychnidis, A. macilenta, A. nitida, A. pistacinoides, A. ruticilla, Agrots bigramma, A. cinerea, A. clavis, A. exclamationis, A. fattidica, A. ipsilon, A. puta, A. segelum, A. simplo-nia, A. trux, A. vestigialis, Allophyeo svyacanthae, Ammoconia caecimacula, A. senex, Amphipoea fucosa, A. lucens, A. oculea, Amphipya berbera, A. cinnamomea, A. livida, A. perflua, A. pyramidea, A. tragopoginis, Anaplectoides prasina, Anarta melanopa, A. myrtilli, A. odontites, A. trifolii, Anorthoa munda, Antitype chi, A. suda, Apamea anceps, A. aquila, A. crenata, A. epomidion, A. furva, A. lityria, A. lateritia, A. lithoxylaea, A. maillardi, A. monoglypha, A. platinea, A. remissa, A. rubrirena, A. scolopacina, A. sordens, A. sublustris, A. unanimis, A. zeta, Aporophyla lutulenta, A. nigra, Apterogenum ypsillon, Archanara dissoluta, A. neurica, Asteroscopus sphinx, Atethmia centrago, Attetis gluteosa, A. hopese, A. pallustris, Kybpha pulmonaris, Auchmis detersa, Autographa aemula, A. bractea, A. gamma, A. jota, A. pulchrina, Axylia putris, Brachionycha nubeculosa, Brachylomia viminalis, Bryophila domestica, B. ereptricula, B. petricolor, B. raptricula, B. ravula, Bryopsis muralis, Calaraita tridens, C. lativiena, C. kadenii, C. montana, C. morpheus, C. selini, C. terrea, C. wullschlegeli, Ceramica pisi, Cerapteryx graminis, Cerastis leucographa, C. rubricosa, Chardrina asperesa, C. clavipalpis, C. fadvergij, C. cuprea, C. fimbriola, C. margaritacea, C. multangula, C. orelina, C. creliaris, Clemathada calberlai, Colocasia coryli, Conistra erythrocephala, C. liguta, C. rubiginosa, C. torbiginosa, C. tortida, C. vaccinii, Cosmia affinis, C.						

	furcifera, L. leautieri, L. ornitopus, L. semibrunnea, L. socia, Litoligia literosa, Luperina dumerilii, L. testacea, Lu- teohadena luteago, Lycophotia porphyrea, Macdunnoughia confusa, Mamestra brassicae, Melanchra persicar- iae, Mesapamea secalis aggr., Mesogona acetosellae, M. oxalina, Mesoligia furuncula, Mniotype adusta, M. satura, M. solieri, Moma alpium, Mormo maura, Mythimna albipuncta, M. anderreggii, M. congrua, M. conigera, M. ferrago, M. impura, M. I-album, M. pallens, M. pudorina, M. riparia, M. sicula, M. straminea, M. turca, M. unipuncta, M. vitellina, Naenia typica, Noctua comes, N. fimbriata, N. interjecta, N. interposita, N. janthe/janthina aggr., N. orbona, N. pronuba, N. tirrenica, Nonagria typhae, Ochropleura plecta, Oligia dubia, O. latruncula, O. strigilis, O. versicolor, Opigena polygona, Orbona fragariae, Orthosia cerasi, O. cruda, O. gothica, O. gracilis, O. incerta, O. miniosa, O. opima, O. populeti, Pachetra sagittigera, Panchrysia deaurata, P. v-argenteum, Panemeria tenebrata, Panolis flammea, Panthea coenobita, Papestra biren, Paradiarsia punicea, Parastichtis suspecta, Peridroma saucia, Phyllophila obliterata, Plusia festucae, Polia bombycina, P. hepatica, P. nebulosa, P. serratilinea, Polychrysia moneta, Polymixis rufocincta, P. xanthomista, Polyphaenis sericata, Protolampra so- brina, Pseudeustrotia candidula, Pyrrhia umbra, Rhizedra lutosa, Rhyacia helvetina, R. lucipeta, R. simulans, Rusina ferruginea, Sedina buettneri, Sideridis kitti, S. lampra, S. reticulata, S. rivularis, S. turbida, Spaelotis rav- ida, S. senna, Spodoptera exigua, Standfussiana lucernea, S. wiskotti, Staurophora celsia, Sunira circellaris, Syngrapha ain, S. hochenwarthi, S. interrogationis, Thalpophila matura, Tholera cespitis, T. decimalis, Tiliacea aurago, T. citrago, Trachea atriplicis, Trichoplusia ni, Trigonophora flammea, Tyta luctuosa, Xanthia togata, Xes- tia alpicola, X. ashworthii, X. baja, X. c-nigrum, X. castanea, X. collina, X. ditrapezium, X. lorezi, X. ochreago, X. rhaetica, X. sexstrigata,
Nolidae	Bena bicolorana, Earias biplaga, E. clorana, E. vernana, Meganola albula, M. strigula, M. togatulalis, Nola aeru- gula, N. confusalis, N. cucullatella, N. subchlamydula, Nycteola asiatica, N. degenerana, N. revayana, N. sicu- lana, Pseudoips prasinana
Notodontidae	Cerura erminea, C. vinula, Clostera anachoreta, C. anastomosis, C. curtula, C. pigra, Drymonia dodonaea, D. obliterata, D. querna, D. ruficornis, D. velitaris, Furcula bicuspis, F. bifida, F. furcula, Gluphisia crenata, Harpyia milhauseri, Leucodonta bicoloria, Notodonta dromedarius, N. tritophus, N. ziczac, Odontosia carmelita, Peridea anceps, Phalera bucephala, Pheosia gnoma, P. tremula, Pterostoma palpina, Ptilodon capucina, P. cucullina, Ptilophora plumigera, Spatalia argentina, Stauropus fagi, Thaumetopoea pityocampa, T. processionea

**Table S1.2** Attribution of land-use and land-cover categories distinguished in the "Arealstatistik" to broad land-use types used in this study. Numbers show codes used in the "Arealstatistik".

Land-use type	Arealstatistik categories
Forests	Forests (without agricultural usage) (NOLU300)
Grasslands	Natural meadows (NOLU222), Pastures (NOLU223), Alpine meadows (NOLU241),
	Alpine and Jura pastures (NOLU242), Alpine sheep pastures (NOLU243)
Croplands	Orchards (NOLU201), Vineyards (NOLU202), Horticulture (NOLU203), Arable land
	(NOLU221)
Sealed area	Paved areas (NOLC11), Buildings (NOLC12), Greenhouses (NOLC13)

Table S1.3 Detailed model results for the models analysing the relation of elevation, landscape composition, weather, season and other covariates to moth abundance, richness, and biomass. Fixed effects of linear effects and splines and standard deviations of random factors and splines are given. For factors, sum-to-zero contrasts were used. Point estimates and 95% credible intervals (95%-CI) are given. If 95%-CI do not include zero, numbers are bold.

			Abundance			Richness			Biomass		
Para- meter	Туре	Variable	Estimate	Lower 95%-Cl	Upper 95%-Cl	Estimate	Lower 95%-Cl	Upper 95%-Cl	Estimate	Lower 95%-Cl	Upper 95%-Cl
		Proportion forests	0.377	0.215	0.532	0.228	0.115	0.341	0.310	0.150	0.476
		Proportion grasslands	0.00396	-0.160	0.169	-0.0365	-0.154	0.0692	-0.00262	-0.157	0.159
		Proportion croplands	0.000358	-0.135	0.133	-0.0435	-0.135	0.0512	-0.00280	-0.136	0.130
		Proportion sealed area	0.0971	-0.0149	0.206	0.0627	-0.00646	0.137	0.0970	-0.00918	0.199
		Precipitation	0.0138	0.00202	0.0254	0.00405	-0.00306	0.0115	0.0206	0.00817	0.0325
Fixed	Fixed	Temperature	0.727	0.703	0.752	0.597	0.582	0.611	0.524	0.500	0.549
		Trap type (contr. sum 1)	-0.426	-0.737	-0.112	-0.325	-0.543	-0.106	-0.320	-0.637	-0.00668
		Trap type (contr. sum 2)	-1.03	-1.62	-0.454	-0.494	-0.918	-0.0831	-0.982	-1.56	-0.398
		Lamp type (contr. sum 1)	-0.300	-0.619	0.0186	-0.174	-0.375	0.0277	-0.281	-0.588	0.0435
effect		Lamp type (contr. sum 2)	-0.0653	-0.721	0.594	-0.125	-0.500	0.269	-0.207	-0.859	0.489
		Lamp type (contr. sum 3)	-0.378	-0.689	-0.0532	-0.189	-0.389	0.0214	-0.377	-0.688	-0.0541
		Nr. of traps (linear)	0.323	-0.677	1.30	0.245	-0.391	0.920	0.263	-0.691	1.18
		Nr. of traps (quadratic)	-0.408	-1.16	0.305	-0.280	-0.762	0.183	-0.513	-1.22	0.196
		Nr. of traps (cubic)	-0.337	-0.701	0.0257	-0.176	-0.408	0.0706	-0.391	-0.767	-0.0303
		Sampl. prev. night (contr. sum 1)	-0.106	-0.169	-0.0421	-0.0635	-0.103	-0.0222	-0.131	-0.190	-0.0699
		Elevation	1.97	-3.10	5.20	0.246	-3.06	2.44	3.19	-0.838	6.09
	Spline	Day of year	-23.3	-28.0	-18.7	-8.57	-12.3	-4.76	-18.7	-23.2	-14.4
		Hrs. active	6.63	1.85	11.2	3.97	0.878	7.49	5.54	0.843	10.2
		Spat-temp. cluster	0.267	0.196	0.334	0.133	0.0907	0.173	0.270	0.204	0.337
	Random	Sampling night × Location	0.795	0.774	0.816	0.481	0.472	0.489	0.599	0.579	0.619
SD		Site ID	0.521	0.453	0.601	0.369	0.321	0.421	0.501	0.434	0.575
		Site ID × Year	0.234	0.196	0.276	0.141	0.120	0.164	0.228	0.190	0.271
		Elevation	1.60	0.0461	5.87	0.789	0.0489	2.47	1.06	0.0347	3.63
	Spline	Day of year	12.6	8.07	20.5	5.88	3.79	9.30	11.0	7.11	17.3
		Hrs. active	1.87	0.938	3.49	1.21	0.528	2.46	1.91	0.890	3.84

Nr. of traps: Number of traps

Sampl. prev. night: Sampling in previous night Spat.-temp. cluster: Spatio-temporal cluster



**Fig. S1.1** Pictures of the three trap types that were used for sampling. (a) fixed trap ("type 1"), (b) manual trap, (c) fixed trap ("type 2"). Pictures from Rezbanyai-Reser (2014, 2018a).



Fig. S1.2 Number of sites per year with respect to the number of traps that were active. Panels on the left show fixed trap samples, panels on the right show manual trap samples.



**Fig. S1.3** Number of sites per year with respect to the lamp type that was used. Panels on the left show fixed trap samples, panels on the right show manual trap samples.



**Fig. S1.4** Spatial distribution of sampling sites in Switzerland. Points show sampling sites, colour indicates traptype and point size indicates the number of years in which the site was sampled. Shading of the map shows elevation (darker shading for lower elevation). The top left inlet shows the distribution of study sites across the elevation gradient (meter above sea level).



**Fig. S1.5** Overview of single sampling nights, arranged chronologically across the whole study period. Each vertical line connects samples from one site and one year. They build blocks of one year, indicates by the shading of the background (starting top left with 1972, ending bottom right with 2021). The *y* axis denotes the day of the year (between 1 and 366) of the sampling night. Single sampling night are shown as points (which might overlay for very dense sampling periods), colors differentiate the fixed samplings (blue) and manual samplings

(red).



**Fig. S1.6** Comparison of empirical data distribution and 100 draws of the posterior predictive distribution from the (**a**) abundance, (**b**) richness and (**c**) biomass models. Lines show kernel density estimates for empirical data (turquoise) and posterior predictive (purple) distributions, bars show histograms of the empirical data distributions. For abundance and richness, a zero-inflated negative binomial distribution was used, whereas for biomass, a hurdle gamma distribution was used. Note that the *x* axes are on log scale (after adding the minimal non-zero value to all values).



**Fig. S1.7** Conditional effects of different model covariates in the abundance, richness, and biomass model. The *y* axis shows predicted abundance, richness, or biomass. Point estimates are in green, shaded areas or error bars show 95% uncertainty intervals. Underlying points show data per sampling night (n = 35,847). Detailed model results in Table S1.3.