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ORIGINAL PAPER

Moths in the Pyrénées: spatio-temporal patterns and indicators of elevational assemblages

E. J. Dale[1] · R. L. Kitching[1] · C. Thebaud[2] · S. C. Maunsell[1,3] · L. A. Ashton[1,4,5]

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Abstract

Understanding how assemblages of invertebrates change over continuous elevational gradients not only generates an understanding of current rules of community assembly but may also be useful for predicting the future distributions of species under global change. Temperature decreases predictably with increasing elevation and, accordingly, gradients in elevation permit the study of adjacent climates within small geographical areas. The present study examines if and how assemblages of moths change with increasing elevation in the eastern French Pyrenees. Elevation had a strong effect on the assemblage composition of moth species in both seasons. The species sets which contributed most to this strong pattern differed completely across seasons. Analysis of restrictions and fidelity to particular elevational ranges generated a set of indicator species which can be used to monitor future changes in distribution. Twelve species were identified as elevation-specific indicators (the 'predictor set') from the spring samples and summer samples. We note the strong contrasts between species that produce overall statistical pattern and those that show strong fidelity to particular elevations and discuss this in terms of the biologies of the species concerned. We discuss best practice for the identification and use of indicator species for monitoring future responses to climate change.

Keywords Moths · Elevational gradients · Indicator species · Assemblage turnover

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✉ L. A. Ashton
lashton@hku.hk

[1] Environmental Futures Research Institute, Griffith University, Brisbane 4111, Australia

[2] Laboratoire Evolution & Diversité Biologique (EDB, UMR 5174), CNRS/ENSFEA/IRD/Université Toulouse III, 118 Route de Narbonne, 31062 Toulouse, France

[3] Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

[4] Department of Life Sciences, Natural History Museum, London W127BX, UK

[5] School of Biological Sciences, The University of Hong Kong, Hong Kong, China

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Introduction

Moths are one of the preferred targets in community and landscape ecology. They are taxonomically better known across more biogeographical regions than other large Orders of insects; they are sufficiently abundant to produce sample sizes with statistical power (Common 1990; Scoble 1992); they represent a wide diversity of evolutionary lineages (Highland et al. 2013); and, are ecologically diverse (Kitching et al. 2000). In addition, they can be readily mass sampled using automated light traps producing large samples that generate power for the detection of spatial and temporal patterns. As a group, and in contrast to the other three insect 'mega'-orders (Coleoptera, Diptera and Hymenoptera), moths are predominately herbivorous which connects them functionally to their hosts (Common 1990; Kitching et al. 2015) and the plant associations within which they occur. For all of these reasons moths have become a popular target of ecologists examining community turnover and environmental heterogeneity (Alonso-Rodríguez et al. 2017; Ashton et al. 2014; Axmacher and Fiedler 2008; Beck et al. 2002; Fiedler et al. 2007; Kitching et al. 2013; Nöske et al. 2008; Truxa and Fiedler 2016).

Elevational gradients present the opportunity to examine, at relatively small geographical scales, changes in ecological diversity and dynamics in response to varying climate-related environmental conditions (Colwell et al. 2016; Hodkinson 2005; Kitching et al. 2011). Moths, again, have become a popular target group in this respect with recent studies within Australian (Odell et al. 2016), Oriental (Ashton et al. 2016a; Chen et al. 2009), Afrotropical (Axmacher and Fiedler 2008), European (Beck et al. 2010) and Neotropical (Brehm et al. 2007, 2016) forested regions. Cross continental comparisons have also proved feasible and valuable (Beck et al. 2017; Colwell et al. 2016).

The Pyrenean transect described here is the latest in a series of such studies we have carried out in subtropical and tropical Australia (4 transects) (Ashton et al. 2011, 2016b; Odell et al. 2016) and tropical to subalpine, south-western China (3 transects) (Ashton et al. 2016a; Ji et al. 2013).

These earlier studies, mostly within tropical and sub-tropical forests have two limitations which, ultimately, limit the interpretation of their results. First the species encountered are frequently undescribed or, for a variety of reasons, cannot be readily identified. Second, and, in part consequential on this limited taxonomic knowledge, even when a species can be identified the amount of specific-level life-history information available from these regions is limited (Axmacher and Fiedler 2008; Odell et al. 2016). These locations simply lack the immense base of accessible historical taxonomic and natural historical information that is required to convert diversity data into functionally based ecological information. It was for these reasons that we have extended our tropical and subtropical work to the eastern French Pyrénées.

Within the European context, the Pyrénées (and, in particular, the Eastern Pyrénées) have been shown to retain important remnants of primary forest with accordingly high conservation values (Sabatini et al. 2018). Although our sites were located on the northern slopes of the ranges (most of the key locations identified by Sabatini et al. (2018) are on the south-facing slopes in Spain rather than France) they nevertheless are close to these areas of high diversity.

Based on general considerations of moth biology we make the following predictions.

1. Moth species richness will decline with elevation reflecting the more demanding local climate.

2. The species composition of the moth assemblage will shift with changing elevation.
3. There will be a general correlation of the elevation-driven changes in the moth assemblages with the local plant assemblages, at least at the plant-generic level (the level at which most host-plant specialization occurs) (Novotny et al. 2002).
4. A subset of species of moths will drive the elevational patterns we observe statistically, generally based on their relative abundances.
5. A second subset of species, which may or may not be the same as the first, will form a 'predictor set' of indicator species based on their restricted elevational distributions and fidelity to sites within particular elevational bands.
6. The sets of species which drive elevational partitioning will change with season.

In order to test these predictions, we examine the role of elevation in defining moth assemblages based on species-level data (on both richness and composition) across two seasons and compare these patterns to those shown by a parallel study of plant diversity from the same locations. We extract from these data those species which, through their restrictive elevational distributions and fidelity of occurrence at those elevations, are properly proposed as indicators for future distribution monitoring.

Methods

Study sites

We established our transects within adjacent valleys of the Rivers Aude (and its higher tributary, l'Aiguette) and Rébenty in the French department of Aude (Fig. 1). These rivers drain from the saddle connecting the Pic Carlit (2921 m) and the Dent d'Orlu (2222 m) and flow, generally, north-eastwards. All study sites were located within a limestone landscape, with habitats ranging from Mediterranean to submountainous woodlands and forests (Leguédois et al. 2014). A general account of the geography and natural history of the region is provided by Dendaletche (1997).

Average mean maxima temperature at Axat, the village closest to our 500 m above sea level (a.s.l.) sites (Lat N42.806, Long E2.231, altitude 504 m a.s.l.) varied from 6.0 °C (January/February) to 23 °C (July/August) between 2012 and 2015. Mean minimum varied from −2 °C (January/February) to 10 °C (July/August). Monthly mean precipitation varied from ca 18 mm (January) to ca 60 mm (May) (*Source* www.worldweatheronline.com/axat-weather-averages/languedoc-roussillon/fr.aspx).

Sampling sites were established between 500 m above sea level (a.s.l.) and 1300 m a.s.l. in the spring (May 14th–26th) of 2012 and the summer (Aug. 22nd–Sept 12th) of 2015. Sampling locations were situated in bands separated elevationally by approximately 200 m (±50 m) [500, 700, 900, 1100 and 1300 m a.s.l. (Fig. 1)]. In 2012 four sampling sites within each elevational band were established each separated laterally (wherever possible) by a minimum of 400 m generating a total of 20 locations. In 2015 we expanded the sampling to include a fifth site within each band, resulting in a total of 25 sites being sampled. This new set of five plots at 500, 700, 900, 1100 and 1300 m a.s.l. were located in a geographically separate valley from the existing plots (Fig. 1), in order to minimize spatial-auto correlation. All sites were established within forests and woodlands and, in 2015, a plant survey was conducted around a 20 m radius of moth trapping location. The presence or absence of seed plant genera within this area was recorded.

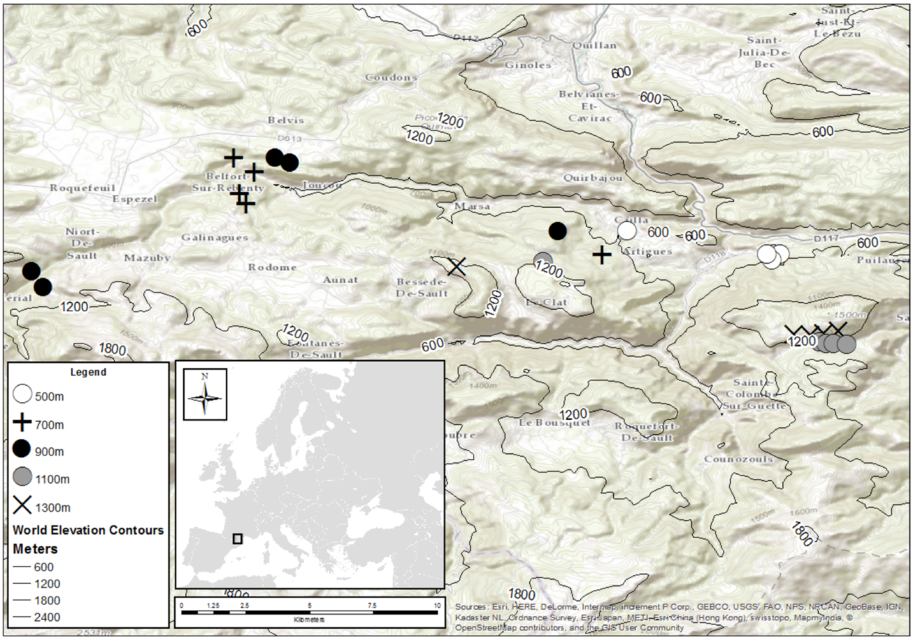


Fig. 1 Map of plots within adjacent valleys of the Rivers Aude (and its higher tributary, l'Aiguette) and Rébenty in the French department of Aude

Insect sampling

The general approach and experimental design for the survey of moths employed within this study are essentially the same as employed within the 'IBISCA' projects (Ashton et al. 2011; Didham and Fagan 2003; Kitching et al. 2011) and subsequent projects in Yunnan, China (Ashton et al. 2016a) and Australia (Ashton et al. 2016b; Odell et al. 2016). We used modified Pennsylvanian-style light traps, the same design as was used in the IBISCA studies (Kitching et al. 2005). These traps comprise a vertical actinic tube mounted among three transparent vanes, above a collecting funnel and bucket. A dichlorvos™-impregnated resin strip is used as a killing agent. A single trap was run at each site for 3–4 nights (with, wherever possible, all sites within an elevational band being run simultaneously). The moon phase is known to affect the efficacy of light traps (Yela and Holyoak 1997) so we avoided trapping in the week around the full moon.

All conventionally designated macromoths, all Pyraloidea and Tortricoidea were identified and counted. In addition other 'micros' with a forewing length greater than 10 mm were included in our dataset. Moth identification used the full range of guides available for France and the European region (Hausmann 2004; Hausmann and Viidalepp 2012; Leraut 2014; Razowski 2002, 2003; Bachelard et al. 2011; Skou and Sihvonen 2015; Slamka 2006, 2008, 2013; Skinner 1998) as well as key websites (*ukmoths.org.uk*; *lepiforum.de*). Eupitheciine larentiines (Geometridae) were collected and preserved but cannot be readily identified without dissection and were excluded from our analyses. The few tortricids in our collections which could not be identified using external wing pattern features, were also excluded.

Data analysis

For both data sets (2012 and 2015), information from the several trapping nights at each location was combined to form a single data point for each sampling site in each of the two seasons.

Abundance coverage-based estimator (ACE), an estimation of total species richness, was calculated for each elevation and each season, using the software package EstimateS (Colwell 2006). Assemblage composition for each season based on the data on moth species was visualized using Non-metric Multiple Dimensional Scaling (NMDS) ordination plots using the '*vegan*' (Oksanen et al. 2016) package in R, following construction of Bray–Curtis dissimilarity metrics. To illustrate the relationship between elevation as a continuous variable and moth assemblage composition, we used the 'ordisurf' function in the *vegan* package in R to fit smooth surface response using a gam (generalised additive model) which allows for the detection of non-linear relationships. Ordinations were carried out using abundance data for the moths and presence/absence data for the plant genera. We tested for spatial autocorrelation within the moth data using Moran's I test. The correlation between the moth and plant communities was assessed using a Mantel test with 999 permutations, carried out with the *Relate* function in PrimerE (Clarke and Gorley 2015). We used the same function to examine spatial auto-correlation, comparing the physical distances between plots (m) and moth assemblages. We carried out Mantel tests for 2012 data, and for the 2015 data with and without the additional 5 plots surveyed in 2015. This approach allowed us to tease apart the factors shaping our results and to see if spatial-autocorrelation is a major factor shaping our moth turnover results. For illustrative purposes, moth assemblage data was presented in ordination plots using the '*ordihull*' function within the *vegan* package.

Multivariate generalised linear modelling was used to test the effect of altitude on moth assemblages and each sampling year (season) was analysed separately. Singletons (species recorded only once across all sites during each sampling location) were excluded from the analysis. 221 species were sampled in 2012 and 68 of these were singletons and removed for analysis, leaving 153 species. 265 species were sampled in 2015 and 75 of these were singletons, leaving 190 species. These numbers are comparable/similar given that an additional five sites were sampled in 2015. For each sampling year, we used the 'manyglm' function within the R package "mvabund" (Wang et al. 2012a, b) to fit a multivariate generalised linear model with altitude as the predictor variable and multiple species abundances the response variables. This model-based approach allows for hypothesis testing, and unlike distance-based methods, is not confounded by the mean–variance relationship and location-dispersion effects (Warton et al. 2011). Since data was comprised of counts and contained many zeros, negative binomial regressions were fit for each species and the model assumption of equal variance was validated by plotting residuals against fitted values (which showed no obvious pattern). An assemblage-level effect of altitude on moth distributions was evaluated using the *anova.manyglm* function which resampled the fitted model using 'pit-trap' bootstrapping to resample abundance data to account for correlations among species. p-values were estimated from 999 bootstraps adjusted for each species to account for multiple testing. Individual species that responded most strongly to elevation (adjusted $p > 0.05$) were identified.

This analysis is a regression approach, where altitude was treated as a continuous variable, and is aimed at detecting a linear relationship between altitude and species composition (but assuming a negative binomial distribution to link the linear predictor variable to abundance data) by assessing changes for individual species.

We used the methodology of Dufrene and Legendre (1997) to identify, for each season, a set of species which exhibit both restricted elevational distributions and cross-site fidelity within those elevations. For this purpose we used the package *labdsv* (Roberts 2007) and the functions *indval* and *clust1* in R. We selected those species with an IndVal value greater than or equal to 0.70 (Van Rensburg et al. 1999) as being sufficiently restricted and common at specific elevations to form part of set of indicators. IndVal treats altitude like a factorial variable and is concerned with detecting if species are representative of particular (or groups of) altitudinal bands, rather than looking at gradual changes with incremental increases in altitude (as the multivariate glm does).

We used information available in several reference texts on the life histories of the moths of the Pyrenees (Leraut 2014; Razowski 2002, 2003; Bachelard et al. 2011) to investigate the biologies of both the 'statistical driver species' (those identified as significant in our GLM analyses) and 'indicator species' (significant IndVal species) to link the life histories of these species to the observed elevational turnover.

Results

Summary results on the abundance, richness and diversity of our samples are presented in Table 1. In spring 2012, a total of 2131 individuals representing 196 species were sampled and, in summer 2015, 4796 individuals were collected representing 267 species. ACE extrapolations suggest a spring fauna of 261 ± 2.72 species and a summer fauna of 339 ± 1.1 species indicating that, in spring, we sampled more than two-thirds of the total fauna and, in summer, over three-quarters. In total, we sampled 309 species across the two sampling occasions. In addition, 91 unidentified morphospecies, mostly occurring as singletons, were included in our analyses.

The spring samples were dominated, both in terms of abundance and species richness, by the Geometridae (69% in terms of abundance, 38% in terms of richness). The Noctuidae ranked second in terms of dominance (13 and 18% respectively). The summer samples contained a more even distribution of families although Geometridae and Noctuidae again dominated (Geometridae abundance 37%, species richness 20%; Noctuidae abundance 36%, species richness 35%). The Pyraloidea (Crambidae and Pyralidae) were a very significant part of the summer fauna (abundance 12%, richness 15%) yet were an insignificant fraction of the spring fauna (abundance $< 1\%$, richness 4%).

In the spring of 2012, abundance was highest at 500 m and species richness was fairly uniform between 500 and 1100 m a.s.l., with a sharp decline at 1300 m a.s.l. In the summer of 2015 abundance and richness were highest at 500 m. The results of the NMDS analysis for both the spring and summer are presented as Fig. 2. For the spring data the samples from the two highest elevations cluster tightly together and clearly represent a different species assemblage. The lower elevations are clearly separated from the samples from higher elevations, but also cluster individually according to elevation. The summer samples are, in general, less tightly clustered, but the basic elevational turnover of moth communities seen in spring are maintained.

Mantel tests between moth assemblages and distances between plots showed that there was spatial autocorrelation in spring 2012 moth samples ($\rho = 0.558$, $p = 0.001$). When we tested the correlation between physical distance (m) and moth assemblages for

Table 1 Catch summaries for moths in the Pyrénées for Spring 2012 and late summer 2015

	Spring 2012						Summer 2015					
	Total	500	700	900	1100	1300	Total	500	700	900	1100	1300
Total abundance	2129	506	392	494	450	287	4796	1726	773	817	900	580
Richness	196	84	96	105	89	39	267	177	148	135	129	99
ACE mean	291.17 ± 2.72	169.57 ± 6.44	197.94 ± 9.74	152.48 ± 7.75	175.43 ± 9.75	63.23 ± 7.15	338.67 ± 1.1	239.88 ± 5.34	216.2 ± 10.2	195.75 ± 7.35	188.25 ± 6.71	153.56 ± 5.96
Results for major taxa												
Pyraloidea												
Abundance	20	3	1	9	7	0	568	313	62	66	88	39
Richness	8	1	1	3	5	0	39	25	16	12	21	13
Geometridae												
Abundance	1477	338	253	319	322	245	1796	602	326	287	316	265
Richness	74	43	48	50	31	19	78	58	44	45	38	35
Erebidae												
Abundance	142	35	25	58	9	15	529	288	83	51	91	16
Richness	10	5	8	6	4	5	17	11	12	10	9	3
Noctuidae												
Abundance	279	87	65	58	62	7	1724	460	174	367	383	240
Richness	36	14	15	20	20	4	93	61	59	48	51	41
Other												
Abundance	211	43	48	50	50	20	179	63	128	46	22	20
Richness	68	21	24	26	29	11	40	22	17	20	10	7

Note that 2015 counts are based on five sites per elevation, 2012 on four (see text)

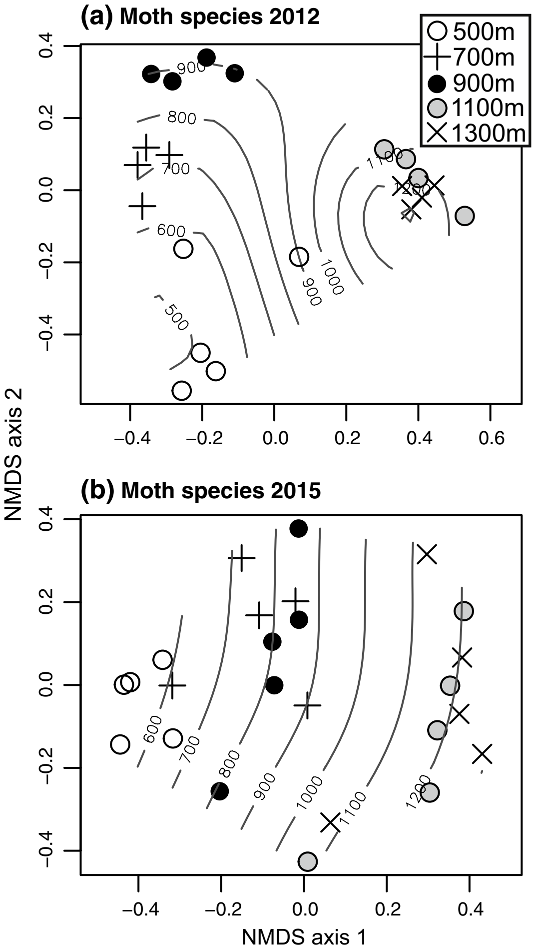


Fig. 2 Multi-dimensional scaling ordination plots of moth assemblages for **a** spring 2012 and summer **b** 2015. Different elevational bands are represented by different symbols. Contour lines illustrate the relationship between elevation as a continuous variable and moth assemblage composition and were fit as a smooth surface response using a generalised additive model

the 20 original plots for summer 2015 moth data, there was also spatial-auto correlation ($\rho = 0.421$, $p = 0.001$). However, when we included an additional 5 plots, at 500, 700, 900, 1100 and 1300 m a.s.l., spread across an adjacent valley, this correlation was reduced ($\rho = 0.277$, $p = 0.002$). This change, through a relatively minor increase in sampling intensity, supports the importance of elevation in driving our results, rather than the observed moth turnover being an artefact of spatial-auto correlation. As expected, there was correlation between the moth and plant assemblages in both spring ($\rho = 0.368$, $p = 0.001$) and summer ($\rho = 0.448$, $p = 0.001$).

The multivariate GLM analyses support the hypothesis that elevation is a significant driver of moth species distribution in both seasons (2012: deviance = 421.89, $p < 0.001$ and 2015: deviance = 716.49, $p < 0.001$). These analyses also identified the species of most statistical importance in generating the more general, assemblage-level result (Table 2). Elevational distributions for these species are shown in Fig. 3. For the spring samples, four of these species (two geometrids, an erebid (Arctiinae) and a noctuid) are lowland specialists with distributions tailing off (or absent) at higher elevations. The remaining species (the geometrid *Entephria flavicinctata*) had its

Table 2 Species with adjusted $P < 0.05$ (to account for multiple testing) when testing the effect of altitude as a continuous predictor variable on individual species abundances using multivariate generalized linear modeling (mvabund)

Year	Family	*Genus*	*Species*	Model deviance	Relationship with elevation	Adjusted *p* value
Spring 2012	Erebidae	*Eilema*	*sororcula*	18.831	Decrease	0.006
Spring 2012	Noctuidae	*Orthosia*	*gothica*	18.795	Decrease	0.006
Spring 2012	Geometridae	*Cyclophora*	*lennigiaria*	17.769	Decrease	0.01
Spring 2012	Geometridae	*Cleora*	*cinctaria*	16.449	Decrease	0.014
Spring 2012	Geometridae	*Entephria*	*flavicinctata*	14.56	Increase	0.034
Summer 2015	Geometridae	*Pachycnemia*	*hippocastanaria*	23.85	Decrease	0.001
Summer 2015	Noctuidae	*Stilbia*	*anomala*	21.05	Decrease	0.005
Summer 2015	Erebidae	*Eilema*	*depressa*	20.588	Decrease	0.005
Summer 2015	Crambidae	*Anania*	*terrealis*	19.183	Decrease	0.009
Summer 2015	Geometridae	*Crocallis*	*elinguaria*	18.532	Decrease	0.009
Summer 2015	Noctuidae	*Noctua*	*janthe*	16.838	Decrease	0.018
Summer 2015	Geometridae	*Cyclophora*	*annularia*	16.545	Decrease	0.022
Summer 2015	Geometridae	*Gerinia*	*honoraria*	16.207	Decrease	0.022
Summer 2015	Drepanidae	*Watsonalla*	*uncinula*	15.998	Decrease	0.026

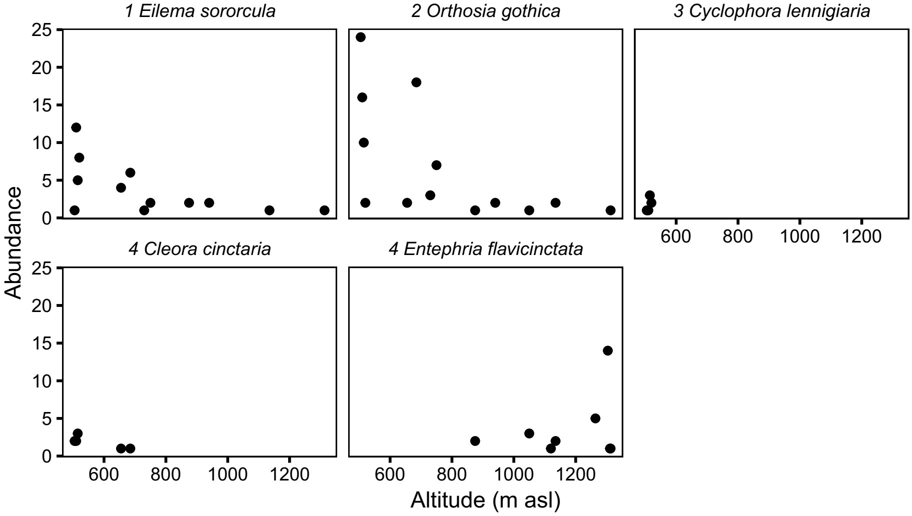
highest abundances at higher elevations and did not occur at all at the two lowest levels. For the summer samples, most species are more abundant at lower elevations, with no higher-elevation specialists contributing to the overall pattern of moth assemblage turnover with elevation.

The results of the indicator value analysis for the spring and summer samples are presented in Table 3. Twelve species are identified for each season with no species being common to both. The species identified as strong indicators for the spring samples comprise nine geometrids, one drepanid, one noctuid and one arctiine (Erebidae). Six species (five geometrids and a drepanid) are indicative of the 500 m samples. A further geometrid indicates 500 and 700 m elevations. Four species (three geometrids and the arctiine) are identified as indicators of the upper two elevations.

The twelve indicator species identified for the summer samples (also Table 3) comprise six geometrids, four noctuids, and two erebids (one hypenine and one arctiine). The 500 m locations are indicated by three geometrids, the highest elevation by six species (three geometrids, two noctuids and an erebid (the hypenine). Two indicator species are characteristic of intermediate elevations (700–1100 m). The noctuid, *Noctua janthe,* is indicative of the 1100 m elevations only. We stress that these results are part of the overall community level analysis (the stated purpose of the study) and that the patterns we found for individual species are site and time specific.

It is noteworthy that only two of the species identified as most significant in the GLM analysis feature in the list of indicators for the spring samples [*Cyclophora lennigiaria* and *Entephria flavicinctata* (Hübner 1813)]. For the summer samples there was a single species (*Noctua janthe*) that overlapped as a significant GLM species and an indicator species.

(a) 2012



(b) 2015

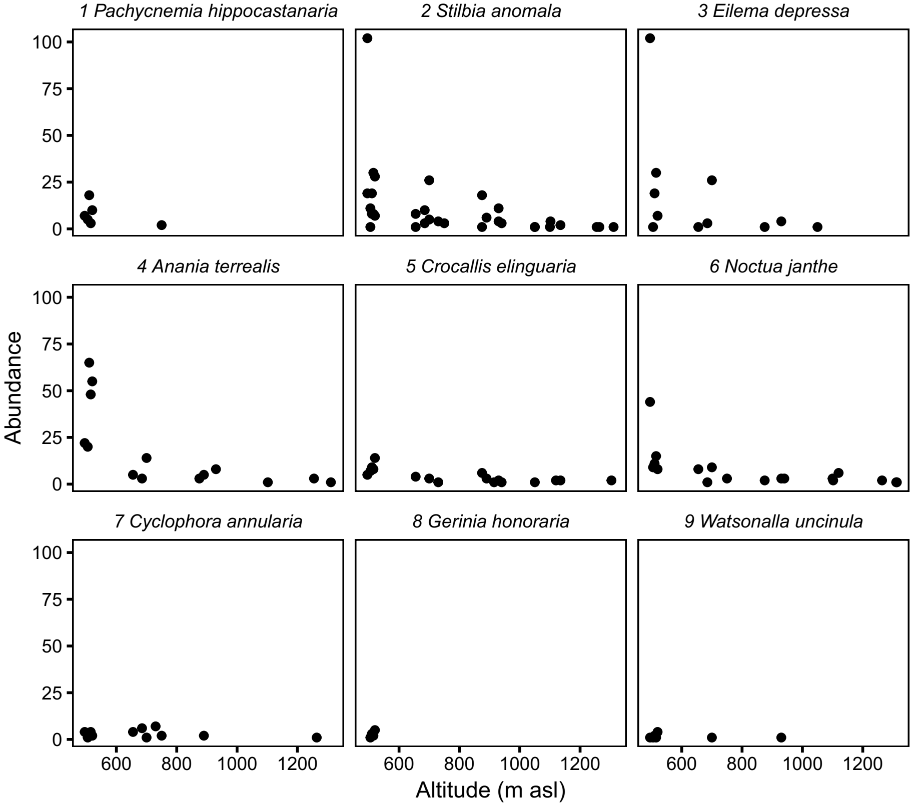


Fig. 3 Species abundances of species which were found to show a significant relationship with elevation (adjusted $p < 0.05$) using multivariate generalized linear modelling (mvabund) in **a** 2012 and **b** 2015. Raw abundances of each species are plotted against the specific altitude of each sampling site

Table 3 Results of the Indicator Value (IndVal) analysis for (a) 2012 and (b) 2015. The Table lists all species that exhibited and indicator value >0.7 in each of the seasons sampled. The shaded areas indicate the elevational ranges of each species. The three species in bold are the only indicator species that were also identified as significant in the glm analyses for the same season

Species	Family: Subfamily	Indicator Value	*p* value	Distribution				
				500m	700m	900m	1100m	1300m
Spring 2012								
Cyclophora lennigiaria	Geometridae: Sterrhinae	1	0.0008	▨				
Isturgia miniosar ia	Geometridae: Ennominae	0.994	0.0004	▨				
Macaria liturata	Geometridae: Ennominae	0.957	0.001	▨				
Watsonalla uncinula	Drepanidae	0.944	0.003	▨				
Gerinia honoraria	Geometridae: Ennominae	0.811	0.0046	▨				
Macaria alternata	Geometridae: Ennominae	0.72	0.0104	▨				
Pachycnemia hippocastanaria	Geometridae: Ennominae	0.921	0.0004	▨	▨			
Entephria flavicinctata	Geometridae: Larentiinae	0.887	0.0036				▨	▨
Watsonarctia casta	Erebidae: Arctiinae	0.818	0.0044				▨	▨
Thera britannica	Geometridae: Larentiinae	0.95	0.002				▨	▨
Thera variata	Geometridae: Larentiinae	0.778	0.0002				▨	▨
Last summer 2015								
Peribatodes abstersaria	Geometridae: Ennominae	0.909	0.003	▨				
Perigune narbonea	Geometridae: Ennominae	0.828	0.0002	▨				
Xanthorhoe fluctuata	Geometridae: Larentiinae	0.737	0.01	▨				
Xestia rhomboidea	Noctidae: Noctuinae	0.9	0.003		▨	▨	▨	
Eilema sororcula	Erebidae: Arctiinae	0.757	0.002		▨	▨	▨	
Noctua janthe	Noctuidae: Noctuinae	0.748	0.0002				▨	
Campaea margarita ria	Geometridae: Ennominae	0.906	0.0002					▨
Hypena proboscidalis	Erebidae: Hypeninae	0.887	0.002					▨
Epirrhoe alternata	Geometridae: Larentiinae	0.771	0.0015					▨
Xestia c-nigrum	Noctuidae: Noctuinae	0.727	0.002					▨
Opisthograptis luteolata	Geometridae: Ennominae	0.719	0.04					▨
Eugnorisma depuncta	Noctuidae: Noctuinae	0.709	0.04					▨

Discussion

We have provided evidence to suggest that elevation is a significant assemblage-level driver of the distribution of moth species in both spring and summer. These results are consistent with the findings of other studies in the Afrotropics (Axmacher and Fiedler 2008), Neotropics (Brehm et al. 2016), Oceania (Kitching 2011), Oriental Regions (Beck et al. 2002; Chen et al. 2009), Australasia (Ashton et al. 2016b; Odell et al. 2016) and the Palaearctic Region (Beck et al. 2010; Choi and An 2010; Hodkinson 2005; Jaroš et al. 2014; Merckx 2015).

Moths are adapted to particular climates reflecting their physiological tolerances (rather than environmental traits) (Majerus 2002) and, in consequence, may be expected to track local climate. This is confirmed in the general pattern observed in this study. Our ordinations identify two major groupings in both seasons (500 m, 700 m and 900 m vs. 1100 m and 1300 m). We suggest that the uppermost elevations may have a different climate from the lower zones, not only because of the decline in temperature and precipitation, but perhaps also related to diminished canopy cover and the persistence of a cloud cap and winter snow cover. This is reflected in the fact that the lowermost sites are mainly a mixture of the meso- and supra-Mediterranean vegetation types while uppermost sits are Mountain-Mediterranean and Mixed Mountain forests (Dupias 1985). The presence of particular species at particular sites may also reflect the availability of larval hosts at those sites: we address this point below.

Our results show strong seasonal variation in the moth species that shape the turnover of moth communities across elevation. Understanding these patterns is best approached through considering the biologies of individual species. We note, first, that the spring samples are much more tightly grouped in ordination space than are the summer ones. It is likely that Spring species bred, overwintered and emerged more or less in situ leading to a close correspondence between elevation and occurrence which translates to the community level in our ordinations. The moth assemblages in summer, in contrast, represent not only resident species but also those that have migrated into the region either as individuals or as the progenitors of a second, higher elevation generation.

There was some correlation between the distribution of moth and plant assemblages across the elevational gradient. Linking the distribution of night-flying moths to the local plant assemblages is possible, as many species do not fly large distances (Common 1990), and low-wattage actinic bulb light traps have small attraction distances (Merckx and Slade 2014). However, the occurrence of larval host plants, per se, was not a highly significant determinant of the assemblage structures. Neither statistically significant species nor those identified by the IndVal analysis showed any marked pattern in the functional group of host-plant preferred (Table 4). We note, however, that lichen-feeding species (the lithosiine Arctiinae) and grass-feeders seldom have their host-plants recorded beyond the general functional group (rather than to host species). Our results, then, suggest that the presence of particular food-plant genera (the level at which most host-plant ‘specialization’ occurs) may, in general, not be as important a determinant of moth assemblage structure at particular elevations as the local microclimate. Moths are very efficient at finding host-plants where they exist regardless of the commonness or rarity of the plant genera concerned.

This is not to say, of course, that local abundance levels may not be enhanced by an abundance of appropriate host-plants. In our results, for example, conifer-breeding species feature as drivers of overall pattern and as significant indicators of elevation (see, e.g., *Thera* spp. in the Summer results, indicators of high elevation). In contrast, however, *Macaria liturata,* also a conifer-feeding species, appears as a low-elevation indicator in the Spring results. Conifers do occur at all elevations (although they dominate the tree cover only at the two highest elevations) suggesting, in this case, that it is micro-climate that is determining the occurrence at least of *M. liturata*, rather than the relative abundance of particular host-plants.

The seasonal variation in those species which emerge as significant in our indicator value analysis sound a note of caution for these and similar results. The set of indicator species identified here are *season-dependent*—applying them at other times of year will simply produce confusion. We also suggest that the whole season-specific set of indicators be used simultaneously and an average occurrence of these species be sought. Undoubtedly individual species will not serve as efficient indicators in every year examined and a single absence or presence may not indicate significant change in ecological conditions. Examining the whole set however will circumvent this potential shortcoming.

A further, principally, technical point is worthy of note here. The four named sets of species we have identified in our results (the two sets of six GLM drivers and the two sets of 12 indicator species) overlap little, and not at all across seasons. This is because the species which occur in the GLM results as most significant may do so because they have very high abundance levels in just some of the sites at particular elevations: that is, they may show high abundance but only low to moderate fidelity across elevational plots. The IndVal analysis incorporates fidelity (to four or five plots in each elevational band) which is heavily weighted in the analysis. In four cases, species occur as statistical drivers in one season and indicators in another. In three of these instances (*Pachynemia hippocastanaria*, *Gerinia honoraria* and *Watsonalla uncinula*), they appear as indicator species in the Spring samples and as statistical drivers in the late summer samples. For *Eilema sororcula* the reverse situation pertains. Analytically these differences suggest that each of these species was among the numerically dominant species in the seasons in which they figure as statistical drivers. In the samples in which they appear as Indicator species, these species were more likely to occur across all sites for which they appear as indicators (Table 3) even when not numerically dominant overall. This underlines the fact that the two analyses we

Table 4 Taxonomy and biology of indicator species (identified with IndVal) and 'statistical drivers' (those species identified as contributing significantly to the elevational pattern by GLM analyses) for Spring 2012 and Summer 2015

Family	Subfamily	Species	Statistical driver?	Indicator species?	Larval feeding guild	Host plant specialisation	Voltinism	Range
Crambidae	Pyraustinae	*Anania terrealis*	Summer	–	Herbs	1 genus	2	Europe
Drepanidae	Drepaninae	*Watsonalla uncinula*	Summer	Spring	Trees	1 genus	2	France to Balkan Peninsula
Erebidae	Arctiinae	*Eilema depressa*	Summer	–	Lichens	Unknown	1–2	Europe to Japan
Erebidae	Arctiinae	*Eilema sororcula*	Spring	Summer	Lichens	Unknown	1	Europe to China
Erebidae	Arctiinae	*Watsonarctia casta*		Spring	Herbs	3 genera	1	Europe to China
Erebidae	Hypeninae	*Hypena proboscidalis*	–	Summer	Herbs	4 genera	2–3	Europe to Japan
Geometridae	Ennominae	*Gerinia honoraria*	Summer	Spring	Trees	2 genera	2–3	Europe
Geometridae	Ennominae	*Campaea margaritaria*	–	Summer	Trees	Many genera	2	South-west Europe
Geometridae	Ennominae	*Cleora cinctaria*	Spring	–	Generalist	Many genera	1	Europe to Japan
Geometridae	Ennominae	*Crocallis elinguaria*	Summer	–	Trees, shrubs	14 genera	1	Europe
Geometridae	Ennominae	*Isturgia miniosaria*	–	Spring	Shrubs	6 genera	1	France to North Africa
Geometridae	Ennominae	*Macaria alternata*	–	Spring	Trees, shrubs	13 genera	2	Europe to Siberia
Geometridae	Ennominae	*Macaria liturata*	–	Spring	Conifers	3 genera	2	Europe to Japan
Geometridae	Ennominae	*Opisthograptis luteolata*	–	Summer	Generalist	11 genera	2–3	Palearctic region and Western Asia
Geometridae	Ennominae	*Pachycnemia hippocastanaria*	Summer	Spring	Herbs	4 genera	2–3	Europe
Geometridae	Ennominae	*Peribatodes abstersaria*	–	Summer	Trees	1 genus	1	Iberian Peninsula
Geometridae	Ennominae	*Perigune narbonea*	–	Summer	Herbs	1 genus	2	Iberian Peninsula
Geometridae	Larentiinae	*Entephria flavicinctata*	Spring	Spring	Herbs	3 genera	1	Palearctic region

Table 4 (continued)

Family	Subfamily	Species	Statistical driver?	Indicator species?	Larval feeding guild	Host plant specialisation	Voltinism	Range
Geometridae	Larentiinae	*Epirrhoe alternata*	–	Summer	Herbs	1 genus	2	Palearctic and North America
Geometridae	Larentiinae	*Thera britannica*	–	Spring	Conifers	3–5 genera	2	Europe
Geometridae	Larentiinae	*Thera variata*	–	Spring	Conifers	3–5 genera	2–3	Europe to Japan
Geometridae	Larentiinae	*Xanthorhoe fluctuata*	–	Summer	Herbs	14 + genera	2–3	Palearctic, North Africa to Japan
Geometridae	Sterrhinae	*Cyclophora annularia*	Summer	–	Trees	1 genus	2	Europe
Geometridae	Sterrhinae	*Cyclophora lennigiaria*	Spring	Spring	Trees	1 genus	2	South-west Europe
Noctuidae	Hadeninae	*Orthosia gothica*	Spring	–	Generalist	Many genera	1	Europe
Noctuidae	Noctuinae	*Eugnorisma depuncta*	–	Summer	Herbs	4 genera	1	Europe
Noctuidae	Noctuinae	*Noctua janthe*	Summer	Summer	Generalist	Many genera	1	Europe to North Africa
Noctuidae	Noctuinae	*Xestia rhomboidea*	–	Summer	Herbs	Many genera	1	Europe to northern Iran
Noctuidae	Noctuinae	*Xestia c-nigrum*	–	Summer	Herbs	Many genera	2	Europe to Japan
Noctuidae	Oncocnemidinae	*Stilbia anomala*	Summer	–	Monocots	Unknown	1	Western Europe

have used test quite different aspects of the data. That species appear to feature differently in different seasons is unsurprising as the two analytical approaches are quite independent of each other. Ecologically we note that the first three species, *P. hippocastanaria, G. honoraria* and *W. uncinula*, are generally bivoltine in this southern part of their ranges and the two generations may well present contrasting phenologies. The case of *E. sororcula* is different. This species is generally regarded as univoltine and its widespread occurrence in the late summer samples is unexpected. This could be because although univoltine, emergence is spread throughout the warmer months: with larvae feeding on ubiquitous lichen this is not entirely improbable. Alternatively its ‘univoltine’ designation may be questionable in the warmer (southern) part of its range. Finally, as a wild card, *Eilema* is a challenging genus taxonomically and the status of the two seasonal populations would bear further examination using modern taxonomic techniques.

It is of interest that the significant species we identified (as both statistical drivers and indicators) were generally (24 of 30) species of wide distributions across Europe and beyond (Table 4, Column 8). This result parallels some of the findings of Kaltsas et al. (2018). These authors examined elevational stratification of butterflies on two Greek mountain massifs and found that at least some of the key species were super-abundant and widespread species. Along with these authors we note that this may, in some instances, simply represent relative abundance and, hence, dominance in any abundance-based statistical analysis. We reiterate, however, that our intention has been to examine stratification at the community level to identify the set of species which reflect changes in elevation. Inevitably such a set is likely to be dominated by the commonest species, as will be any implied changes in ecosystem functioning. As others before us (e.g., Gaston 2010), we suggest that overlooking the role of common species in a conservation context, especially when we focus on ecosystem functioning, is inappropriate.

We return, in summary, to the six predictions we posed in the introduction.

1. Moth species richness generally declines with elevation reflecting the more demanding local climate at higher elevations. The ACE estimators in Table 1 flesh out this pattern which is clear in the late summer samples. The spring samples show how a more complex pattern but again with the fewest species at the highest elevations.
2. There is clear turnover in species composition of the moth assemblages with both elevation and season although the two highest elevations (1100 m and 1300 m) form a single category in this regard.
3. Although there is a general correlation of the elevation-driven changes in the moth assemblages with the local plant assemblages, our data are not fine-grained enough to rate the relative importance of climate versus food-plant availability in determining assemblage composition at each elevation.
4. Two distinct sets, one of six and one of nine species of moths did indeed drive the elevational patterns in spring and summer.
5. Two additional subsets, each of twelve species did form a ‘predictor set’ of indicator species for each season. Only four of these 24 species featured in the set of statistical ‘driver’ species in the same season.
6. Finally, as indicated above, different moth assemblages occurred in each of the two seasons studied and the predictor set for each is not transferrable across seasons.

We conclude with a note of caution. We did not target the highest Pyrenéean forested elevations which may occur up to 1700 m above sea level with, in places, a woody shrubby vegetation at even higher elevations (Dupias 1985). Accordingly, our moth samples did not include, necessarily, alpine or subalpine specialists. Our transect, by design, however, did capture the transition between mesophyllous and coniferous vegetation. We suggest, our results and interpretations not only confirm that moths have great potential as indicators of environmental conditions but also that, when combined with good natural history, throw light on ecological mechanisms which structure communities across landscapes.

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Data availability Data has been deposited at https://osf.io/w2tdz/.

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