

Life-history traits of Central European moths: gradients of variation and their association with rarity and threats

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Abstract. 1. Analysing faunal changes using life-history traits (LHT) represents a promising venue in community ecology. We prepared traits table for 1234 species of Central European macro-moths (Lepidoptera), a species-rich insect group rather neglected by LHT analyses.

2. Table of 27 LHTs, split into 44 trait states, was subjected to ordination analyses, aiming to disclose the main gradients in the traits' covariance organising the regional fauna.

3. The main ordination gradient was related to habitats. It contrasted large-ranging, tree foliage feeding and large-winged species of humid and wooded habitats from small, trophic specialists feeding on reproductive plants parts and inhabiting non-wooded, xeric habitats. This gradient sustained control for phylogeny, as well as omission of habitats- and biogeography-related traits from the analyses. The secondary gradient, perpendicular to the former, distinguished multivoltine and univoltine species, the former often mobile and having a long adult period. Two minor gradients were related to defences/seasonality and to adult diurnal activity.

4. The habitats and voltinism gradients predicted current commonness and red-list status of individual species reasonably well.

5. Life histories are linked to habitat use, commonness and threat levels of individual moths species in Central Europe. The overwhelming importance of habitat association mirrors the diversity of habitats used by Central European moths. Species of closed woodlands tend to be more common and less threatened than species of rarer grassland types; multivoltine and mobile species are least threatened. The compiled LHT table will be of use for further conservation-oriented analyses of the moths communities.

Key words. Biogeography, habitat selection, life-history traits, macrolepidoptera, moths conservation, ordination.

Introduction

Viewing animal communities or entire faunas through the lens of life-history traits (LHT) of constituent species has become a major current in community ecology and

biogeography (McGill *et al.*, 2006; Gagic *et al.*, 2015). Communities consist of species, but the species' traits have evolved in response to environmental filters. Environmental change shifts the representation of species in communities, and hence the representation of functional traits (e.g. Ockinger *et al.*, 2010; Webb *et al.*, 2010; Games-Virues *et al.*, 2015).

One group where LHT analyses have progressed quite far is that of butterflies, the popular but rather species-

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poor (ca. 18 500 species globally) diurnal subgroup of Lepidoptera (ca. 180 000 species). In temperate faunas and communities, butterfly LHTs tend to form a gradient from highly fecund and mobile species forming multiple generations per year, overwintering in late stages and utilising wide ranges of resources, to species with opposite trait states [generalists-specialist (herein g/s) continuum: Dapporto & Dennis, 2013; Bartonova *et al.*, 2014]. Some attributes of the continuum correspond with the *r*-*K* selection theory (Pianka, 1970). More recent analyses have revealed that traits associated with development speed (e.g. voltinism, body size) are related to host plant form [constrained voltinism (herein cV) continuum] (Bartonova *et al.*, 2014), and that nutrients' quality affect development and phenology (WallisDeVries, 2014). Still, the g/s continuum has provided a conceptual framework to study responses to altitude (Stefanescu *et al.*, 2011; Carnicer *et al.*, 2013), changing climate (Poeyry *et al.*, 2009; Altermatt, 2010), habitat declines (Barbaro & van Halder, 2009; Franzén *et al.*, 2012; Boerschig *et al.*, 2013), restoration actions (Woodcock *et al.*, 2012), reserves design (Bartonova *et al.*, 2016) and long-term community change (Habel *et al.*, 2016).

Much less work has been done on LHTs of the species-richer moths. The order Lepidoptera is traditionally (e.g. Sterneck, 1929; Koch, 1984) and non-phylogenetically divided into micro-moths and macro-moths. The group consists of diurnal monophyletic butterflies and nocturnal paraphyletic macro-moths (herein "moths"), not to be confused with the narrower monophyletic clade of Macrolepitoptera, or Macroheterocera (Timmermans *et al.*, 2014; Mitter *et al.*, 2017). With advancing sampling techniques, moths increasingly complement butterflies in community ecology and conservation (e.g. Leps *et al.*, 1998; Merckx *et al.*, 2010; Slade *et al.*, 2013; Novotný *et al.*, 2015; Truxa & Fiedler, 2016). Some LHT analyses exist on combined moths and butterflies data (Altermatt, 2010; Franzén *et al.*, 2012), some studies have related LHTs to moths' distribution trends and extinction risk in Northern Europe (Mattila *et al.*, 2006, 2008; Franzén & Johannesson, 2007; Hunter *et al.*, 2014) and several recent papers studied distribution of moths' traits related to land use changes (Mangels *et al.*, 2017). Further progress, however, seems to be hindered by a lack of comprehensive sources listing moths' LHTs for entire faunas. The situation has much improved recently, with new publications summarising the knowledge of major taxa and regions (e.g. Hausmann, 2001; Schintlmeister, 2008; Witt & Ronkay, 2011).

We tabulated LHTs of macro-moths inhabiting Central Europe and subjected them to multivariate analysis, seeking to unravel major gradients in the traits' diversity and their relationships to the analysed species' rarity and conservation status. Central Europe represents a suitable region for such analysis, as its moths fauna is well-known (Macek *et al.* 2007, 2009, 2012) and moderately rich. It hosts more species, and presumably higher LHT diversity, than northern and western Europe, allowing

generalisation of the patterns for most of the European continent.

Using the thus compiled traits table, we addressed the following questions: (i) What are the main gradients of variation in LHTs of Central European moths? (ii) How robust are the variation gradients against including or excluding traits defining the moths' habitat affiliations and biogeography ranges? (iii) What are the relationships between the LHT gradients, species rarity and levels of threat?

Materials and methods

Taxonomic and geographical scope

We worked with traditional (e.g. Sterneck, 1929) macro-moths families, i.e. Hepialidae, Cossidae, Limacodidae, Drepanidae, Lasiocampidae, Lemonidae [= Brahmaeidae], Endromidae, Saturniidae, Sphingidae, Geometridae, Notodontidae, Thaumetopoeidae, Noctuidae (in the traditional concept), Arctiidae and Lymantridae [the latter two recently classified as Erebiidae (Zahiri *et al.*, 2013)]. We included all species occurring in any of the countries of Central Europe: Austria, Czech Republic, Germany, Hungary, Poland and Slovakia. We excluded species restricted to the Alps, as high alpine fauna forms a separate biogeographical unit (cf. Dennis *et al.*, 1991) and non-native invasive species (Mlikovsky & Styblo, 2006). The total material includes 1234 species (Appendix S1).

Life-history traits

The primary source for compiling LHTs was the three-volume handbook by Macek *et al.* (2007, 2008, 2012), supplemented, for missing traits, by other monographs, papers, Internet sources and consultations with moths experts. In the case of conflicting information, we preferred those from Central Europe over those from elsewhere, those from nature over those from captive breeding, those from low altitudes over those from high altitudes, and newer/primary literature over older/secondary. After finishing the compilation, the information for a single trait was checked during a single day, to ensure compatibility across species.

A total of 27 LHTs, split into 44 trait states, forming the following thematic groups, was tabulated.

- 1 Traits related to mobility, voltinism and related themes pivotal to the g/s and cV continua (Bartonova *et al.*, 2014). (1) *Wing span*, expressed as forewing length, a possible proxy for dispersal ability (Sekar, 2012), also related to development speed (WallisDeVries, 2014) and host plant use (Cizek *et al.*, 2006); a numeric variable. (2) *Overwintering stage*, influencing year-round dispersal and resource location (Boerschig *et al.*, 2013), ordinal value from egg – 1, to adult – 4. (3) *Voltinism*, the mean number of

- generations per year (higher in generalists: Dapporto & Dennis, 2013; and related to development speed: WallisDeVries, 2014). (4) *Semivoltine* development, i.e. > 1 year, factor (1/0). (5) *Migrations*, for species known to migrate over long distances (0/1). (6) *Apterous*, i.e. reduced wings in the female sex (0/1).
- 2 Traits related to the duration and timing of adult stage, the former proportional to dispersal ability (Bubova *et al.*, 2016), the latter linked to habitats and resource use (e.g. Zografou *et al.*, 2015). (7) *Flight period*, or time of the year when adults occur, 5-states factor (early spring, spring, summer, autumn, winter). (8) *Flight period length*, numeric variable defined as the sum of above flight periods.
- 3 Traits related to larval feeding, describing larval niche breadth and affecting the development speed (Cizek *et al.*, 2006). (9) *Trophic range*, ordinal (1 – monophages, feeding on < 4 genera from a single family or on < 3 genera from different families; 2 – oligophages; and 3 – polyphages, > 3 plant families). (10) *Host plant form* defining the host plants' spatiotemporal availability (i.e. apparency) and linked to anti-herbivore defences (Altermatt, 2010); ordinal (1 – forbs, 2 – grasses, 3 – shrubs, 4 – trees, 5 – non-vascular plants, e.g. lichens, fungi, etc.). (11) *Host plant part*, defining the width of larval feeding window, as the more nutritious plant parts such as flowers are available only for a restricted time. Three-state factor: flower/seeds, leaves and stems/roots. (12) *Larval carnivory*, including the opportunistic one, which modifies the effects of plant nutrition quality (0/1). (13) *Detritivory*, i.e. feeding on dead or decaying plant material (0/1).
- 4 Traits related to larval defences. Costly defences require resources, but may enhance survival compared to species not possessing them. (14) *Larval sociality*, a trait with assumed defensive function (Allen, 2010), ordinal (1 – solitary, 2 – small groups in at least some instars, 3 – large aggregations in at least some instars). (15) *Hairy larvae*, with dense larval fur covering the entire body (0/1).
- 5 Adult resources, defences, or crypsis. (16) *Adult feeding* increases longevity and egg production (Tammaru & Haukioja, 1996) but complicates habitat quality demands (0/1). (17) *Adult activity*, a 0/1 factor distinguishing nocturnal and diurnal activity, fuzzy coded (0.5/0.5) if both activities exist. (18) *Sexual dimorphism* in adults (0/1), sometimes linked to differing diurnal activity profiles (Fuldner, 2000) or diversified resource requirements (Alarcón *et al.*, 2010). (19) *Seasonal polyphenism* in adults (0/1), possibly linked to differences in selection pressures or resource use (Kivela *et al.*, 2013).
- 6 Habitat use in Central Europe. (20) *Altitude range*, numeric (1–3) variable describing how many of the following three altitudinal bands a species inhabits: lowlands (< 250 m a.s.l.), highlands (> 250 and < 1000 m a.s.l.) and mountains (over 1000 m a.s.l.). (21) *Habitats range*, the number of habitat types listed for particular species in Macek *et al.* (2007), who distinguished twelve categories: xerophilous1 (barrens to xeric grasslands), xerophilous2 (dry shrublands), xerophilous3 (warm woodlands), mesophilous1, mesophilous2 and mesophilous3 (following the same logic), hygrophilous1 (open wetlands), hygrophilous 2 (wooded wetlands), hygrophilous (warm wetlands and swamps), tyrphophilous (peat bogs), alpine (grasslands above the tree line), ubiquitous (no specific requirements). The following four traits, all ranked, were obtained by translating the 12 above habitat categories into ranked variables: (22) *Habitat 3-D structure* (1–3); (23) *Habitat temperature* (1–3), 3 for xerophilous and 1 for alpine and tyrphophilous species; (24) *Habitat humidity* (1–3), 1 for xerophilous and 3 for hygrophilous, hygrophilous and tyrphophilous species; and (25) *Habitat acidity* (1–3), 1 for hygrophilous and 3 for tyrphophilous species.
- 7 Species range. (26) *Range size*, referring to global range, ranked variable (1–4) from small (e.g. a part of Europe) to huge (e.g. Holarctic realm) ranges. (27) *Range type*, eleven-state factor, distinguishing (cf. Macek *et al.*, 2007): Atlanto-Mediterranean, Continental, European, Eurosiberian, Holarctic, Cosmopolitan, Mediterranean, Palaearctic, Pantropical, Pontomediterranean, West-Palaearctic.
- The total data matrix (Appendix S1) contained 54 295 cells. Of these, we did not obtain trait states information for 358 cells (0.66% of the total); these cells were filled by mean values for individual traits.
- For a crude control for phylogeny, we used recent view of membership of species in superfamilies and families (van Nieukerken *et al.*, 2011), from which we built a matrix hierarchically coding individual species' taxonomic positions (Appendix S2).

Rarity and distribution trends measures

We used information from the Czech Republic, a country situated centrally in the study region and hosting (except for exotics, species encountered only once and doubtful records) 1069 of the 1234 originally analysed species (Appendix S3).

- 1 A *commonness* measure, obtained by inquiring four national moths experts, who ranked all Czech Republic species into four categories: extremely rare – 1, rather rare – 2, rather common – 3, extremely common – 4; the means from their answers were the species' commonness measure.
- 2 *Red list status* from a recent source (Hejda *et al.*, 2017a) compiled by inquiring national experts. The IUCN were used to rank the variable: least concern – 1, near threatened – 2, vulnerable – 3, endangered – 4, critically endangered – 5, regionally extinct – 6.

Statistical analyses

To detect the major directions in LHT variation and to visualise the relationships among the traits, we subjected the traits x moths table to principal component analyses (PCA), an indirect linear ordination, computed in four variants. PCA1 used all 27 traits. PCA2 also used all traits but considered phylogeny using the taxonomic matrix as covariates. The next two analyses investigated, assuming that both habitats and distribution ranges filter from species according to their traits (Shreeve *et al.*, 2001; Pavlikova & Konvicka, 2012), how would the patterns described by traits change after removing traits specifically describing habitat affiliations and geographical distributions (traits 20–27, above), PCA3. Finally, PCA4 excluded habitats and geographical distribution of species, but considered phylogeny as covariate matrix.

We used CANOCO for Windows v. 5 (Ter Braak & Šmilauer, 2012). We coded factor and binary traits as “dummy” variables, centred all response variables (i.e. traits) to zero mean and standardised all response variables to unit norm, thus performing PCA on correlation matrix (Šmilauer & Lepš, 2014, p. 10).

To assess how the ordinations excluding habitats (traits 20–25) and biogeography (26–27) were related to habitat affiliations and biogeography patterns, we used the most stringent of all ordinations not containing habitats and biogeography, i.e. PCA4, for adding pre-defined habitat types (the 12 categories from Macek *et al.*, 2007, above) and range types (trait 27, above), as supplementary variables.

Finally, we regressed the moths' commonness and red list status in the Czech Republic against the ordination scores returned by the PCA1–4 analyses. We used the glm module with identity link in R (R Core Team 2013), constructed linear and 2nd-degree polynomial regressions and compared their fits with null models (response ~ +1) according to the Akaike information criterion (Akaike, 1974).

Results

Variation gradients in traits distribution

The PCA with all 27 life-history traits (PCA1) returned ordination eigenvalues 0.085, 0.068, 0.060, 0.052 (cumulative explained variation 26.43), revealing four similarly strong gradients. The first axis distinguished species inhabiting large ranges (correlation coefficient between the trait's value and axis, $r = -0.625$), feeding on apparent plants (−0.574), from humid habitats (−0.538), consuming leaves (−0.535), with developed 3D habitat structure (−0.516), inhabiting the Palaearctic range (−0.470) and having large wingspan (−0.385); from species with opposing trait states, i.e. feeding on plant reproductive parts (0.548), from warm habitats

(0.496), with adults feeding (0.416), inhabiting the Mediterranean (0.387), Pontomediterranean (0.271) or European (0.209) ranges. The second axis distinguished species with long flight period (0.698), multivoltine (0.678), flying in spring (0.648), overwintering in late stages (0.508) and often migratory (0.409); from species with opposite trait states that often feed on apparent plants (−0.259), and may be apterous (−0.249). Positive values on the third axis corresponded to species with frequent sexual dimorphism (0.451), sometimes with apterous (0.402) or diurnally active (0.398) adults and hairy (0.938) or gregarious (0.363) larvae; from species with solitary larvae, with adult feeding (−0.507), from humid habitats (−0.497) with nocturnal adults (−0.398). The fourth axis distinguished diurnal (0.669) and nocturnal (−0.669) moths.

The above patterns remained practically unchanged when controlled for phylogeny (PCA2) (eigenvalues 0.077, 0.063, 0.053, 0.048, cumulative explained variation 25.59) (Fig. 1).

After removing habitats and biogeography traits (PCA3; eigenvalues 0.117, 0.101, 0.087, 0.077, cumulative explained variation 38.28), the first axis still distinguished species feeding on leaves (0.643) of apparent plants (0.557), with hairy larvae (0.485), sometimes sexually dimorphic (0.477), large-winged (0.445), with broad trophic range (0.393) and gregarious larvae (0.388); from species of opposite traits, often feeding on plant reproductive parts (0.644), whose imagoes intake food (−0.618) and who overwinter in later stages (−0.252). The second axis distinguished species with long flight period (0.818), occurring in spring (0.682) or early spring (0.418), multivoltine (0.671), overwintering in late stages (0.621), sometimes seasonally dimorphic (0.300) or migratory (0.260); from species with opposite trait states, feeding on roots or stems (−0.310), displaying nocturnal activity (−0.210) or semivoltine development (−0.102). The third axis distinguished diurnal (0.827) and nocturnal adults (−0.827) adult activity; the former tend to be sexually dimorphic (0.341), consume plant reproductive parts (0.324), can be apterous (0.267) and may have hairy larvae (0.257). In the latter, larvae tend to feed on leaves (−0.330), imagoes tend to accept food (−0.307) and occur in autumn (−0.280). Positive values of the fourth axis were occupied by moths flying in winter (0.539), early spring (0.521) or in autumn (0.329), often apterous (0.348), feeding on plants reproductive parts (0.336) and overwintering in late stages (0.287). Negative values occupied moths flying in summer (−0.624) or spring (−0.167); their larvae may develop on decaying material (0.394) or leaves (0.375) and may have broad tropic ranges (0.240).

The main patterns did not change much if controlled for phylogeny (eigenvalues 0.103, 0.087, 0.080, 0.072, cumulative explained variation 39.54) (Fig. 2).

In all analyses, the main gradient distinguished woodland from grassland/steppic species (herein *habitats gradient*); the second stood for voltinism and flight period

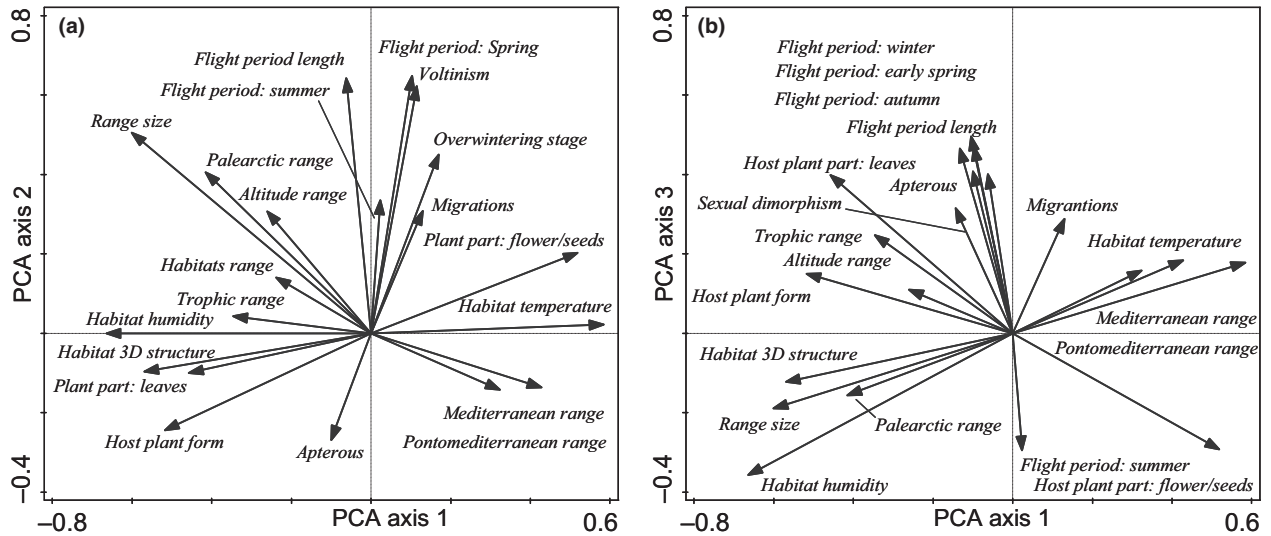


Fig. 1. Principal component analyses (PCA) ordination plot showing mutual relations of life-history traits of 1234 Central European macro-moths in ordination space. Analysis PCA2, containing all 27 life-history traits compiled (44 traits states) and controlled for phylogeny. (a) 1st and 2nd ordination axes, i.e. *habitats gradient* and *voltinism gradient*. (b) 1st and 3rd ordination axes, i.e. *habitats gradient* and *defence/season gradient*. Only traits with the best fit to ordination space are depicted.

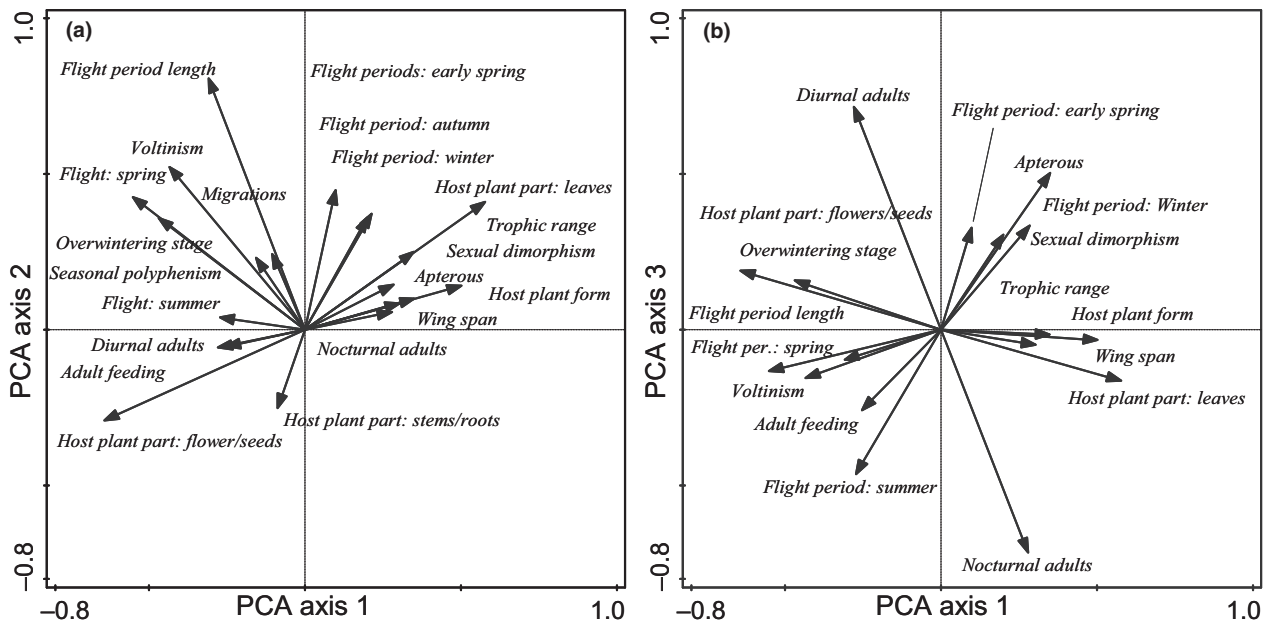


Fig. 2. Principal component analyses (PCA) plots showing mutual relations of life-history traits of 1234 Central European macro-moths in ordination space. Analysis PCA4, excluding traits describing habitat associations and biogeography (traits 20–27; i.e. 19 traits and 26 traits states; see Materials and Methods) and controlled for phylogeny. (a) 1st and 2nd PCA axes, i.e. *habitats gradient* and *voltinism gradient*. (b) 1st and 3rd axes, i.e. *habitats gradient* and *defence/season gradient*. Only traits with the best fit to ordination space are depicted.

length (herein *voltinism gradient*), the third accounted for major defence modes in association with adult phenology (*defence-season gradient*) and the fourth distinguished diurnal vs. nocturnal adult activity (*diurnal gradient*). After exclusion of habitats and geography from analyses,

the gradients described by the third and the fourth axes switched their relative importance.

See Appendix S4 for positions of all analysed species and traits on the ordination axes returned by the four PCA analyses.

Traits gradients, habitats and ranges

Fitting the 12 pre-defined habitats from Macek *et al.* (2007) as supplementary variables onto the LHT ordination PCA4 returned the following pseudo-canonical correlations with the four ordination axes: 0.491, 0.325, 0.302, 0.255, explaining 4.9% of total variation. In parallel with *habitats gradient*, there was distinction between woodland habitats on the one hand, and grasslands, especially xeric ones, on the other hand. High values of *voltinism gradient* correlated with ubiquitous habitats, whereas low values correlated with alpine, tyrphophilous and thermophilous habitats (Fig. 3a).

Fitting range types as supplementary variables to PCA4 returned pseudo-canonical correlations: 0.258, 0.180, 0.312, 0.230, explaining 3.7% of total variation. High values of the *habitats gradient* (closed woodlands) correlated with West-Palaeartic and Atlanto-Mediterranean distributions; high values (xeric grasslands) correlated with Pontomediterranean, Mediterranean and Continental elements. High values of *voltinism gradient* correlated with two large-ranged faunal element, Palaeartic and Holarctic, as well as with Cosmopolitan and Pantropical elements. Negative values of this gradient correlated with Eurosiberian and European elements (Fig. 3b).

Relation of traits to rarity and conservation status

For all Czech Republic moths (Table 1), regressing *commonness* against *habitats gradient* (the first ordination axes) from PCA1-4 showed that commonness decreased,

either polynomially or monotonously, from larger-sized polyphagous moths inhabiting woodlands and feeding on apparent plants foliage towards small monophagous moths feeding on unapparent plants' reproductive parts; or from species associated with woodlands towards those associated with grasslands (Fig. 4a). Along the *voltinism gradients* (the second PCA axes), commonness always increased with flight period length, number of generations, overwintering in later stages and migration ability (Fig. 4b). Responses to the *defence-season gradient* were more complex. If not controlled for phylogeny, commonness decreased from moths that have gregarious hairy larvae, diurnal and/or sexually dimorphic adults and tend to fly in extreme times of year (winter, autumn) towards moths with solitary glabrous larvae flying in spring or summer (Fig. 4c). The pattern was opposite if controlled for taxonomy, indicating that traits forming the *defence-season gradient* covaried with phylogeny. No responses to *defence-season gradient* were returned from analyses without habitats and biogeography (PCA3, PCA4) – recall that here, the mutual ranking of third and fourth ordination axes switched, so that axes 3 stood for *diurnal* and axes 4 for *defence-season gradient*. Finally, the responses to *diurnal gradients* revealed polynomial or linear decreases, indicating that moths with diurnal adults appeared as more common than nocturnal moths.

Responses of red list status to *habitats gradients* either monotonously increased (PCA2) or followed U-shaped polynomials (PCA1, PCA3), indicating either that more red-listed species were associated with grasslands, or that they were over-represented in the ordination extremes, i.e. xeric grasslands and closed woodlands (Fig. 4d).

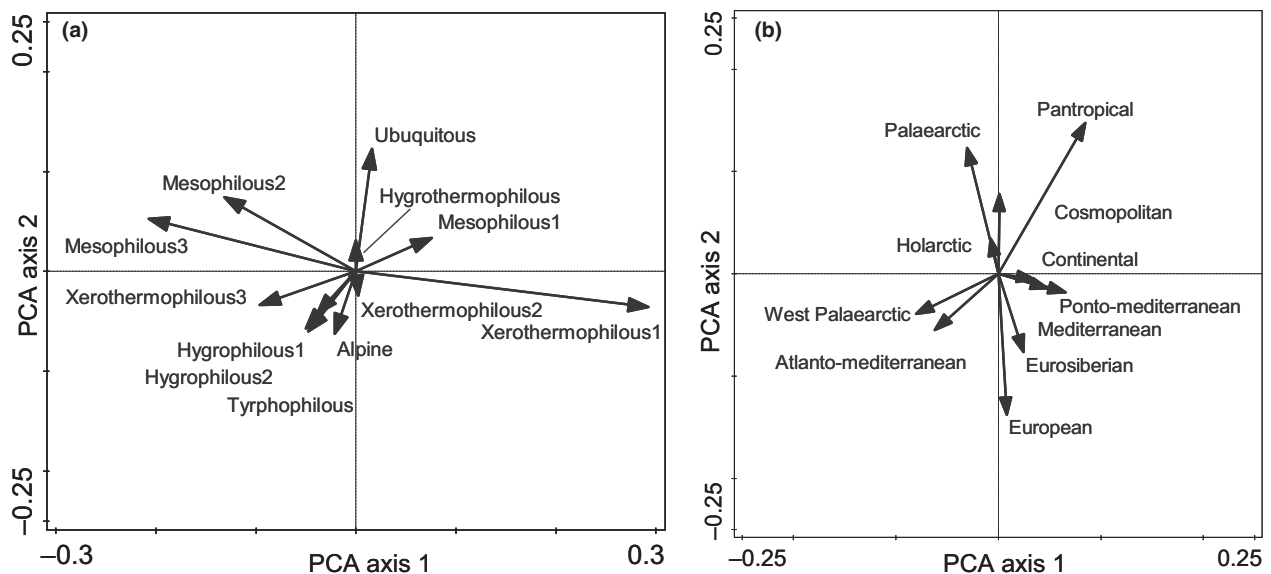


Fig. 3. Results of fitting supplementary variables (taken from Macek *et al.*, 2007) onto the ordination analysis of moths' life-history traits PCA4 (cf. Fig. 2), i.e. the analysis not containing traits defining habitat affiliation and range types. (a) Pre-defined habitat affiliations fitted as supplementary variables. (b) Range types fitted as supplementary variables.

Table 1. Results of regressions relating Commonness and Red list status of 1069 moths occurring in the Czech Republic against ordination scores of individual species, returned from PCA analyses of Central European moths' life-history traits. Null models fit the response variable to $\sim +1$. Models PCA1-4 stand for ordination of all available life-history traits (PCA1); all traits controlled for phylogeny (PCA2); ordination excluding traits describing habitat affiliation and distribution ranges (PCA3); and as before but controlled for phylogeny (PCA4).

	PCA axis 1 – Habitats gradient			PCA axis 2 – Voltinism gradient			PCA axis 3 – Defence/season or Diurnal gradient*			PCA axis 4 – Diurnal or Defence/season gradient*		
	Coefficients	res.D	AIC	Coefficients	res.D	AIC	Coefficients	res. D	AIC	Coefficients	res.D	AIC
Commonness												
Null model		670.2	2539									
PCA1	–9.26 –2.07P	580.1	2388	0.07	665.8	2533	–0.08	664.5	2531	–0.68 –1.77P	666.6	2537
PCA2	–0.31	579.0	2384	0.11	658.7	2522	0.05	667.8	2537	0.72 –4.07P	653.1	2515
PCA3	3.97 –1.31P	652.7	2514	0.08	662.9	2529	–0.09	661.9	2527	0.14 + 0.89P	665.2	2535
PCA4	0.18	659.4	2523	0.26	648.8	2506	ns			ns		
Red list status												
Null model		1263.0	3216									
PCA1	–1.76 + 5.37P	1231.0	3193	–2.11 –2.68P	1263.0	3210	8.88 + 4.45P	1164.0	3133	6.63 + 3.85P	1204.0	3169
PCA2	0.13	1247.0	3204	–2.46 –349P	1245.0	3204	ns			3.27 + 3.27P	1242.0	3202
PCA3	6.18 + 3.93P	1209.0	3174	1.30 –2.76P	1261.0	3212	0.25	1200.0	3164	ns		
PCA4	ns			–2.80 –2.47P	1249.0	3208	0.21	1252.0	3208	ns		

Key: All null models are with 1068 degrees of freedom. The fitted functions are either for linear (i.e. $y \sim ax + \text{intercept}$, d.f. = 1067, a is presented) or 2nd-degree polynomial (i.e. $y \sim ax + bx^2 + \text{intercept}$, d.f. = 1066, presented as $a + bP$). Res.D – residual deviance of the fitted function. AIC – Akaike information criterion. ns – “non-significant” relationships, i.e. relationships in which the model AIC > null model AIC.

Bold values refer to AIC values of null models, used to compare the performance of all other models.

*The mutual positions of defence/season and diurnal gradients switched between analyses PCA1 + 2 (where axis3 stands for defence/season gradient) and PCA3 + 4 (where axis 3 stands for diurnal gradient).

Responses to *voltinism gradients* were always polynomial, decreasing or domed in a shallow way (Fig. 4e), suggesting fewer generations, shorter flight period and earlier overwintering stages in red-listed moths. With *defence-season gradient*, red-listed status increased towards positive values, but only in the analyses not controlled for phylogeny (PCA1: Fig. 4f). With *diurnal gradients*, the red-listed status always increased, polynomially or monotonously.

Discussion

Gradients of variation defined by life-history traits

The main gradients of variation, revealed by ordinations of life-history traits of Central European macro-moths, differed from patterns revealed for European butterflies (e.g. Dapporto & Dennis, 2013). In butterflies, the main gradient distinguishes generalist and specialist species, the former displaying high mobility, low population density, wide habitat and host plant ranges and overwintering in late stages. The secondary gradient(s), depending on the selection of traits used, then reflect relationships

among habitat use, voltinism, larval host forms and presumably larval defences (Bartonova *et al.*, 2014; WallisDeVries, 2014). High generations number (related to smaller body size) associates with feeding on qualitatively defended forbs, whereas low generations number (and large size) associates with feeding on quantitatively defended trees or shrubs foliage (Cizek *et al.*, 2006; Altermatt, 2010). The latter distinction contains a habitat signal, however: large-bodied univoltine butterflies feeding on apparent plants tend to occur in woodlands, whereas small-bodied, forbs feeding polyvoltine species tend to inhabit grasslands, ruderals or arable habitats (cf. Hodgson, 1993; Shreeve *et al.*, 2001; Dennis *et al.*, 2004).

For the moths, in contrast, the major gradient of variation carried an unequivocal habitat signal, distinguishing tree foliage feeders associated with humid woodlands from species developing on forbs, often on flowers and seeds, associated with xeric grasslands. A dominant role of woodlands – grasslands gradient was also found by Pavlikova and Konvicka (2012), in an analysis limited to species-poor macro-moths families, i.e. excluding Geometridae and (traditional) Noctuidae. In this study, it was the secondary gradient that pointed to the associations between high generations number, long adult flight,

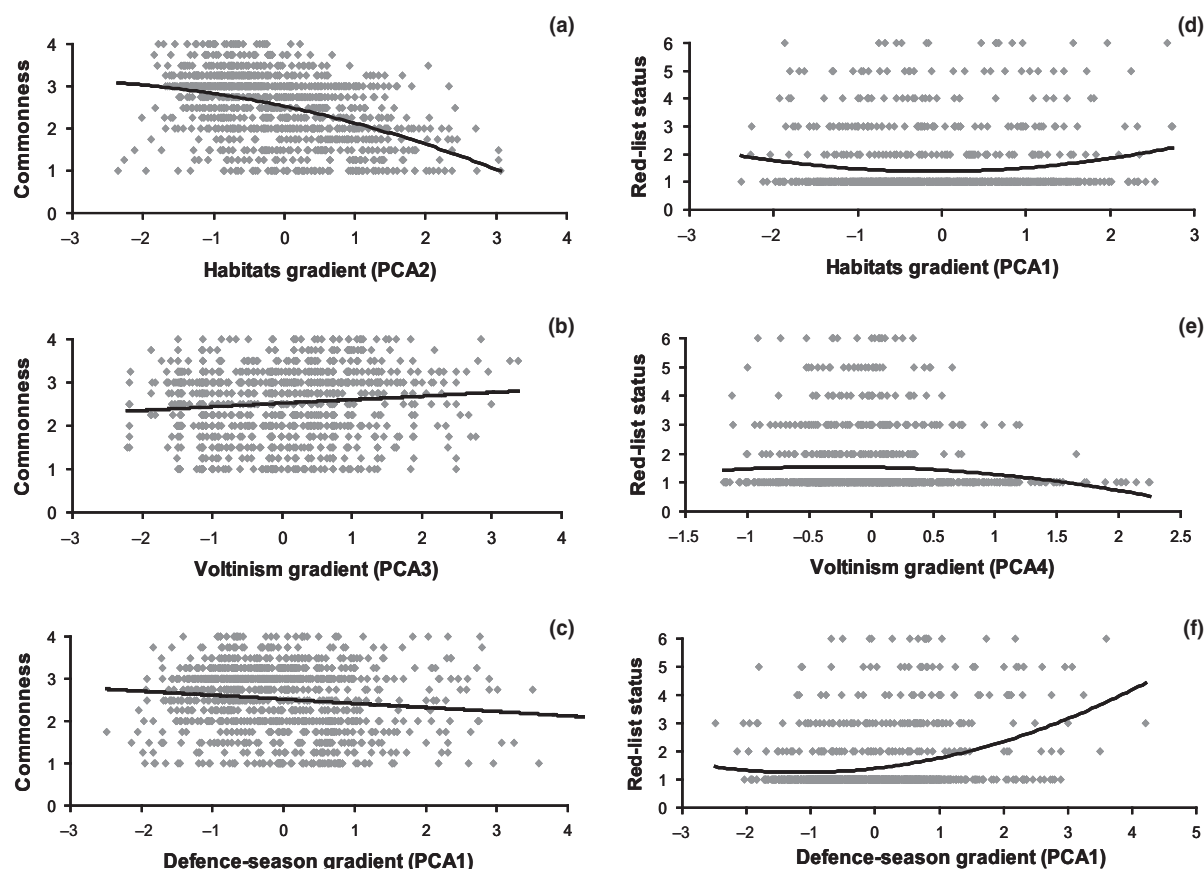


Fig. 4. Regression lines from selected regression models that fitted commonness (panels a–c) and red-list status (panels d–f) against ordination axes obtained by principal component analyses of Central European moths' life-history traits. See Table 1 for regression coefficients, explained deviance and AIC values.

migratory status and feeding on unapparent plants. This *voltinism gradient* applicable to moths thus combines the g/s and cV gradients of butterflies (Bartonova *et al.*, 2014). The third and fourth moths traits gradients, relating phenology to larval and adult defences (larval hair, gregarism, etc., versus species with cryptic solitary larvae) and diurnal vs. nocturnal adult activity, have no parallels in butterfly studies, although it has been sometimes suggested (Dennis *et al.*, 2004) that defence modes might reflect habitat use.

The differences in patterns revealed for butterflies and moths might be partly caused by the different quality of information on crucial traits states. For European butterflies, there exist fairly good (albeit incomplete: cf. Dennis *et al.*, 2008) information on such traits as mobility or population density, whereas not even vague knowledge exists for many moths (cf. Nieminen *et al.*, 1999; Betzholtz & Franzén, 2011, 2013). Moths, in contrast, are more variable in such traits as host plant part consumed, adult aptery, or adult diurnal activity profiles.

The ranking of variation axes – habitats more important than voltinism, which is more important than defence-seasonality and diurnal profile – withstood exclusion of

traits describing habitat use and biogeography from the analyses. Importantly, pre-defined habitat types correlated with results of thus restricted ordination (i.e. PCA4), demonstrating that the moths' habitat associations can be reconstructed from traits not describing habitat use, a phenomenon previously demonstrated by Shreeve *et al.* (2001) for British butterflies and Pavlikova and Konvicka (2012) for a subset of Central European moths. This supports the conjecture that certain habitat conditions filter certain life-history traits combinations (e.g. Southwood, 1977; Cornwell *et al.*, 2006), sometimes in obvious ways (e.g. tree foliage feeding in woodlands, high mobility in ruderal species), sometimes more subtly (e.g. stem borers frequent in wetlands, species with diurnal adults more frequent at xeric grasslands).

Range types also correlated with the ordinations excluding habitats and biogeography. The *habitats gradient* paralleled increasing continentality of ranges, with close woodlands species corresponding to distributions in western or south-western Europe, species with intermediate values on the gradient (i.e. open woodlands or “savanna” species) corresponding to West-Palaearctic and Euro-Siberian ranges, and open grasslands species

corresponding to Continental or Mediterranean ranges. These results agree with vegetation reconstructions (Bohn, 1993), and may contribute to the ongoing debates within the conservation community regarding the natural openness of Western Palaearctic vegetation (Vera, 2000; Šebek *et al.*, 2015). They suggest that Atlantic Europe would indeed be largely forested in the absence of humans, whereas the wide areas stretching from Central Europe to West Asia, the homeland of “Eurosiberian” faunal and floral elements, would be covered by grassland-forests mosaics (Chytrý *et al.*, 2010; Kunes *et al.*, 2015), supporting moths with intermediate positions on the *habitats gradient*. Such species would often develop on shrubs or large forbs, would display intermediate requirements for habitats temperature and humidity, would form more than one generation per year, and would display intermediate mobility. The importance of open woodlands, or grasslands-woodland mosaics, for insects declining in Europe is now well established for many butterflies (e.g. Bergman & Kindvall, 2004; Slámová *et al.*, 2013), and other groups (e.g. Spitzer *et al.*, 2008) including moths (Šebek *et al.*, 2015). Finally, the (sub)tropical migrants, ranking highly on the *voltinism axis*, share similar traits combinations as West Palaearctic and Euro-Siberian species, again suggesting their origin in mosaic-like landscapes.

Given the herbivorous larval diet, and the association of moths with their host plants, it is tempting to relate the ordination of moths according to their life histories to the R-C-S system describing plants’ life histories (Grime, 1977) and discussed for butterflies by Hodgson (1993), Dennis *et al.* (2004) and Bartonova *et al.* (2014). Developing on competitive plants (C strategy) should be associated with negative values of *habitats gradient* in PCA1 + 2, or positive values in PCA3 + 4. Stress tolerant host plants (S strategy) should correspond to the opposite side of *habitats gradient* coupled with negative values of *voltinism gradient* which are, notably, occupied by moths of high altitudes, waterlogged sites or bogs. Finally, moths developing on ruderal hosts (R strategy) should occupy high values of the *voltinism gradient*.

Life-history traits versus rarity and threats

The measure of Czech moths’ commonness fitted the *habitats gradient* in logical ways. Forest-dwelling moths tend to be more common, as forests of all types cover over 30% of the country, their area has increased during the last century and they still assume the largest share of “natural” vegetation. Reports for numerous taxa (e.g. birds: Reif *et al.*, 2008; Orthoptera: Marini *et al.*, 2009) reveal the good status, or even an increase, of Central European forest fauna at the expense of non-forest species. Some open habitat types, in contrast, have always existed only as small islets in the region and have further decreased during the recent past (e.g. continental sand dunes: Tropek *et al.*, 2013; salt marshes: Rickert *et al.*, 2012; riverine gravels: Sadler *et al.*, 2004). The historically

more common seminatural grasslands of all kinds have deteriorated with the decline of traditional land use throughout the continent (Rakosy & Schmitt, 2011; Botham *et al.*, 2015).

Responses of commonness to *voltinism gradient* were even more straightforward, supporting the widely held conjecture that species with multiple generations, often migrants or wide-ranging vagrants, tend to be widespread, highly fecund, abundant and frequently encountered (e.g. Spitzer *et al.*, 1984; Betzholtz & Franzén, 2011, 2013). Mangels *et al.* (2017) recently showed that moths with such traits prevail at intensively used grasslands in Europe. The responses to *defence-season gradient*, with explanatory power (cf. the AIC values in Table 1) much lower than in the previous cases, were less trivial. They were sensitive to controlling or not controlling for phylogeny, and in the controlled ordinations they suggested that species relying for protection on hair, conspicuous coloration, etc., appear as more common to Lepidoptera experts. This might be a result of their easier detectability and the same might apply to the *diurnal activity gradients*.

The red list status responses to *habitats gradients* did not merely mirror the commonness responses. Instead, they sometimes followed U-shaped patterns, implying an increased chance for red listing for both species of dry, xeric grasslands and species of close-canopy humid woodlands. This pattern, notably resembling a pattern found for threatened invertebrates of Britain (Thomas *et al.*, 1994), should be viewed with caution, however. The Czech Republic moths red list was compiled according to experts’ consensus and therefore, it mirrors the experts’ tastes and prejudices. Still, it appears that species restricted to undisturbed conditions of certain forest types [e.g. adler carrs: *Phragmitiphila nexa* (Hübner, 1808) (cf. Jaroš & Spitzer, 1987), forested canyon screes: *Venusia blomeri* (Kurtis, 1832) (cf. Šumpich, 2011)] are either declining, or more likely to be red-listed. Improving distribution data is the only way to resolve this riddle.

The domed responses of red list status to *voltinism gradient* agrees with the established knowledge. Extremely polyvoltine and migratory species include, e.g. a wide range of Noctuidae pests (cf. Hill & Gatehouse, 1993; Anderson *et al.*, 2016) and such tropical migrants as *Agrius convolvuli* (Linnaeus, 1758) and *Macroglossum stelarum* (Linnaeus, 1758), which efficiently locate resources over wide geographical scales (cf. Kelber, 2010; Johnson & Raguso, 2016) and thus unlikely face declines. On the other hand, obligatorily monovoltine species with extremely short flight period restricted to early spring and late autumn are often associated with extremely common resources (e.g. polyphagous development on deciduous trees foliage; Wynne *et al.*, 2003). Despite having apterous females, they efficiently disperse via larval ballooning (Leggett *et al.*, 2011) and their population dynamics can be synchronised via large spatial scales (Tenow *et al.*, 2013). It follows that red-listed species concentrate in the middle values of the *voltinism gradient*.

Red-list status also increased with *defence-season gradient* (in PCA1 only) and with *diurnality gradient* (consistently in PCA1-4), notably contrasting with responses of commonness. Arguably, species employing such conspicuous defence strategies as communal larval nests, as well as diurnal species, are easier to detect in the field, and hence rank relatively highly when commonness is considered, and at the same time are more likely to be noticed to decline (Groenendijk & van der Meulen, 2004). Consequently, such species are often included into conservation programmes (e.g. Albrecht *et al.*, 2011; Chrzanowski *et al.*, 2013; Kuźmiński *et al.*, 2014).

Conclusion

Central European moths' fauna can be understood as filling a multi-dimensional space, organised according to gradients of habitat use (from close canopy forests to grasslands and barrens), demography/dispersal (from r- to K-selected species) and seasonality combined with larval and adult defences. These gradients perform robustly with respect to the life-history traits considered. They also account for biogeography patterns, namely range types (close woodland species associated with oceanic and xerophilous species with continental ranges, ubiquitous species with huge ranges). The *habitats*, *voltinism* and *defence-season gradients* are related to commonness/rarity within the study region, and to the red list status of individual species.

The LHT table presented in Appendix S1 may be used to analyse community changes in Central European moths, similarly as in the case of butterflies (Bartonova *et al.*, 2016), plants (Lososova *et al.*, 2006) or birds (Reif *et al.*, 2016). For instance, one may expect community shifts along the *habitats gradient* with successional changes, presence of invasive plant species (cf. Hejda *et al.*, 2017b), or even with changes of climatic conditions, or shifts along *voltinism gradient* with land use intensification. Although knowledge of Central European moths' life histories is still incomplete, and such crucial traits as fecundity remain largely unknown, understanding community change in terms of traits changes may bring more mechanistic insights than mere counting of species, or even counting of endangered species, whose listing is also prone to serious biases.

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Supporting Information

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

Appendix S1. List of Central European macro-moths analysed in this paper, with their life-history traits. Unknown trait states, for which we used mean values of individual matrix columns, are indicated at the bottom of the matrix.

Appendix S2. Matrix coding the membership of the analysed moths species in superfamilies and families, used as the covariate matrix in analyses crudely controlled for phylogeny, i.e. PCA2 and PCA4.

Appendix S3. List of commonness measures and red list status values for moths of the Czech Republic, used in the analyses regressing species ordination scores against their commonness and red list status.

Appendix S4. PCA scores of all analysed species from analyses PCA1-4 (list1), and correlation coefficients of all life-history traits values analysed with ordination axes returned from analyses PCA1-4 (list 2).

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