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Life-history traits and climatic responsiveness in noctuid moths

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Emergence phenology has been shown to advance considerably in the past decades in many lepidopterans. Noctuid moths (Noctuidae) constitute a species-rich family of lepidopterans with a large diversity of life history traits presumably driving climatic responsiveness. In our study we aim to assess the role of life-history and ecological traits in climatic responsiveness of noctuid moths, whilst controlling for phylogenetic dependence. We used a long-term dataset of European noctuid moths collected from a light-trap in northeastern Hungary. As the study site is located at the intersection of several biogeographical zones harbouring a large number of noctuid moth species, our dataset provides a unique possibility to investigate the moths' climatic sensitivity. To estimate the role of life-history traits and ecological factors in driving lepidopterans' response to climatic trends, we employed three proxies related to the species' ecology (habitat affinity, food plant specialization and food type) and two robust types of life-history traits (migration strategy and hibernation form). The degree of temporal shifts of various measures of emergence phenology was related to hibernation stage, food type and migration strategy. Large-scale phylogenetic relatedness exerted little constraint in all models fitted on each measure of phenology. Our results imply that noctuid moths overwintering as adults exhibited greater degrees of phenological shifts than species hibernating as larvae or pupae. It implies that moths hibernating as adults are forced to suspend activity in our climate and the prolongation of autumn activity might be the result of increased plasticity in flight periods.

During the past decades an increasing number of studies have reported on the effects of global climatic change on ecosystem structure and functioning (Parry et al. 2007, Walther 2010, Burrows et al. 2011). Climatic processes influence phenology, population dynamics and life-history traits in a broad range of organisms, including a large number of endangered taxa (Parmesan 2006, Forrest and Miller-Rushing 2010, Jenouvrier and Visser 2011). Specifically, evidence is accumulating that temporal shifts in insect phenology as a response to climatic alteration has accelerated over the past few decades (Singer and Parmesan 2010, Hodgson et al. 2011). For instance, emergence phenology has been shown to advance considerably in the past decades in many **[AQ3]** lepidopterans (Stefanescu et al. 2003, Hekkinen et al. 2010, Diamond et al. 2011). Besides, studies have recently detected that the annual number of generations of night-active moths has changed over the last decades (Altermatt 2010a, Kocsis and Hufnagel 2011, Gimesi et al. 2012). Global warming is assumed to be one of the most probable drivers of the increasing number of generations presumably by allowing more time for activity (Altermatt 2010a). Nocturnal moths have also been found to respond strongly to global warming by advancing spring flight periods but an immense number of species respond in a varied way to climatic changes in this taxa (Hodgson et al. 2011, Valtonen et al. 2011).

European noctuid moths constitute a representative taxonomic group for studying the effects of climatic trends on insect phenology, as they represent one of the most species-rich insect families subdivided into a large number of subfamilies and tribes characterised by a high diversity of life history, possibly related to the observed variation in climatic responsiveness (Karsholt and Razowski 1996, references in Supplementary material Appendix 1). A specific explanation for this large variation in climatic responsiveness may be that the ability of lepidopterans to track food plant phenology is assumed to be constrained by a number of ecological and life history factors (van Asch and Visser 2007, Altermatt 2010b, Breed et al. 2013). As a consequence, declining population sizes in butterflies (and also in moths) are often attributed to spatial mismatches between their distribution area and changing climatic envelopes, leading to regional or total extinctions of entire subspecies (Devictor et al. 2012).

The developmental stage in which individuals hibernate has already been shown to affect climatic responsiveness. For instance, species overwintering as adults were shown to exhibit higher degrees of phenological flexibility than lepidopterans hibernating as larvae or pupae, as these taxa can emerge immediately after hibernation (Diamond et al. 2011).

Recent studies have detected that climatic warming seems to enhance the range of migratory movements of some moth species, as migrant populations might track climatic trends faster owing to their large mobility (Sparks et al. 2007).

Evidence is accumulating that climatic responsiveness shows contrasting regional patterns across Europe, both in the frequency of supplementary generations and temporal patterns of emergence phenology of lepidopterans (Tobin et al. 2008, Altermatt 2010a, Pöyry et al. 2011, Kharouba et al. 2014).

In our study we aim to assess the role of life-history and ecological traits in climatic responsiveness in a species-rich lepidopteran family (Noctuidae) with a control for phylogenetic dependence. To accomplish this objective, we used a long-term dataset of European noctuid moths collected by a light-trap in Jósvafő (Aggtelek karst, northeastern Hungary, 48.5°N, 20.51°E, 287 m a.s.l), eastern Europe, where such investigations are still scarce.

Although a recent study has shown that many life-history traits might have important roles in climatic responsiveness in lepidopterans (Radchuk et al. 2013), we aim to assess only those which emerged as substantial predictors of climatic responsiveness in lepidopterans. Accordingly, we employed three proxies related to the species' ecology (habitat affinity, characterised as habitat specialist or generalist; food plant specialization and food type, defined as herbaceous or woody) and two types of life-history traits (migration strategy, and hibernation form) already shown to affect the climatic sensitivity of lepidopterans (Forrest and Miller-Rushing 2010, Diamond et al. 2011).

Specifically, our hypotheses are as follows: 1) species with broader habitat range would be less responsive to climatic change, as these noctuids are less constrained by climate-induced changes in habitat phenology. 2) Food-generalist noctuid moths would exhibit smaller degrees of advancement in emergence phenology (as estimated by capture dates) than specialist species as they are less dependent on the phenology of one or a few specific food plants. 3) Migrant moths would track climatic variability to a greater degree than resident ones, as they have more developed sensitivity to weather conditions promoting flexible onsets of northward migration (Sparks et al. 2007, Alerstam et al. 2011). 4) Finally, noctuids which hibernate as adults might track climatic trends faster than species hibernating as larvae or pupae as these moths can emerge immediately after finishing hibernation (Nyman et al. 2012).

Material and methods

Study area

The moth fauna of the Aggtelek karst area has been intensively surveyed over the last decades of the last century (Varga 1999, Szabó et al. 2007). We collected data during a long term light trap survey. The Jermy-type light trap was established in 1988 on the northeast-facing slope of the Tohonya Valley in Aggtelek National Park, northeast Hungary (48.1°N, 20.51°E, 287 m). The trap equipped with a 125 W mercury bulb was activated in 1988 and operated in each year for a 20-year period until 2007 between March and November, spanning 4788 days in total. The study area provides a unique opportunity to investigate the moths' climatic sensitivity, as this part of the Carpathian basin is located in the intersection of several biogeographical zones harbouring 407 noctuid moth species, an unusually high number in central Europe (Varga 1999, 2012). Furthermore, the study area is surrounded by a broad variety of habitats hosting a set of noctuid taxa highly representative for the region. The light trap was located in an abandoned orchard, presently used as a semi-dry haymeadow, surrounded by scattered rests of karstic oak–hornbeam *Waldsteinio–Carpinetum* and xerothermic oak forests (*Corno–Quercetum pubescentis*) and hazel shrub *Coryletum avellanae* communities (Szabó et al. 2007).

Climate data

Weather data were obtained from the nearest meteorological station at Miskolc (48°1N, 20°4E), 60 km from the light-trap. Out of a numerous set of climatic variables, daily mean temperature and daily precipitation were available for the studied period. To assess temporal patterns in climatic predictors relevant for lepidopteran biology, we calculated monthly and seasonal (March to May for spring, June to August for summer, September to November for autumn and December to February for winter) means and variances of daily average temperature and monthly as well as seasonal precipitation sums and variances. Further, we computed temporal patterns in cumulative temperature, a biologically more relevant predictor of climatic responsiveness than temperature itself (Pöyry et al. 2011). The computation went as follows: we set a temperature limit of 5.0°C, and summed daily average temperature values above this limit for the following periods in each year,: 1) 1 January to 31 March, 2) 1 January to 31 April, 3) 1 January 1 to 31 May, 4) 1 March to 31 May. To detect temporal trends in weather proxies, we fitted linear regressions on these variables as a function of years.

Noctuid data

In each year the light trap was operated from the first days of March until the first days of November (with a small, 1–2 day variation per year due to accidentally unfavourable weather conditions), totalling 4788 days (mean ± SD = 239.4 ± 12 days per year). Captured specimens were collected on a daily basis and were stored in cotton layers or pinned until identification. Species-level identification was carried out by SSz and ZV and the data were entered into a database by recording date, taxon and number of individuals.

During the study period 128 045 individuals of 417 noctuid taxa were collected. To acquire robust measures on climatic responsiveness, we used only the data of species with records from at least ten years spanning for at least 15 years, yielding 200 species in total. In the following step we retained only species with more than twenty individuals caught in total in every year, to be able to obtain reliable estimates of the annual population development. As a result, we used the records of 70 species in subsequent analyses (filtered species hereafter; Supplementary material Appendix 2). To test the robustness of the above filtering conditions, we removed noctuids with less than ten distinct capture dates per year from the set of 200 species and repeated all analyses.

To test the effects of first and final operation dates of the light trap, we calculated the distribution of capture dates of filtered species. This shows that the percentage of first and last capture dates within seven days from first and last operation dates, respectively, were less than 0.1%. Therefore it is unlikely that between-year variation in first and final operation dates can influence phenological patterns.

To derive standard measures of climatic responsiveness for each species, we calculated slopes of linear regressions fitted on years using the following estimates of emergence phenology as response variables: 1) first, 2) median and 3) last julian dates (day-of-year number) of capture and 4) activity length (defined as the number of days between first and last capture dates), calculated using corresponding capture dates. We refer to these response variables as climatic responsiveness of first, median and last julian days as well as activity length. High slopes from these regressions indicate that a given species can respond faster to climatic changes. The linear regression slopes were then applied in phylogenetic least squares models as response variables to investigate which ecological and life history traits influence climatic responsiveness. To test the robustness of the emergence predictors, we applied the approach proposed by van Strien et al. (2008) to our dataset. Accordingly, we calculated 1) the date of the 25th individual captured (FA25) and 2) the date of the first 25% of all observed individuals in the entire flight period (FP25) for each species in the filtered dataset. In the next step we calculated Pearson's correlation coefficients medium capture dates and only FP25 which revealed significant relationships ($r = 0.73$, $p < 0.03$) between medium capture dates and those proposed by van Strien et al. (2008).

Ecological and life-history predictors

We obtained data on ecological variables and life-history traits from the series of Noctuidae Europae (Ronkay et al. 2001, Hacker et al. 2002, Fibiger et al. 2009, 2010). Habitat affinity was classified as specialist or generalist. Feeding strategy was characterized by diet specialization (categorised as food specialist or food generalist) and food type (classified according to the food type of caterpillars: herbaceous or woody). Migration strategy was categorised as resident and migratory. Hibernation type was classified as imago, pupal and larval stages (Varga et al. 2005).

All used data on the species' life history and ecology are presented in the Supplementary material Appendix 2.

Phylogenetic and statistical analyses

In the first step we constructed a composite tree (Supplementary material Appendix 3) using the data of the most recent molecular survey applying gradual branch lengths (Mitchell et al. 2006, Zahiri et al. 2011). To account for the lack of knowledge of species-level tree topology, we included only subfamily-level information provided by the most recent molecular phylogenetic analyses (Mitchell et al. 2006, Zahiri et al. 2011).

To evaluate the degree of association between climatic responsiveness measures and ecological and life-history predictors, we fitted phylogenetic generalized least squares (PGLS) models controlling for the non-independence among taxa by incorporating a variance–covariance matrix that represents their phylogenetic relationships (Martins and Hansen 1999, Pagel 1997, 1999). The degree of phylogenetic dependence (λ) was set to the most appropriate value obtained for each model by likelihood ratio statistics (Freckleton et al. 2002). In the following step we calculated the strength of phylogenetic relatedness in each trait separately by quantifying the maximum-likelihood value of λ with its statistical significance estimated by likelihood ratio tests (i.e. by comparing the log-likelihood of the model in which λ is set to the most appropriate value to the log-likelihood of a model in which $\lambda = 0$). As recent studies on the phylogeny of Noctuidae have suggested a number of major changes in the structure of the phylogenetic tree (references provided in the Supplementary material Appendix 4), we repeated assessing phylogenetic signal in response and predictor variables by formulating linear mixed models that include only genus nested in subfamily as a random term, and compared model performance by ANOVA tests.

After model fitting, the relative importance of life-history traits and ecological variables was calculated using information-theoretic model-comparison (Burnham and Anderson 2002). First we obtained the values of Akaike's information criterion corrected for small sample size (AIC_c) and the corresponding Akaike weight of each model (ω). Second, we selected models with substantial support ($\Delta_i = AIC_i - AIC_{min} < 2.0$) and calculated model-averaged parameter estimates (β) and unconditional standard errors (SE_u; Burnham and Anderson 2002) of each variable by the sums of their Akaike weights across all models with substantial support containing the given predictor. Akaike differences in the range 0–2 indicate substantial level of empirical support of a given model, whereas $\Delta_i > 7$ implies very weak support (Burnham and Anderson 2002).

For all analyses we used the R statistical computing environment including its 'ape' (Paradis et al. 2011), 'geiger' (Harmon et al. 2009), 'MuMIn' (Barton 2011) and 'nlme' (Pinheiro et al. 2009) packages.

Results

Climatic patterns

During the 20 years of data collection monthly mean temperature has significantly increased only in June ($b = 0.140$°C year^{-1}, $F_{1,17} = 7.292$, $p = 0.015$, Fig. 1). Seasonal mean and cumulative temperature has not shown significant trends. Further, we detected no clear temporal patterns in variance of monthly temperature and all precipitation metrics (results not shown).

Temporal trends in capture data

Noctuids showed a considerable amount of variation in slopes of various estimates of emergence phenology as a function of years. Out of the 70 taxa in our study, 38 shifted

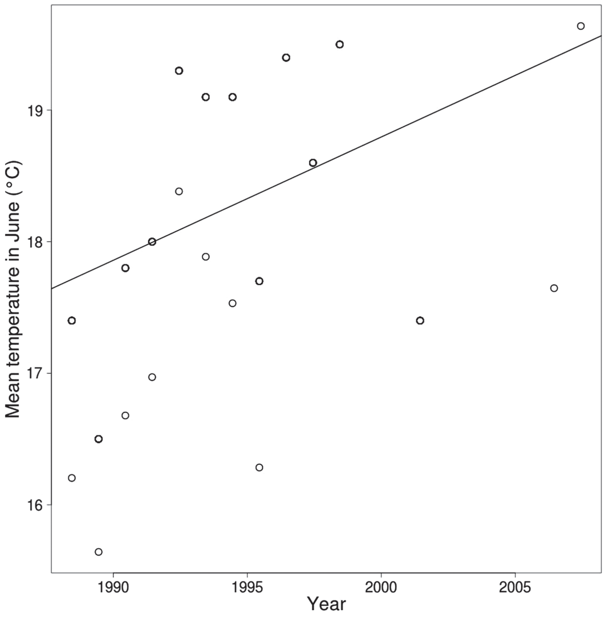

Figure 1. June mean temperature as a function of years during the study.

their first capture to earlier dates with four of them exhibiting significant advance. Median capture dates, indicative of the climatic responsiveness of the bulk of the population, showed similar patterns with 34 noctuids emerging earlier but the trend was only significant for a single species. Last julian dates of annual records have advanced in 27 taxa, four of which were significant (Supplementary material Appendix 2, Fig. 2).

In contrast, first capture of 32 noctuids shifted to later dates with only a single species showing significant patterns. Median capture date was detected to change to later dates in 36 noctuids including three species with significant trends. Last capture dates of 43 noctuids have shifted later, five of which exhibited significant temporal patterns. Although activity length shortened in 28 species with significant trends in three species, it became longer in 42 noctuids including significant relationships for nine taxa (Supplementary material Appendix 2).

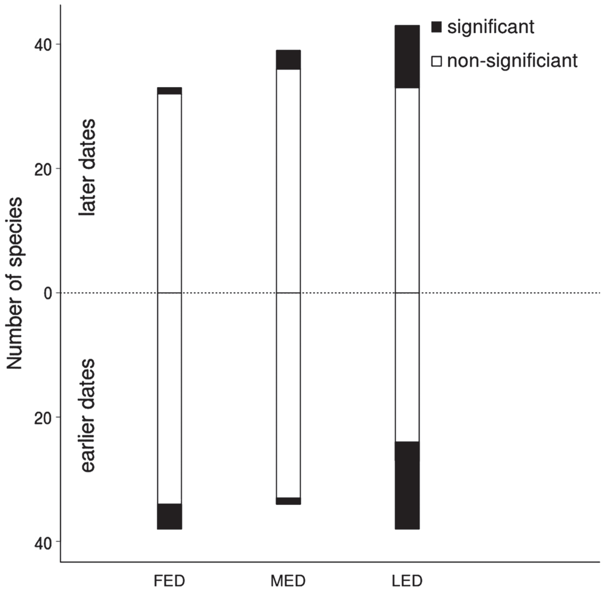

Figure 2. Number of species shifting emergence phenology to earlier and later dates.

Table 1. λ-statistics for phylogenetic signal in the investigated response variables and predictors. λ = 0 indicates no phylogenetic signal.

Variable	λ	Likelihood ratio	p
Slope of first capture date	0.000	0.000	0.999
Slope of median capture date	0.000	0.000	0.999
Slope of last capture date	0.000	0.000	0.999
Slope of activity length	0.000	0.000	0.997
Migration type	0.000	0.000	0.999
Hibernation type	0.000	0.000	0.422
Food specialisation	0.543	0.898	0.343
Food type	0.811	2.249	0.134
Habitat affinity	0	0.001	0.98

On average, noctuids shifted their first capture dates by 4.705 (SE = 0.902) days to later dates after 1998 than before this year across all species considered. Similarly, median capture occurred 4.525 (SE = 2.210) days later in the second period than in the first one. In contrast, overall last emergence shifted by 7.547 (SE = 1.325) days to later dates, representing a delay almost twice as long as the delay at the beginning of the flight season. As a result, activity length increased by 2.842 (SE = 1.151) days calculated over the filtered set of species.

Ecological and life history correlates of phenological change

Phylogenetic signal (λ) was zero for all measures of all response and proxy variables (Table 1). Quantitatively similar results were obtained by linear mixed models which showed no significant effect of genus nested within subfamily (p = 0.067).

Responsiveness of first capture dates was significantly affected by food type and migration strategy – parameter estimates of which had confident intervals not overlapping with zero. Noctuids with larvae feeding primarily on woods are shifting first emergence to later dates while species feeding on herbaceous plants advance first capture dates ($\sum = 0.826$; Table 2, 3; Supplementary material Appendix 5).

Our results show that migratory strategy has emerged as the second most important proxy of climatic responsiveness measured as first capture dates based on its Akaike sums in PGLS-models fitted on first capture dates ($\sum = 0.749$; Table 2, 3; Supplementary material Appendix 5): resident noctuids advanced climatic responsiveness measured as first capture dates to a greater degree than migratory species. Parameter estimates for all other variables have confidence intervals overlapping with zero, therefore we consider their effects as non-significant.

Considering last emergence phenology hibernation stage has emerged with the highest Akaike scores calculated over supported models fitted on the slope of last capture dates ($\sum = 1.0$, Table 2). Hibernation stage was the only predictor

Table 2. Akaike sums, model-averaged parameter estimates (β), standard errors (SEu) and 95% confidence intervals for predictors across best supported models ($\Delta_i < 2.0$).

Slope of first emergence date	Slope of median emergence date	Slope of last emergence date	Slope of activity length
Food type $\Sigma = 0.826$ $\beta(SE_u) = -0.395$ (0.145) 95% CI = (−0.678; −0.111)	Migration strategy $\Sigma = 0.483$ $\beta(SE_u) = -0.497$ (0.575) 95% CI = (−1.625; 0.631)	Hibernation stage $\Sigma = 1.0$ $\beta(SE_u) = -2.674$ (0.543) 95% CI = (−3.737; −1.61)	Hibernation stage $\Sigma = 1.0$ $\beta(SE_u) = -3.018$ (0.608) 95% CI = (−4.21; −1.826)
Migration strategy $\Sigma = 0.749$ $\beta(SE_u) = -0.547$ (0.243) 95% CI = (−1.023; −0.07)	Food type $\Sigma = 0.404$ $\beta(SE_u) = -0.376$ (0.365) 95% CI = (−1.091; 0.339)	Migration strategy $\Sigma = 0.246$ $\beta(SE_u) = -0.227$ (0.406) 95% CI = (−1.023; 0.57)	Migration strategy $\Sigma = 0.282$ $\beta(SE_u) = 0.265$ (0.467) 95% CI = (−0.651; 1.18)
Habitat affinity $\Sigma = 0.296$ $\beta(SE_u) = 0.252$ (0.15) 95% CI = (−0.099; 0.548)	Habitat affinity $\Sigma = 0.299$ $\beta(SE_u) = 0.206$ (0.36) 95% CI = (−0.499; 0.912)	Food type $\Sigma = 0.209$ $\beta(SE_u) = -0.217$ (0.301) 95% CI = (−0.807; 0.373)	Habitat affinity $\Sigma = 0.213$ $\beta(SE_u) = -0.212$ (0.287) 95% CI = (−0.774; 0.35)
Food specialisation $\Sigma = 0.212$ $\beta(SE_u) = 0.224$ (0.165) 95% CI = (−0.099; 0.548)	Food specialisation $\Sigma = 0.293$ $\beta(SE_u) = 0.052$ (0.404) 95% CI = (−0.74; 0.843)	Food specialisation $\Sigma = 0.183$ $\beta(SE_u) = 0.151$ (0.293) 95% CI = (−0.424; 0.725)	Food type $\Sigma = 0.195$ $\beta(SE_u) = 0.099$ (0.339) 95% CI = (−0.564; 0.763)
Hibernation stage $\Sigma = 0.151$ $\beta(SE_u) = 0.386$ (0.303) 95% CI = (−0.208; 0.981)	Hibernation stage $\Sigma = 0.278$ $\beta(SE_u) = 0.097$ (0.755) 95% CI = (−1.384; 1.577)	Habitat affinity $\Sigma = 0.142$ $\beta(SE_u) = -0.018$ (0.252) 95% CI = (−0.512; 0.475)	Food specialisation $\Sigma = 0.186$ $\beta(SE_u) = -0.06$ (0.331) 95% CI = (−0.708; 0.588)

of last capture dates and activity length in the best supported models: species hibernating as imagos shifted last capture to later dates and prolonged activity length to a greater degree than noctuids hibernating as larvae or pupae (Table 2, Fig. 3, 4; Supplementary material Appendix 7).

We obtained qualitatively similar results for species with more than ten capture dates per year (Supplementary material Appendix 6).

Discussion

In this study we aimed to 1) describe the extent of phenological responses presumably caused by ongoing climate change in a species-rich group of noctuid moths and 2) investigate the possible ecological and life history correlates of these responses. We believe that our results are based on a unique combination of methodological elements. First, our dataset was collected over 20 years applying highly standardised collection methodology. Second, the single collection site allows high-level replication of species-specific climatic responsiveness of large number of noctuid taxa allowing multispecies analyses of 70 species after rigorous filtering. Third, we calculated multiple phenological estimates in order to avoid collection bias primarily affecting first emergence phenology.

Considering noctuid phenology, we detected no clear patterns in changes of emergence phenology, which might be related to the diversity in a number of life history traits of the studied species, as shown by recent investigations (Altermatt 2010a or b????). [AQ2] Additionally, complex trends of emergence phenology can also be a result of our finding that significant trends in climatic patterns were only found for June temperature, which is in line with a number of recent studies showing no clear temperature trends after 1990 (reviewed by Stocker et al. 2013). Although Hungary has experienced considerable increase of annual mean temperature over the past century (Molnár V. et al. 2012), our study covered only two decades and was located in an area where the foothills of the Carpathian Mountains might have had a buffering effect.

Our findings show that the degree of temporal shifts of various measures of emerging phenology was primarily related to hibernation stage, food type and migration strategy.

Table 3. Supported models ($\Delta_i < 2.0$) fitted on all types of response variables.

Response	Model formula	DF	AICc	Δ_i	w
Slope of first emergence date	food type + migration strategy	4	123.811	0	0.279
	food type + habitat affinity + migration strategy	5	124.904	1.092	0.161
	food type	3	125.321	1.509	0.131
Slope of median emergence date	migration strategy	3	246.815	0	0.123
	food type	3	247.018	0.203	0.111
	food type + migration strategy	4	247.695	0.88	0.079
	hibernation stage	4	247.858	1.043	0.073
	food specialisation	3	247.881	1.067	0.072
	habitat affinity	3	247.996	1.181	0.068
	habitat affinity + migration strategy	4	248.586	1.771	0.051
Slope of last emergence date	hibernation stage	4	203.804	0	0.395
Slope of activity length	hibernation stage	4	219.033	0	0.362
	hibernation stage + migration strategy	5	220.947	1.914	0.139

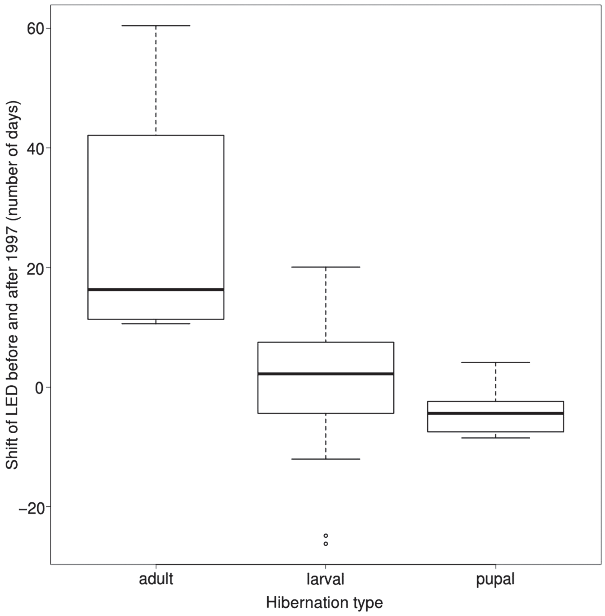

Figure 3. Shift of last capture date as a function of hibernation stage in noctuid moths.

Specifically, hibernation stage is the strongest predictor of climatic responsiveness measured as last capture dates and activity length in noctuid moths, similarly to the results of Diamond et al. (2011). This might indicate that noctuid moths overwintering as adults exhibited greater degrees of phenological shifts than species hibernating as larvae or pupae. This finding extends the results of a recent study reporting that species with more advanced overwintering stages have experienced relatively greater advances in their date of first appearance (Diamond et al. 2011). However, the difference between the reactions of the bulk of the population and last active individuals to climatic trends seems to be different in our case. Since noctuids hibernating as adults in our database showed no shifts in median emergence to earlier dates, the last individuals of these moths have prolonged capture dates over the study period in comparison to species hibernating in larval or pupal form. Prolonged autumn activity may allow longer time for replenishing fat reserves before hibernation which can increase survival chances and improve reproductive success. Moreover, all of these species are winter-active moths in the southern part of their distribution areas implying that noctuid taxa hibernating as imagos are forced to suspend activity in our climate and the prolonged autumn activities of the last emerging individuals might be the result of enhanced temporal plasticity of the timing of autumn emergence (László et al. 2000).

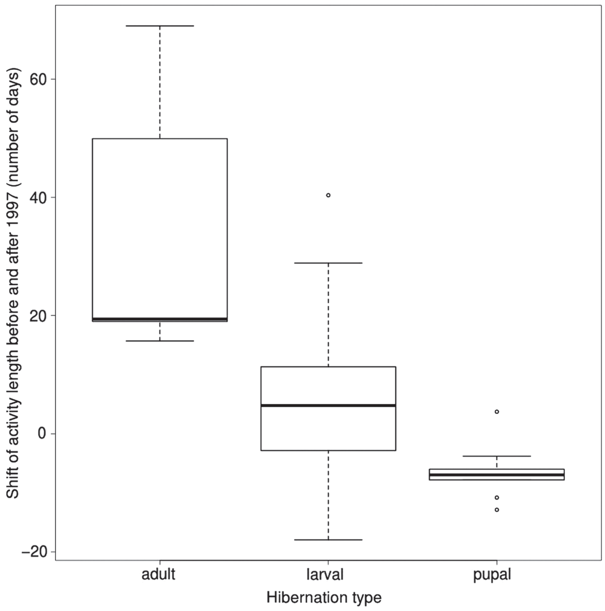

Figure 4. Shift of activity length as a function of hibernation stage in noctuid moths.

Food type was included in best supported models for climatic responsiveness measured as first capture dates, similarly to previous investigations: noctuids feeding on herbaceous plants advanced first capture dates to a greater degree than species connected to woody materials (Diamond et al. 2011, Altermatt 2010a or b????). **[AQ2]** Although a previous study showed that herbaceous plants were more likely than woody plants to advance phenology (Walther et al. 2002), our results imply that moths feeding on herbaceous plants are able to track plant phenology faster than noctuids feeding on woody plants which evokes the following hypotheses. First, as herbaceous plants are shorter-lived on average than woody taxa, their herbivores are forced to synchronise phenology to a greater degree than moth larvae feeding on woody plants. Second, woody plants are on average larger than herbaceous species implying higher levels of phenological variance of plant parts consumed by herbivores in individual trees which allows for a wider range of phenological synchronisation. However, the complexity of climatic responses driven by trophic interactions is enhanced by the fact that the highly diverse family of Noctuidae is linked to a great variety of larval food plants (references in Supplementary material Appendix 1). For instance, the majority of these species is connected to forested habitats and majority of spring- and autumn-active moths are linked to woody food plants (details shown in Supplementary material Appendix 2; references in Supplementary material Appendix 1). A large group of genera (Supplementary material Appendix 2) use a wide variety of food plants which are most often herbaceous (grasses for mostly monovoltine *Apamea*, and often Urticaceae for the phenologically more plastic Plusiinae), or partly herbaceous and woody (Acronictinae) (Supplementary material Appendix 2).

Migration strategy has emerged as a supported predictor of climatic responsiveness. Migrant noctuids have shifted first captures to later dates than resident moths which implies that migratory species arriving from southern regions may detect warming spring weather later than locally hibernating taxa (Alerstam et al. 2011). Indeed, migrant moths need time to reach central Europe and thus are outcompeted in advancements of climatic responsiveness measured as first capture dates by locally wintering moths hibernating as imagos.

Throughout our analyses we detected no phylogenetic relatedness on the subfamily level in climatic responsiveness of noctuid moths. As the existing politomies are largely unresolved, this implies that the absence of phylogenetic signal in climatic responsiveness of noctuid moths can be considered as the result of poor resolution of clades rather than missing phylogenetic relationships. Since the majority of noctuid taxa in our dataset belongs to the tribe Hadenini previously merged into the subfamily Noctuinae by Lafontaine and Schimdt (2011), for which recent investigations on evolutionary relatedness do not provide better phylogenetic resolutions, we were not able to detect phylogenetic signal on finer scales (Zahiri et al. 2013). This warrants further research on phylogenetic relatedness among noctuid moths to be able to detect if climatic responsiveness is independent of phylogenetic relatedness in noctuid species as shown by a number of investigations showing that phenological shifts are not driven by common descent in a broad range of taxa (Végvári et al. 2010, Diamond et al. 2011). However, the lack of phylogenetic signal in emergence phenology of the species in our dataset can also be an outcome of phenotypic plasticity which drives phenological patterns as a response to climatic variability, suggested by the findings of recent studies across a number of taxonomic levels (Hoffmann and Sgrò 2011). [AQ4] The similar results of Diamond et al. (2011) showing that phylogenetic relatedness among species predicted very little variation in butterflies' phenological responses imply that climatic responsiveness in lepidopterans can be treated as a species-specific reaction rather than driven by evolutionary relatedness (Altermatt 2010a).

Our study implies recommendations for lepidopteran conservation, as a reflection to current declining trends in a number of insect species on a global scale. We found that noctuid moths hibernating as adults are able to track climatic trends faster than species overwintering in less developed stages which suggest higher declining probabilities in these taxa, considering current climatic predictions (Stocker et al. 2013). Our result that resident moths are responding to ongoing climatic patterns to a greater degree than migratory taxa, calls for more intensive surveys of migrating lepidopterans populations.

In summary, we have demonstrated in a diverse set of noctuid moth species that temporal trends in emergence phenology (which is associated with a measure of temperature increase in the study area) is primarily related to hibernation stage, diet specialisation and migration strategy.

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