Hibernation stage predicts climatic responsiveness in noctuid moths

Journal:	*Oikos*
Manuscript ID:	OIK-01655
Wiley - Manuscript type:	Research
Date Submitted by the Author:	24-Mar-2014
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Keywords:	climate change, phylogenetic control, model selection
Abstract:	Emergence phenology has been shown to advance considerably in the past decades in many lepidopterans. Noctuid moths constitute a species-rich family of lepidopterans with a unique diversity of life history traits driving climatic responsiveness. In our study we aim to assess the role of life-history and ecological traits in climatic responsiveness of noctuid moths (Noctuidae) with a control for phylogenetic dependence. We used a long-term dataset of European noctuid moths collected by a light-trap in North-Eastern Hungary. As the study site is located in 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 emerging phenology was primarily related to hibernation stage, food type and migration strategy. Large-scale phylogenetic relatedness exerted little constraint in all models fitted on all measures of capture dates. Our results imply that noctuid moths overwintering as adults exhibited greater degrees of phenological shifts than species hibernating as larvae or pupae. It follows that this group is forced to hibernate as imagos in our climate and the prolonged autumnal activities of the last emerging individuals might be interpreted as a return

	to their original life-cycle. The missing subfamily-level phylogenetic signal in climatic responsiveness of noctuid moths implies that responses to climatic trends are primarily governed by life-history and ecological adaptations rather than large-scale phylogenetic relatedness.

Hibernation stage predicts climatic responsiveness in noctuid moths

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Running head: Climatic responsiveness of noctuid moths

Summary

Emergence phenology has been shown to advance considerably in the past decades in many lepidopterans. Noctuid moths constitute a species-rich family of lepidopterans with a unique diversity of life history traits driving climatic responsiveness. In our study we aim to assess the role of life-history and ecological traits in climatic responsiveness of noctuid moths (Noctuidae) with a control for phylogenetic dependence. We used a long-term dataset of European noctuid moths collected by a light-trap in North-Eastern Hungary. As the study site is located in 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 emerging phenology was primarily related to hibernation stage, food type and migration strategy. Large-scale phylogenetic relatedness exerted little constraint in all models fitted on all measures of capture dates. Our results imply that noctuid moths overwintering as adults exhibited greater degrees of phenological shifts than species hibernating as larvae or pupae. It follows that this group is forced to hibernate as imagos in our climate and the prolonged autumnal activities of the last emerging individuals might be interpreted as a return to their original life-cycle. The missing subfamily-level phylogenetic signal in climatic responsiveness of noctuid moths implies that responses to climatic trends are primarily governed by life-history and ecological adaptations rather than large-scale phylogenetic relatedness.

Key words: Noctuidae, climate change, phylogenetic control, model selection

Introduction

During the past decades an increasing number of studies have reported about the effects of global climatic change on ecosystem structure and functioning (Parry et al. 2007, Walther 2010, Burrows et al. 2011). These effects 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 lepidopterans (Stefanescu et al. 2003, Hekkinen et al. 2010, Diamond et al. 2011) and, 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 diversely respond to climatic changes in this taxa (Hodgson et al. 2011, Valtonen et al. 2011).

European noctuid moths constitute an ideal 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, possible related to the observed variable climatic responsiveness (Karsholt and

Razowski 1996, references in Appendix 1). A specific explanation for variation in responses may be that the ability of lepidopterans to track food plant phenology is often 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 seem to enhance the range of migratory movements of some moth species, as migrant populations might track climatic trends faster owing to their increased 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 in eastern Europe where such investigations are still scarce. To accomplish this objective, we used a long-term dataset of European noctuid moths collected by a light-trap in Jósvafő (Aggtelek karst, North-Eastern Hungary, 48.5ºN, 20.51ºE, 287 m a.s.l). This 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.

Although a recent study has shown that many life-history traits might have important role in climatic responsiveness in lepidopterans, we aim to assess only those which are more likely to be relevant for noctuid moths (Radchuk et al. 2013). Hence, 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 robust 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 the hibernation (Nyman et al. 2012).

Materials 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 light trap was established in 1988 on the North-East-facing slope of the Tohonya Valley in Aggtelek National Park, North-East Hungary (48.1° N20.51° E, 287 m). 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 recorded by an automatic meteorological station, located 50 meters from the light trap. Out of a numerous set of climatic variables, daily mean temperature and daily precipitation were available for the studied period.

As it was not possible to obtain meteorological data between 1996-2005, we compared existing data with those of the nearest meteorological station at Miskolc (N48.1, E20.4), 60 kilometres from the light-trap by computing Pearson correlation coefficients. Since the strength of correlation between the monthly mean temperatures and precipitation sums was highly significant (median r= 0.89, minimum r= 0.68, all $p < 0.01$) for all months, we considered meteorological data from Miskolc representative for the study site. 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) January 1-March 31 (2) January 1-April 31 (3) January 1-May 31 (4) March 1-May 31. To detect temporal trends in weather proxies, we fitted linear regressions on these variables as a function of years.

Noctuid data

The Jermy-type light trap (Szabó et al. 2007) equipped with a 125 W mercury bulb was activated in 1988 and operated in each year for a 20 year period until 2007. 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 ± 39 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 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, in order 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; 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 faster respond to climatic changes. The linear regression slopes were then applied in phylogenetic least squares models as response variables to investigate what ecological and life history traits influence climatic responsiveness.

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, Fibiger et al. 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 has the categories of 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 Appendix 2.

Phylogenetic and statistical analyses

In the first step we constructed a composite tree (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 tribal-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 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 (R Development Core Team, 2013) 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 in June (b = 0.140 °C/year, $F_{1,17} = 7.292$, $p = 0.015$). 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 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 (Appendix 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 (Appendix 2).

On average, noctuids shifted their first capture dates by 4.705 (SE=0.902) days to later dates after 1998 than in the first half of the study period 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 complete 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 with the random factor genus nested within subfamily (results not shown).

First capture dates were affected by significant effects of 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).

Our results show that migratory strategy has emerged as the second most important proxy of climatic responsiveness based on its Akaike sums in PGLS-models fitted on first capture dates ($\sum = 0.749$; Table 2, 3): 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.

Overall, 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 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, Appendix 5; Fig 1, Fig 2).

We obtained qualitatively similar results for species with more than ten capture dates per year (results not shown.)

Discussion

In this study we aimed to (i) describe the extent of phenological responses presumably caused by ongoing climate change in a species-rich group of noctuid moths and (ii) investigate the possible ecological and life history correlates of these responses.

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.

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. 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. 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 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. Parallely, all of these species are winter-active moths in the southern part of their distribution areas which group is forced to hibernate as imagos in our climate and the prolonged autumn activities of the last emerging individuals might be interpreted as a return to their original life-cycle (László et al. 2000).

Food type was included in best supported models for climatic responsiveness measured as first capture dates: noctuids feeding on herbaceous plants advanced first capture dates to a greater degree than species connected to woody materials. Although a recent survey of British plants showed that annuals were more likely than perennials to advance phenology (Fitter and Fitter 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 that the highly diverse family of Noctuidae is connected to a great variety of larval food plants. For instance, 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 Appendix 2). A large group of genera (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) (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. This result is in line with a number of investigations showing that the advancement in spring phenology is not driven by common descent in a broad range of taxa (Végvári et al. 2010, Diamond et al. 2011). The lack of phylogenetic signal in emergence phenology of the species in our dataset evokes several explanations (1) climatic sensitivity is a species-specific response (2) phenotypic plasticity might play a role in driving phenology dynamics as a response to climatic variability, paralleling the findings of recent studies across a number of taxonomic levels (Hoffmann and Sgrò 2011). However, the resolution of current phylogenetic studies of noctuid moths does not allow us to draw more general conclusions on the existence of phylogenetic signal in climatic responsiveness of night-active lepidopterans. 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. Further, lacking phylogenetic relatedness in climatic sensitivity probably contributes to fast adaptations to global change, observed in a wide range of insect taxa (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 call for more intensive survey of migrating lepidopterans populations.

In sum, 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.

Acknowledgements

This research was supported by the European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP-4.2.4.A/ 2-11/1-2012-0001 'National Excellence Program'.The support of the nature conservation authorities of Hungary is highly appreciated. ZB was supported by a Hungarian Research Fund grant (OTKA K75696).

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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

Table 2. Akaike sums, model-averaged parameter estimates (beta), 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 $\sum = 0.826$ $\beta(SE_u)$= -0.395 (0.145) 95% CI = (-0.678; -0.111)	Migration strategy $\sum = 0.483$ $\beta(SE_u)$ = -0.497 (0.575) 95% CI = (-1.625; 0.631)	Hibernation stage $\sum = 1.0$ $\beta(SE_u)$ = -2.674 (0.543) 95% CI = (-3.737; -1.61)	Hibernation stage $\sum = 1.0$ $\beta(SE_u)$ = -3.018 (0.608) 95% CI = (-4.21; -1.826)
Migration strategy $\sum = 0.749$ $\beta(SE_u)$ = -0.547 (0.243) 95% CI = (-1.023; -0.07)	Food type $\sum = 0.404$ $\beta(SE_u)$ = -0.376 (0.365) 95% CI = (-1.091; 0.339)	Migration strategy $\sum = 0.246$ $\beta(SE_u)$ = -0.227 (0.406) 95% CI = (-1.023; 0.57)	Migration strategy $\sum = 0.282$ $\beta(SE_u)$ = 0.265 (0.467) 95% CI = (-0.651; 1.18)
Habitat affinity $\sum = 0.296$ $\beta(SE_u)$ = 0.252 (0.15) 95% CI = (-0.099; 0.548)	Habitat affinity $\sum = 0.299$ $\beta(SE_u)$ = 0.206 (0.36) 95% CI = (-0.499; 0.912)	Food type $\sum = 0.209$ $\beta(SE_u)$ = -0.217 (0.301) 95% CI = (-0.807; 0.373)	Habitat affinity $\sum = 0.213$ $\beta(SE_u)$ = -0.212 (0.287) 95% CI = (-0.774; 0.35)
Food specialisation $\sum = 0.212$ $\beta(SE_u)$ = 0.224 (0.165) 95% CI = (-0.099; 0.548)	Food specialisation $\sum = 0.293$ $\beta(SE_u)$ = 0.052 (0.404) 95% CI = (-0.74; 0.843)	Food specialisation $\sum = 0.183$ $\beta(SE_u)$ = 0.151 (0.293) 95% CI = (-0.424; 0.725)	Food type $\sum = 0.195$ $\beta(SE_u)$ = 0.099 (0.339) 95% CI = (-0.564; 0.763)
Hibernation stage $\sum = 0.151$ $\beta(SE_u)$ = 0.386 (0.303) 95% CI = (-0.208; 0.981)	Hibernation stage $\sum = 0.278$ $\beta(SE_u)$ = 0.097 (0.755) 95% CI = (-1.384; 1.577)	Habitat affinity $\sum = 0.142$ $\beta(SE_u)$ = -0.018 (0.252) 95% CI = (-0.512; 0.475)	Food specialisation $\sum = 0.186$ $\beta(SE_u)$ = -0.06 (0.331) 95% CI = (-0.708; 0.588)

Table 3. Supported models ($\Delta_i < 7.0$) fitted on all types of response variables.

response	Model formula	df	AICc	Δ_i	w
Slope of first emergence date	foodtype + migratory	4	123.811	0	0.279
	foodtype + habpr2 + migratory	5	124.904	1.092	0.161
	foodtype	3	125.321	1.509	0.131
	foodspec + foodtype + migratory	5	125.964	2.152	0.095
	foodtype + hiber3 + migratory	6	127.997	4.186	0.034
	foodspec + foodtype + habpr2 + migratory	6	128.104	4.293	0.033
	foodspec + foodtype	4	128.213	4.402	0.031
	foodtype + habpr2 + hiber3 + migratory	7	128.514	4.702	0.027
	migratory	3	128.692	4.881	0.024
	habpr2 + hiber3 + migratory	6	128.772	4.961	0.023
	foodspec	3	128.832	5.021	0.023
	habpr2 + migratory	4	128.974	5.162	0.021
	hiber3	4	128.999	5.187	0.021
	foodspec + migratory	4	129.064	5.253	0.02
	hiber3 + migratory	5	129.069	5.258	0.02
	foodtype + habpr2	4	129.11	5.299	0.02
	foodtype + hiber3	5	129.653	5.842	0.015
	habpr2	3	130.275	6.463	0.011
	foodspec + hiber3 + migratory	6	130.285	6.473	0.011
Slope of median emergence date	migratory	3	246.815	0	0.123
	foodtype	3	247.018	0.203	0.111
	foodtype + migratory	4	247.695	0.88	0.079
	hiber3	4	247.858	1.043	0.073

	foodspec	3	247.881	1.067	0.072
	habpr2	3	247.996	1.181	0.068
	habpr2 + migratory	4	248.586	1.771	0.051
	hiber3 + migratory	5	248.847	2.032	0.044
	foodspec + migratory	4	249	2.185	0.041
	foodspec + foodtype	4	249.3	2.485	0.035
	foodtype + habpr2	4	249.545	2.731	0.031
	foodtype + habpr2 + migratory	5	249.724	2.91	0.029
	foodtype + hiber3	5	249.754	2.939	0.028
	foodspec + foodtype + migratory	5	250.039	3.224	0.024
	foodspec + hiber3	5	250.2	3.385	0.023
	foodspec + habpr2	4	250.22	3.406	0.022
	habpr2 + hiber3	5	250.382	3.568	0.021
	foodtype + hiber3 + migratory	6	250.552	3.738	0.019
	habpr2 + hiber3 + migratory	6	250.76	3.946	0.017
	foodspec + habpr2 + migratory	5	250.878	4.063	0.016
	foodspec + hiber3 + migratory	6	251.176	4.361	0.014
	foodspec + foodtype + habpr2	5	251.805	4.99	0.01
	foodspec + foodtype + habpr2 + migratory	6	252.089	5.275	0.009
	foodspec + foodtype + hiber3	6	252.117	5.303	0.009
	foodtype + habpr2 + hiber3	6	252.41	5.595	0.007
	foodtype + habpr2 + hiber3 + migratory	7	252.678	5.864	0.007
	foodspec + habpr2 + hiber3	6	252.709	5.895	0.006
	foodspec + foodtype + hiber3 + migratory	7	252.992	6.177	0.006
	foodspec + habpr2 + hiber3 + migratory	7	253.188	6.373	0.005
Slope of last emergence date	hiber3	4	203.804	0	0.395
	hiber3 + migratory	5	205.899	2.095	0.139
	foodtype + hiber3	5	206.245	2.44	0.117

	foodspec + hiber3	5	206.554	2.75	0.1
	habpr2 + hiber3	5	207.16	3.355	0.074
	foodtype + hiber3 + migratory	6	208.222	4.418	0.043
	foodspec + hiber3 + migratory	6	208.585	4.781	0.036
	habpr2 + hiber3 + migratory	6	209.142	5.338	0.027
	foodspec + foodtype + hiber3	6	209.159	5.354	0.027
	foodtype + habpr2 + hiber3	6	209.627	5.823	0.022
	foodspec + habpr2 + hiber3	6	209.815	6.011	0.02
Slope of activity length	hiber3	4	219.033	0	0.362
	hiber3 + migratory	5	220.947	1.914	0.139
	foodtype + hiber3	5	221.667	2.634	0.097
	habpr2 + hiber3	5	221.717	2.684	0.095
	foodspec + hiber3	5	221.778	2.745	0.092
	habpr2 + hiber3 + migratory	6	223.106	4.073	0.047
	foodtype + hiber3 + migratory	6	223.564	4.531	0.038
	foodspec + hiber3 + migratory	6	223.695	4.662	0.035
	foodspec + foodtype + hiber3	6	224.438	5.405	0.024
	foodtype + habpr2 + hiber3	6	224.462	5.428	0.024
	foodspec + habpr2 + hiber3	6	224.479	5.446	0.024
	foodtype + habpr2 + hiber3 + migratory	7	225.877	6.844	0.012
	foodspec + habpr2 + hiber3 + migratory	7	225.961	6.928	0.011

Predictors are abbreviated as:

hiber3: hibernation stage

migratory: migration strategy

habpr2: habitat affinity

foodtype: food type

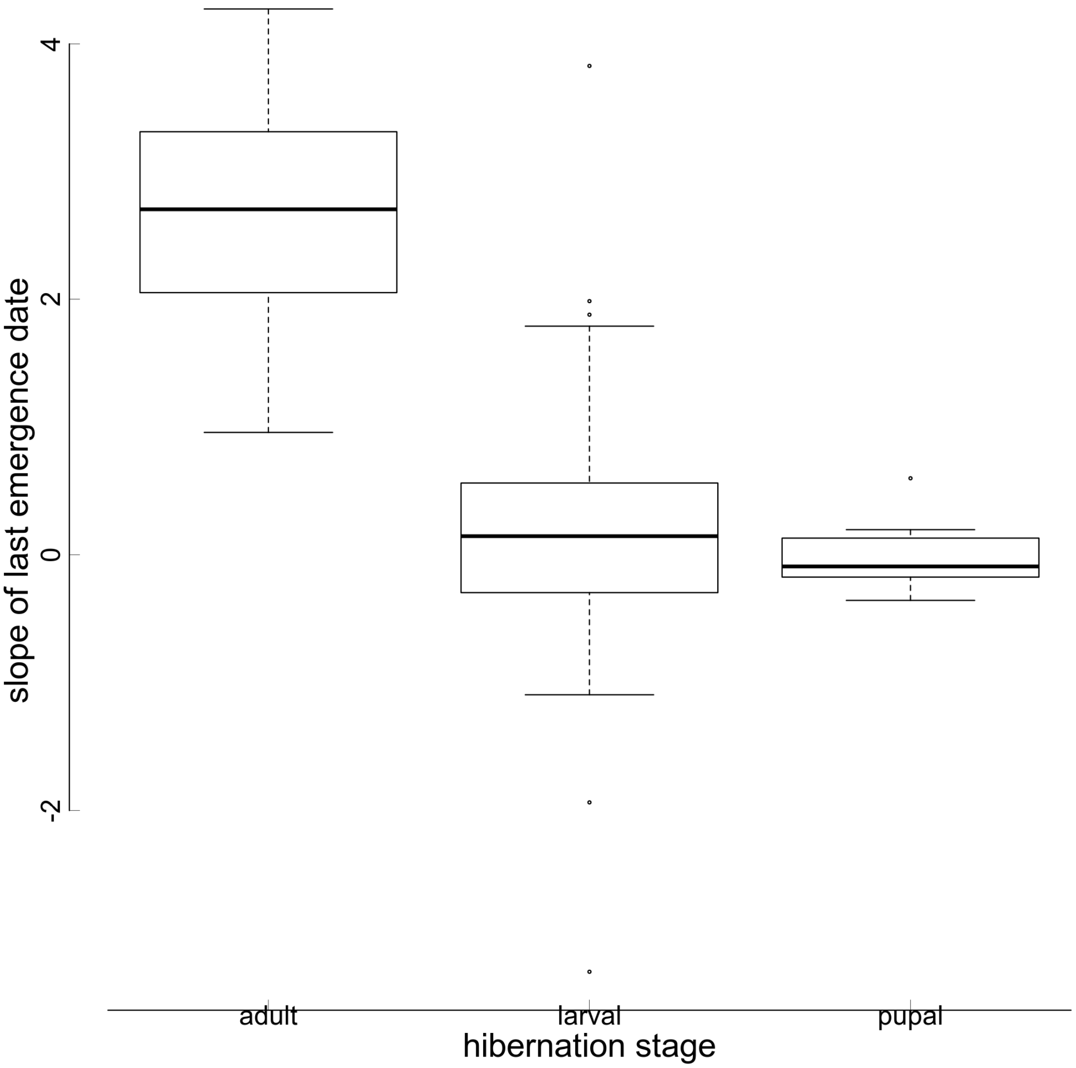
foodspec: food specialisation

Figure legends

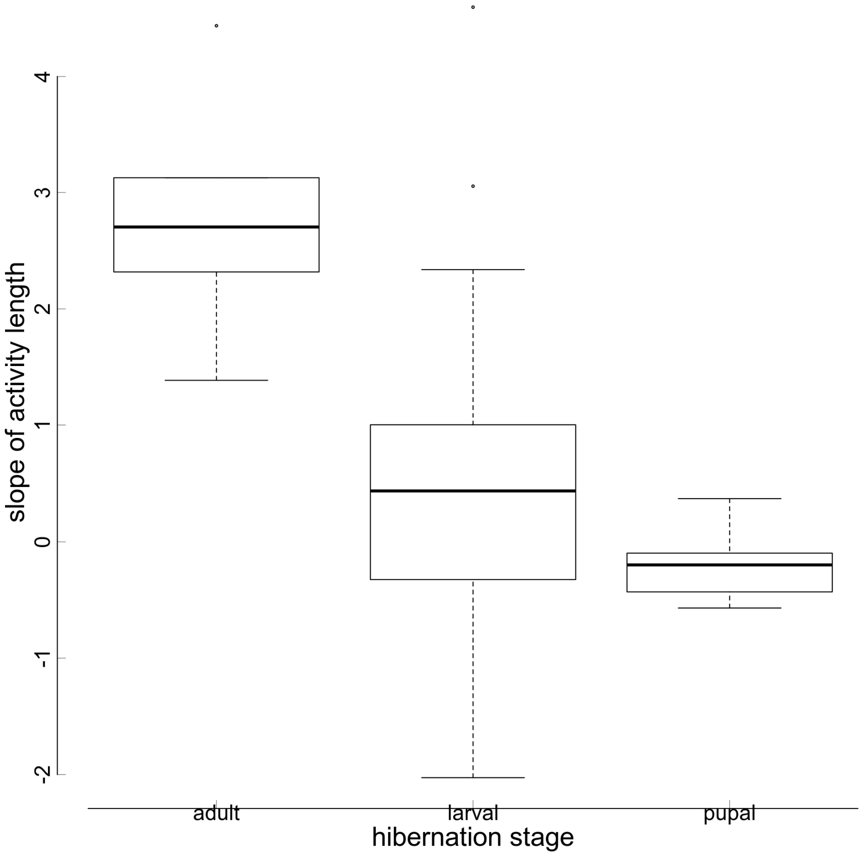
Fig 1. Slope of last capture date as a function of hibernation stage in noctuid moths.

Fig 2. Slope of activity length as a function of hibernation stage in noctuid moths.

Fig. 1.


slope of last emergence date
4
2
0
-2
adult
larval
pupal
hibernation stage

534 **Fig. 2.**


slope of activity length
4
3
2
1
0
-1
-2
adult
larval
pupal
hibernation stage

Appendix 1. References for ecological and life-history traits of Noctuid moths.

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Appendix 2. Life-history traits, ecological predictors and measures of climatic responsiveness of noctuid moths. In the table we use the following abbreviations: FED=first emergence date; LED= last emergence date; MED=median emergence date.

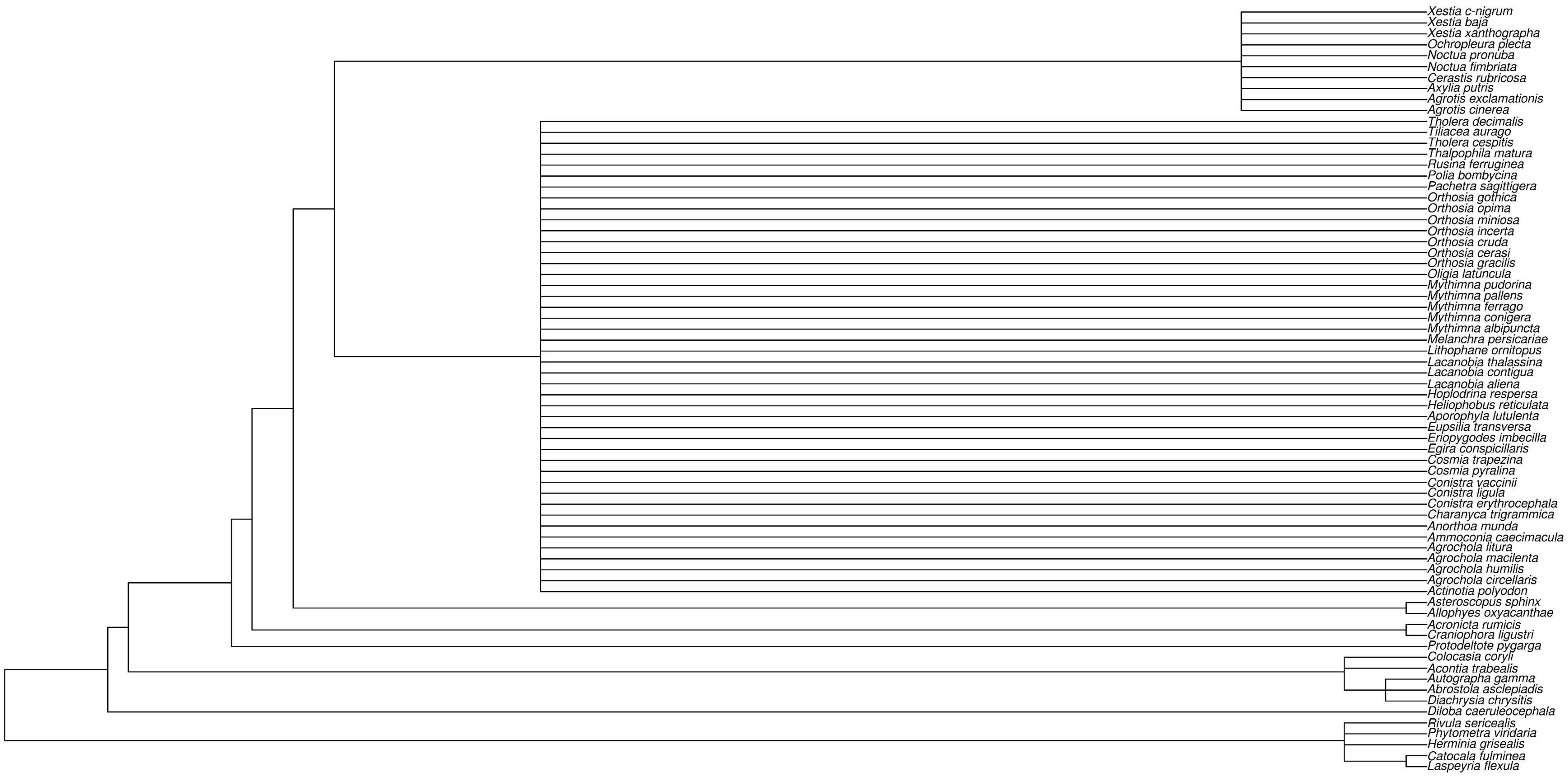
Taxon	Subfamily	Hibernation stage	Migration strategy	Habitat affinity	Food specialization	Food type	FED slope (p-value)	LED slope (p-value)	MED slope (p-value)	Slope of activity length (p-value)
Abrostola asclepiadis	Plusiinae	larval	resident	stenoecious	specialist	herbaceous	-0.383 (-0.383)	1.415 (0.119)	-0.101 (0.949)	1.798 (0.013)
Acontia trabealis	Acontiinae	larval	resident	euryoecious	gene	herbaceous	-1.641 (-1.641)	1.418 (0.158)	1.152 (0.697)	3.058 (0.08)
Acronicta rumicis	Acronictinae	larval	resident	euryoecious	generalist	herbaceous	-0.743 (-0.743)	1.043 (0.26)	-1.155 (0.55)	1.786 (0.036)
Actinotia polyodon	Xyleninae	larval	resident	stenoecious	generalist	herbaceous	0.253 (0.253)	0.056 (0.951)	-0.759 (0.619)	-0.198 (0.824)
Agrochola circellaris	Xyleninae	egg	resident	stenoecious	generalist	woody	0.854 (0.854)	0.562 (0.334)	1.249 (0.141)	-0.292 (0.743)
Agrochola humilis	Xyleninae	egg	resident	stenoecious	generalist	woody	-0.218 (-0.218)	0.511 (0.053)	0.537 (0.376)	0.729 (0.157)
Agrochola litura	Xyleninae	egg	resident	stenoecious	generalist	woody	0.102 (0.102)	0.567 (0.006)	0.701 (0.169)	0.465 (0.277)
Agrochola macilenta	Xyleninae	egg	resident	stenoecious	specialist	woody	0.1 (0.1)	0.378 (0.444)	0.103 (0.859)	0.277 (0.699)
Agrotis cinerea	Noctuinae	larval	resident	stenoecious	generalist	herbaceous	-0.24 (-0.24)	-0.663 (0.003)	-0.554 (0.172)	-0.423 (0.131)
Agrotis exclamationis	Noctuinae	larval	resident	euryoecious	generalist	herbaceous	-0.774 (-0.774)	0.387 (0.576)	-0.868 (0.4)	1.161 (0.097)
Allophyes oxyacanthae	Psaphidinae	egg	resident	stenoecious	specialist	woody	-0.141 (-0.141)	0.804 (0.005)	0.951 (0.027)	0.944 (0.018)
Ammoconia caecimacula	Xyleninae	egg	resident	stenoecious	specialist	herbaceous	-0.192 (-0.192)	0.284 (0.336)	-0.801 (0.078)	0.476 (0.182)
Anorthoa munda	Hadeninae	pupal	resident	stenoecious	specialist	woody	0.494 (0.494)	0.065 (0.821)	0.684 (0.276)	-0.429 (0.326)
Aporophyla lutulenta	Xyleninae	larval	resident	euryoecious	generalist	herbaceous	0.074 (0.074)	1.512 (0.168)	1.012 (0.606)	1.438 (0.135)
Asteroscopus sphinx	Psaphidinae	egg	resident	stenoecious	specialist	woody	0.239 (0.239)	0.348 (0.408)	0.133 (0.777)	0.11 (0.764)
Autographa gamma	Plusiinae	larval	migratory	euryoecious	generalist	herbaceous	0.403 (0.403)	-0.608 (0.403)	1.406 (0.501)	-1.012 (0.326)

Axylia putris	Noctuinae	larval	migratory	euryoecious	generalist	herbaceous	-0.377 (-0.377)	-0.057 (0.939)	-0.239 (0.878)	0.321 (0.654)
Catocala fulminea	Catocalinae	larval	resident	stenoecious	specialist	woody	0.622 (0.622)	-0.812 (0.051)	-0.582 (0.408)	-1.434 (0.001)
Cerastis rubricosa	Catocalinae	pupal	resident	stenoecious	generalist	herbaceous	0.129 (0.129)	-0.107 (0.63)	-0.248 (0.662)	-0.236 (0.623)
Charanyca trigrammica	Xyleninae	larval	resident	stenoecious	generalist	herbaceous	-0.679 (-0.679)	-0.143 (0.741)	0.196 (0.706)	0.536 (0.319)
Colocasia coryli	Pantheinae	larval	resident	stenoecious	generalist	woody	0.582 (0.582)	0.15 (0.787)	-0.355 (0.846)	-0.432 (0.432)
Conistra erythrocephala	Xyleninae	adult	resident	stenoecious	generalist	woody	-0.163 (-0.163)	4.273 (0.09)	0.309 (0.94)	4.435 (0.092)
Conistra ligula	Xyleninae	adult	resident	stenoecious	generalist	woody	0.182 (0.182)	3.313 (0.305)	6.599 (0.094)	3.131 (0.351)
Conistra vaccinii	Xyleninae	adult	resident	stenoecious	generalist	woody	0.002 (0.002)	2.706 (0.336)	-0.937 (0.814)	2.704 (0.328)
Cosmia pyralina	Xyleninae	larval	resident	stenoecious	generalist	woody	-0.178 (-0.178)	1.985 (0.052)	-0.124 (0.877)	2.163 (0.042)
Cosmia trapezina	Xyleninae	larval	resident	euryoecious	generalist	woody	-0.399 (-0.399)	-0.121 (0.767)	-1.723 (0.121)	0.279 (0.696)
Craniophora ligustri	Acronictinae	larval	resident	stenoecious	specialist	woody	-0.735 (-0.735)	0.531 (0.422)	-0.346 (0.851)	1.267 (0.145)
Diachrysia chrysitis	Plusiinae	larval	resident	stenoecious	generalist	herbaceous	-0.948 (-0.948)	-0.118 (0.881)	-0.84 (0.58)	0.83 (0.286)
Diloba caeruleocephala	Dilobinae	egg	resident	euryoecious	generalist	woody	-0.313 (-0.313)	0.706 (0.025)	0.311 (0.523)	1.019 (0.011)
Egira conspicillaris	Hadeninae	pupa	resident	stenoecious	generalist	herbaceous	0.232 (0.232)	0.602 (0.167)	0.367 (0.562)	0.37 (0.408)
Eriopygodes imbecilla	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	-0.424 (-0.424)	0.097 (0.82)	0.268 (0.553)	0.521 (0.24)
Eupsilia transversa	Xyleninae	adult	resident	euryoecious	generalist	woody	-0.267 (-0.267)	2.051 (0.45)	-2.568 (0.491)	2.318 (0.39)
Herminia grisealis	Herminiinae	larval	resident	euryoecious	generalist	herbaceous	-1.237 (-1.237)	-3.263 (0.012)	-2.453 (0.343)	-2.026 (0.224)
Heliophobus reticulata	Hadeninae	larval	resident	stenoecious	specialist	herbaceous	0.002 (0.002)	-0.383 (0.342)	-0.5 (0.213)	-0.385 (0.375)
Hoplodrina respersa	Xyleninae	larva	resident	stenoecious	generalist	herbaceous	-0.816 (-0.816)	-1.062 (0.042)	-2.162 (0.056)	-0.246 (0.756)
Lacanobia aliena	Hadeninae	larval	resident	stenoecious	specialist	herbaceous	-0.011 (-0.011)	0.146 (0.812)	0.404 (0.73)	0.157 (0.839)
Lacanobia contigua	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	-0.828 (-0.828)	1.281 (0.025)	3.708 (0.002)	2.109 (0.004)
Lacanobia	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	0.313 (0.313)	0.389 (0.61)	-0.29 (0.824)	0.076 (0.92)

thalassina										
Laspeyria flexula	Aventiinae	larval	resident	stenoecious	generalist	herbaceous	-1.402 (-1.402)	0.061 (0.898)	-3.215 (0.039)	1.462 (0.015)
Lithophane ornitopus	Xyleninae	adult	resident	stenoecious	generalist	woody	-0.428 (-0.428)	0.96 (0.181)	-2.277 (0.569)	1.388 (0.108)
Melanchra persicariae	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	-0.025 (-0.025)	-0.223 (0.752)	0.838 (0.27)	-0.198 (0.785)
Mythimna albipuncta	Hadeninae	larval	migratory	euryoecious	generalist	herbaceous	-0.123 (-0.123)	1.879 (0.059)	0.207 (0.918)	2.002 (0.065)
Mythimna conigera	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	0.412 (0.412)	-1.092 (0.005)	-1.489 (0.061)	-1.504 (0.01)
Mythimna ferrago	Hadeninae	larval	resident	euryoecious	generalist	herbaceous	-0.922 (-0.922)	0.064 (0.927)	-0.119 (0.888)	0.986 (0.213)
Mythimna pallens	Hadeninae	larval	migratory	euryoecious	generalist	herbaceous	-2.107 (-2.107)	-1.933 (0.228)	-1.611 (0.451)	0.175 (0.911)
Mythimna pudorina	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	0.011 (0.011)	0.933 (0.161)	1.171 (0.191)	0.921 (0.186)
Noctua fimbriata	Noctuinae	larval	migratory	euryoecious	generalist	herbaceous	0.686 (0.686)	0.331 (0.567)	0.931 (0.498)	-0.355 (0.509)
Noctua pronuba	Noctuinae	larval	migratory	euryoecious	generalist	herbaceous	0.876 (0.876)	-0.33 (0.612)	-0.9 (0.649)	-1.205 (0.308)
Ochropleura plecta	Noctuinae	larval	migratory	euryoecious	generalist	herbaceous	-0.034 (-0.034)	-0.13 (0.889)	0.359 (0.799)	-0.096 (0.911)
Oligia latruncula	Xyleninae	larval	resident	stenoecious	specialist	herbaceous	-1.16 (-1.16)	-0.211 (0.669)	-1.55 (0.04)	0.949 (0.194)
Orthosia cerasi	Hadeninae	pupal	resident	euryoecious	generalist	woody	0.393 (0.393)	-0.174 (0.701)	0.78 (0.152)	-0.567 (0.198)
Orthosia cruda	Hadeninae	pupal	resident	euryoecious	generalist	woody	0.26 (0.26)	0.131 (0.749)	0.087 (0.88)	-0.129 (0.771)
Orthosia gothica	Hadeninae	pupal	resident	euryoecious	generalist	woody	0.208 (0.208)	-0.265 (0.598)	-0.69 (0.256)	-0.474 (0.326)
Orthosia gracilis	Hadeninae	pupal	resident	stenoecious	specialist	woody	0.261 (0.261)	-0.125 (0.735)	1.192 (0.042)	-0.386 (0.49)
Orthosia incerta	Hadeninae	pupal	resident	euryoecious	generalist	woody	-0.197 (-0.197)	-0.356 (0.394)	1.145 (0.072)	-0.159 (0.7)
Orthosia miniosa	Hadeninae	pupal	resident	stenoecious	specialist	woody	0.238 (0.238)	0.197 (0.59)	-0.424 (0.411)	-0.041 (0.905)
Orthosia opima	Hadeninae	pupal	resident	stenoecious	specialist	woody	0.023 (0.023)	-0.074 (0.921)	0.122 (0.893)	-0.097 (0.882)
Pachetra sagittigera	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	0.062 (0.062)	-0.409 (0.585)	-1.058 (0.087)	-0.471 (0.528)
Phytometra viridaria	Phytometrinae	larval	resident	euryoecious	generalist	herbaceous	-0.767 (-0.767)	3.828 (0.504)	0.690 (0.893)	4.595 (0.554)
Polia bombycina	Hadeninae	larval	resident	stenoecious	generalist	herbaceous	0.127 (0.127)	-0.477 (0.496)	-0.313 (0.563)	-0.604 (0.45)

Protodeltote pygarga	Eustrotiinae	larval	resident	euryoecious	generalist	herbaceous	-0.094 (-0.094)	-0.746 (0.275)	0.068 (0.956)	-0.652 (0.332)
Rivula sericealis	Rivulinae	larval	resident	euryoecious	generalist	herbaceous	-0.841 (-0.841)	-0.306 (0.77)	-1.09 (0.442)	0.535 (0.623)
Rusina ferruginea	Xyleninae	larval	resident	stenoecious	generalist	herbaceous	-0.864 (-0.864)	0.422 (0.376)	0.152 (0.809)	1.286 (0.009)
Thalpophila matura	Xyleninae	larval	resident	stenoecious	generalist	herbaceous	0.221 (0.221)	-0.284 (0.437)	0.198 (0.689)	-0.505 (0.415)
Tholera cespitis	Hadeninae	egg	resident	euryoecious	generalist	herbaceous	0.102 (0.102)	0.538 (0.213)	0.533 (0.1)	0.436 (0.467)
Tholera decimalis	Hadeninae	egg	resident	euryoecious	specialist	herbaceous	-0.025 (-0.025)	0.114 (0.663)	0.1 (0.747)	0.139 (0.654)
Tiliacea aurago	Xyleninae	egg	resident	euryoecious	specialist	woody	0.335 (0.335)	1.096 (0.004)	0.599 (0.476)	0.761 (0.145)
Xestia baja	Noctuinae	larval	resident	stenoecious	generalist	herbaceous	-0.702 (-0.702)	0.101 (0.621)	-0.297 (0.704)	0.803 (0.11)
Xestia c-nigrum	Noctuinae	larval	migratory	euryoecious	generalist	herbaceous	-0.548 (-0.548)	1.789 (0.079)	0.212 (0.901)	2.338 (0.028)
Xestia xanthographa	Noctuinae	larval	resident	euryoecious	generalist	herbaceous	0.59 (0.59)	-0.375 (0.093)	-0.004 (0.995)	-0.965 (0.042)

Appendix 3. Phylogenetic tree of noctuid taxa used in PGLS models



Appendix 4. References for creating the phylogenetic tree of noctuid taxa.

Mitchell, A. et al. (2006) Systematics and evolution of the cutworm moths (Lepidoptera : Noctuidae): evidence from two protein-coding nuclear genes. Syst. Ent. 31, 21-46.

Speidel, W. et al. (1996) The phylogeny of the Noctuidae (Lepidoptera). Syst. Ent. 21, 219-251.

Zahiri, R. et al. (2011) A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera). Zool. Script. 40, 158-173.

Appendix 5. Parameter estimates of life-history and ecological predictors in PGLS-models. In the table we use the following abbreviations: FED=first emergence date; LED= last emergence date; MED=median emergence date.

Response	Model ID	Intercept	Migration strategy	Habitat affinity	Food specialisation	Food type	Hibernation stage
FED slope	0	0.557 (0.245)	-0.496 (0.22)			-0.431 (0.138)	
	1	0.534 (0.241)	-0.66 (0.234)	0.26 (0.141)		-0.409 (0.136)	
	2	0.061 (0.11)				-0.354 (0.137)	
	3	0.518 (0.244)	-0.538 (0.22)		0.226 (0.157)	-0.392 (0.139)	
	4	0.377 (0.324)	-0.511 (0.219)			-0.382 (0.163)	0.415 (0.293)
	5	0.509 (0.242)	-0.668 (0.234)	0.223 (0.146)	0.166 (0.16)	-0.383 (0.138)	
	6	-0.002 (0.124)			0.176 (0.161)	-0.318 (0.141)	
	7	0.33 (0.317)	-0.695 (0.232)	0.287 (0.14)		-0.349 (0.16)	0.466 (0.287)
	8	0.126 (0.215)	-0.325 (0.227)				
	9	0.239 (0.323)	-0.628 (0.236)	0.318 (0.143)			0.402 (0.294)
	10	-0.226 (0.077)			0.261 (0.161)		
	11	0.126 (0.21)	-0.524 (0.243)	0.298 (0.149)			
	12	-0.135 (0.25)					0.339 (0.307)
	13	0.126 (0.211)	-0.405 (0.226)		0.313 (0.161)		
	14	0.281 (0.332)	-0.416 (0.222)				0.339 (0.301)
	15	-0.017 (0.148)		0.108 (0.137)		-0.334 (0.14)	
	16	-0.135 (0.246)				-0.31 (0.166)	0.401 (0.303)
	17	-0.267 (0.108)		0.167 (0.139)			
	18	0.352 (0.329)	-0.486 (0.223)		0.282 (0.16)		0.226 (0.303)

	β(SE_u)	0.347 (0.34)	-0.547 (0.243)	0.252 (0.15)	0.224 (0.165)	-0.395 (0.145)	0.386 (0.303)
	95% CI	(-0.32; 1.015)	(-1.023; -0.07)	(-0.042; 0.546)	(-0.099; 0.548)	(-0.678; -0.111)	(-0.208; 0.981)
LED slope	0	2.66 (0.438)					-2.671 (0.536)
	1	2.867 (0.593)	-0.206 (0.398)				-2.671 (0.539)
	2	2.66 (0.439)				-0.212 (0.296)	-2.629 (0.541)
	3	2.66 (0.44)			0.149 (0.287)		-2.731 (0.551)
	4	2.675 (0.482)		-0.018 (0.242)			-2.675 (0.542)
	5	2.929 (0.6)	-0.268 (0.406)			-0.249 (0.303)	-2.621 (0.544)
	6	2.912 (0.601)	-0.252 (0.407)		0.181 (0.293)		-2.744 (0.554)
	7	2.861 (0.599)	-0.232 (0.439)	0.039 (0.266)			-2.663 (0.546)
	8	2.66 (0.442)			0.099 (0.3)	-0.183 (0.311)	-2.674 (0.562)
	9	2.699 (0.484)		-0.048 (0.246)		-0.221 (0.303)	-2.636 (0.547)
	10	2.714 (0.489)		-0.067 (0.258)	0.175 (0.306)		-2.755 (0.563)
	β(SE_u)	2.718 (0.496)	-0.227 (0.406)	-0.018 (0.252)	0.151 (0.293)	-0.217 (0.301)	-2.674 (0.543)
	95% CI	(1.746; 3.691)	(-1.023; 0.57)	(-0.512; 0.475)	(-0.424; 0.725)	(-0.807; 0.373)	(-3.737; -1.61)
MED slope	0	0.282 (0.512)	-0.358 (0.54)				
	1	0.195 (0.27)				-0.366 (0.336)	
	2	0.731 (0.617)	-0.536 (0.555)			-0.449 (0.347)	
	3	0.225 (0.608)					0.076 (0.745)
	4	-0.058 (0.185)			0.081 (0.387)		
	5	-0.137 (0.257)		0.161 (0.331)			
	6	0.282 (0.514)	-0.559 (0.593)	0.301 (0.363)			
	7	0.693 (0.822)	-0.468 (0.551)				0.076 (0.746)

	8	0.282 (0.516)	-0.391 (0.553)		0.131 (0.395)		
	9	0.201 (0.307)			-0.018 (0.398)	-0.369 (0.348)	
	10	0.123 (0.364)		0.1 (0.337)		-0.347 (0.344)	
	11	0.708 (0.62)	-0.701 (0.602)	0.261 (0.363)		-0.426 (0.35)	
	12	0.225 (0.611)				-0.26 (0.412)	0.128 (0.753)
	13	0.725 (0.626)	-0.542 (0.564)		0.033 (0.401)	-0.443 (0.357)	
	14	0.225 (0.612)			0.056 (0.399)		0.054 (0.767)
	15	-0.139 (0.26)		0.155 (0.35)	0.026 (0.409)		
	16	0.111 (0.668)		0.142 (0.336)			0.105 (0.752)
	17	0.777 (0.83)	-0.552 (0.563)			-0.336 (0.42)	0.143 (0.753)
	18	0.652 (0.825)	-0.673 (0.604)	0.308 (0.367)			0.138 (0.751)
	19	0.282 (0.517)	-0.563 (0.599)	0.289 (0.379)	0.051 (0.41)		
	20	0.723 (0.834)	-0.498 (0.564)		0.121 (0.406)		0.028 (0.769)
	21	0.134 (0.375)		0.112 (0.353)	-0.054 (0.416)	-0.356 (0.353)	
	22	0.714 (0.628)	-0.699 (0.607)	0.269 (0.378)	-0.04 (0.416)	-0.432 (0.359)	
	23	0.225 (0.615)			-0.015 (0.418)	-0.264 (0.433)	0.135 (0.782)
	24	0.137 (0.673)		0.111 (0.342)		-0.237 (0.421)	0.146 (0.76)
	25	0.732 (0.835)	-0.731 (0.612)	0.281 (0.37)		-0.304 (0.423)	0.193 (0.758)
	26	0.112 (0.68)		0.142 (0.359)	0.001 (0.425)		0.104 (0.782)
	27	0.785 (0.84)	-0.559 (0.572)		0.041 (0.422)	-0.325 (0.437)	0.125 (0.782)
	28	0.66 (0.84)	-0.675 (0.61)	0.301 (0.386)	0.026 (0.425)		0.126 (0.781)
	β(SE_u)	0.298 (0.598)	-0.497 (0.575)	0.206 (0.36)	0.052 (0.404)	-0.376 (0.365)	0.097 (0.755)
	95% CI	(-0.874; 1.469)	(-1.625; 0.631)	(-0.499; 0.912)	(-0.74; 0.843)	(-1.091; 0.339)	(-1.384; 1.577)
Slope of	0	2.795 (0.49)					-3.01 (0.601)

activity length							
	1	2.585 (0.665)	0.21 (0.446)				-3.01 (0.604)
	2	2.795 (0.494)				0.099 (0.333)	-3.03 (0.608)
	3	2.94 (0.538)		-0.182 (0.27)			-3.046 (0.605)
	4	2.795 (0.494)			-0.07 (0.322)		-2.982 (0.618)
	5	2.622 (0.667)	0.396 (0.488)	-0.279 (0.296)			-3.066 (0.607)
	6	2.552 (0.675)	0.243 (0.457)			0.132 (0.341)	-3.036 (0.612)
	7	2.56 (0.675)	0.235 (0.457)		-0.1 (0.329)		-2.97 (0.622)
	8	2.795 (0.497)			-0.047 (0.338)	0.085 (0.35)	-3.008 (0.632)
	9	2.934 (0.543)		-0.173 (0.276)		0.064 (0.339)	-3.057 (0.613)
	10	2.941 (0.547)		-0.182 (0.289)	0.001 (0.342)		-3.047 (0.63)
	11	2.596 (0.678)	0.415 (0.496)	-0.27 (0.3)		0.102 (0.343)	-3.084 (0.615)
	12	2.619 (0.679)	0.397 (0.493)	-0.275 (0.312)	-0.013 (0.344)		-3.06 (0.632)
	$\beta(SE_u)$	2.757 (0.567)	0.265 (0.467)	-0.212 (0.287)	-0.06 (0.331)	0.099 (0.339)	-3.018 (0.608)
	95% CI	(1.646; 3.867)	(-0.651; 1.18)	(-0.774; 0.35)	(-0.708; 0.588)	(-0.564; 0.763)	(-4.21; -1.826)