



## Effect of land use and climate on the diversity of moth guilds with different habitat specialization

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**Keywords:** Climate change, Habitat specialization, Landscape ecology, Light trapping, Macrolepidoptera.

**Abstract:** An assemblage of moth species at a suburb of Prague (50°5'11"N, 14°18'06"E) was monitored by a highly efficient mercury light trap for 23 years (1967-1976, 1980-1992). Species caught were divided into guilds according to habitat specialisation, and analysed using species richness  $S$ , Shannon's diversity  $H$  and evenness  $J$  as the response variables, and the individual years of monitoring and effects of mean annual temperature and precipitation as the explanatory variables. Overall, 424 species were recorded: 25 early successional arable land species (43% of all caught individuals), 116 forest species feeding on trees and shrubs, 33 forest species feeding on woodland herbs and lichens, 92 forest-steppe species, 116 grassland species, 28 wetland species, and 14 non-specialized generalists. The diversity of habitat-specialised species responded mainly to land use changes, whereas the diversity of generalists reflected long-term meteorological trends. Species richness of specialists whose habitats in the vicinity of the trap have declined in extent decreased, the numbers of those whose habitats remained intact did not exhibit any particular trend, whereas the numbers of generalists increased, and their diversity positively responded to warming. It is concluded that the habitat specialists and generalists react to environmental changes differently. Non-specialised species appear more sensitive indicators of climate changes than habitat specialists because for the latter the indication of climate changes can be overlaid by changes in habitat use.

**Nomenclature** of moths follows Lastuvka (1998).

### Introduction

Climate change and habitat loss represent widely recognised twin threats to global biodiversity, and hence to integrity of Earth's life supporting systems (Parmesan and Yohe 2003, Franco et al. 2006). In terrestrial biomes, the effects of changing climate include spatial shifts in species' ranges (Konvička et al. 2003, La Sorte and Thompson 2007, Wilson et al. 2007), phenological changes such as earlier arrival times or flowering periods (Roy and Sparks 2000, Hassall et al. 2007), and disruptions of finely-tuned biotic interactions (Harrington et al. 1999, Crozier 2004, Davies et al. 2006, Jepsen et al. 2008). The effects of habitat loss are evident in declines of populations and losses of species across wide regions, particularly so in industrial countries (Konvička et al. 2006, Pimm 2008). The losses no longer affect only rare and specialised organisms but apply to widely distributed species as well (Gaston and Fuller 2007). For instance, Britain's common moths have declined in numbers by about one third of their abundance forty years ago (Conrad et al. 2006a,b), likely affecting food supply of insectivorous vertebrates, and hence structuring and stability of food chains. Overall, it has

been estimated that 15-35% of Earth's species suffer losses due to the combined effects of climate change and habitat loss in a near future (Thomas et al. 2004).

Finding efficient responses to the two growing threats is complicated by complex interrelations between climate change and habitat loss effects. In groups in which distribution changes are monitored in detail, such as butterflies, both contrasting and reinforcing impacts of both developments have been detected. About one third of British warm-preferring butterfly species are shifting their ranges northwards, whereas another third fails to respond to increasing temperature, as habitat loss counterbalances the benefits of warmer climate (Warren et al. 2001). Changing climate increased the magnitude of population fluxes of the Bay checkerspot (*Euphydryas editha* B.) in California, eventually leading to population extinction (McLaughlin et al. 2002) and complex effects increasing extinction proneness have been observed elsewhere (Wallisdeevries and Van Swaay 2006). It is increasingly clear that without disentangling the climate change and habitat loss effects, we cannot produce reliable predictive models of responses of biotic communities to either of these two factors.

Here, we explore a unique opportunity to separate climate and habitat effects on diversity of moth light trap catches, using 23-years long data series originating from a single, but particularly efficient light trapping method. The trap was situated at a single location for the entire period, illuminating a section of landscape which remained unchanged, whereas adjacent parts underwent substantial land use changes. The trap attracted both specialists of several habitat types and generalists. While habitats of some specialists have declined rapidly, habitats of others did not change and hence increased in proportion. This situation allows us to compare the temporal changes of diversity of specialised and unspecialised species, as well as of species that have lost habitats with those not losing them.

The unique setting, and concurrent recording of meteorological data, allow us to test the hypothesis that the diversity of habitat-specialised species will respond mainly to land use changes, whereas the diversity of generalists will reflect long-term meteorological trends. More specifically, the diversity of specialists whose habitats in the vicinity of the trap have declined in extent should decrease, the diversity of those whose habitats remained intact should not exhibit any particular trend, whereas the diversity of generalists should increase, mainly as warming climate brings forth prolonged season and colonisation by a higher diversity of migrants that tend to be habitat generalists (cf. Sparks et al. 2005, 2007).

### Material and methods

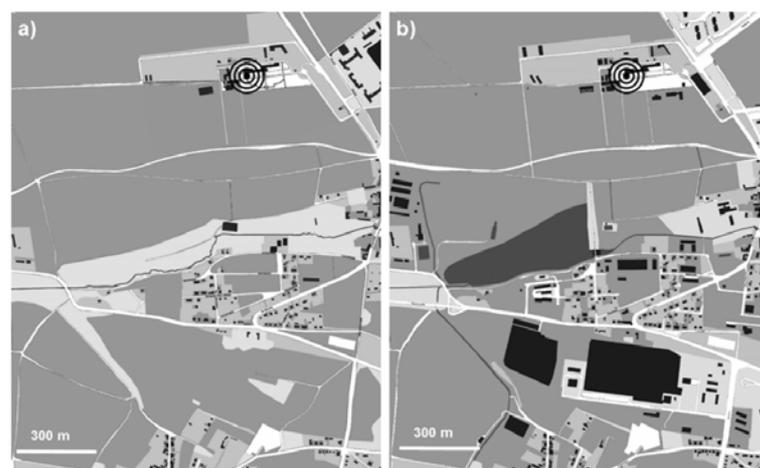
Moths were trapped at Ruzyně crop research station, at the outskirts of Prague (50°5'11"N, 14°18'06"E) using a highly efficient mercury-vapour light trap (Novák 1983). The trap was placed 8 m above the ground on the southern wall of a large building. It illuminated an arboretum with a

collection of deciduous trees and shrubs (2.7 ha), further surrounded by small arable land. Further away, but still in the range of the trap operation, there were dry and mesic grasslands with shrubs, intervened by small anthropogenic woodlands, lines of trees, small trampled areas, and riverine carr fen scrubs. During the period of the light trap operation, the park in front of the trap remained unchanged, while wet habitats were largely destroyed by the establishment of a pond, and small arable fields and forest-steppe habitats were both gradually abandoned, and part of them finally converted in build-up areas (Fig. 1).

The trap has been operating consistently throughout the growing seasons (March–November), from 1967 to 1992, and the catches were sorted to species by I.N. Yearly catches of all species belonging to families of traditional “macrolepidoptera” (i.e., the monophyletic *Macrolepidoptera sensu* Kristensen et al. 2007, plus primitive *Hepialidae*), which are available for 23 years, are analyzed here. Catches from 1977–1979, when only the 19 most abundant species were monitored, are excluded from this analysis.

Seven distinct habitat preference guilds of the moths were distinguished, based on preferences of both adult and larval stages (Fajčík 1998, Fajčík 2003): arable land species; forest species feeding on woodland herbs and lichens; forest species feeding on trees and shrubs; forest-steppe species; grassland species; wetland species; and generalists, occurring in many types of habitats (Appendix 1). Mean annual temperatures and precipitations originated from a local meteorological station.

Species diversity in each of 23 years was expressed, separately for all species and all species belonging to the specified guilds, as (i) species richness  $S$  (square rooted to



**Figure 1.** Proportional distribution of main habitat types and components in monitored region, **a)** situation in 1967, **b)** in 1992. Black concentric circles show the approximate position of the light-trap.

Legend of map:

	Parks		Field (arable land)
	Meadows		Water sheets
	Gardens		Buildings

normalize the data, e.g., Sokal and Rohlf 1995), (ii) Shannon's index of diversity  $H$

$$H = -\sum_{i=1}^n p_i \ln p_i,$$

where  $p_i$  is the proportion of individuals of the  $i$ -th species in the total number of individuals of all species,  $n$  is the total number of species, and  $\ln$  is the natural logarithm (e.g., Pielou 1966), and (iii) evenness  $J$  (e.g., Magurran 1988)

$$J = \frac{H}{\ln S}.$$

Diversity was then analysed by multiple regression models that included interactions between explanatory variables. In the first model, the number of species  $S$ , diversity index  $H$  and evenness  $J$  were the response variables, and the explanatory variables were linear and quadratic terms of the individual years of monitoring (1967-1976, 1980-1992) and mean annual temperatures and precipitations in that years. In the following models, the effects on the response variables of the means of the meteorological factors for the period when the species on the wings, for the period when the species in a dormant stage, of monthly averages of temperatures and precipitations, and of one - year lag meteorological data were also analysed, together with the linear and quadratic terms of the years of monitoring. The square powers of the explanatory variables were added in the analyses to test for non-linear relationships. Because the explanatory variables were measured on different scales, they were standardized to zero mean and unit variance. The standardization enabled direct comparisons of the variable effects because steeper regression slopes directly indicated larger effects. Using the standardized values, collinearity was checked with a matrix of correlation coefficients and by calculating tolerance values following Quinn and Keough (2002, p. 128). Low tolerance values, indicating a high correlation, would negatively affect the estimates of model parameters (see Quinn and Keough 2002, p. 127-130).

We sought to obtain the minimal adequate models where all parameters of explanatory variables and their interactions were significantly ( $p < 0.05$ ) different from zero and from one another, and all non-significant terms were removed (e.g., Crawley 1993, p. 188-191). This was achieved by a step-wise process of model simplifications, beginning with the maximal model (containing all explanatory variables and their interactions) and proceeding with elimination of non-significant terms (through deletion tests from the maximal model) and retention of significant terms (e.g., Pyšek et al. 2002). To prevent biases to model structures caused by correlation between variables, we simplified by a backward elimination from the maximal models using step-wise analysis of deviance tables (Crawley 1993, p. 192-197). Thus, the results were not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification. To keep the recommended number of explanatory variables 6-10 times smaller than the number of observations (Neter et al. 1996), only the quadratic terms of explanatory variables which appeared significant in preliminary regressions of the response variable on the single indi-

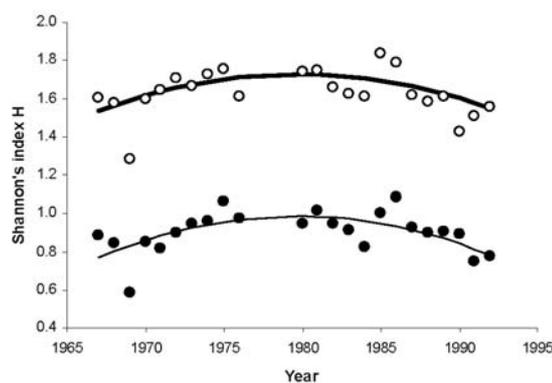
vidual explanatory variables were included in the maximal models. Appropriateness of the fitted models was checked by plotting standardized residuals against fitted values and by normal probability plots. All calculations were made in SPPLUS<sup>®</sup> v. 6.2.1 (Insightful Corp.).

## Results

Overall, during 23 years, 424 macro-moth species and 800,690 individuals were recorded: 25 species of early successional arable land (365,820 individuals), 116 forest species feeding on trees and shrubs (49,123 individuals), 33 forest species feeding on woodland herbs and lichens (33,059 individuals), 92 forest-steppes species (88,310 individuals), 116 grassland species (184,539 individuals), 28 wetland species (4,281 individuals), and 14 non-specialized generalists (75,558 individuals). Mean annual temperature and precipitation had an insignificant tendency for increase: the temperature by 0.1 °C ( $F = 0.45$ ;  $df = 1, 21$ ,  $P = 0.5$ ), and the precipitation by 2.5 mm per year ( $F = 2.08$ ;  $df = 1, 21$ ;  $P = 0.16$ ). Only the first model, in which species richness  $S$ , diversity  $H$  and evenness  $J$  were regressed on years of observations and meteorological factors in the years of monitoring, appeared significant. There were no significant results for any of the remaining models.

Species richness  $S$ , except of forest species feeding on trees and shrubs and of non-specialized generalists, significantly decreased in time, most notably those of early successional arable land species (Table 1). Grassland species significantly decreased also with increasing precipitation. The only guild significantly increasing in time was that of habitat generalists, and the only guild not affected by any changes were forest species feeding on trees and shrubs (Table 1).

Diversity  $H$  of species total followed a domed relationship, with the highest diversity about 1980, symmetrically decreasing both towards the beginning (1967) and the end (1992) of the monitoring period (Figure 2). This pattern was due to arable land species (Figure 2), which formed 43% of all caught individuals, and the reason was the highest evenness  $J$  for these species in the mid of the observation (Table 1).



**Figure 2.** Diversity  $H$  plotted against the years of observation for species total (empty circles and thick line) and early successional arable land species (full circles and thin line). Statistics are given in Table 1.

**Table 1.** Intercepts, significant ( $P < 0.05$ ) slopes of explanatory variables and test statistics ( $F$ ,  $df$ ,  $P$ ,  $R^2$ ) for minimal adequate models of species number (richness,  $S$ ), diversity (Shannon's index  $H$ ) and evenness ( $J$ ). Results on standardized values, enabling direct comparisons on the same scale; larger slopes mean larger effects.

	Intercept	Slopes of explanatory variables				Test statistics			
		year	year <sup>2</sup>	temp	precipitation	$F$	$df$	$P$	$R^2$
<b>Species number <math>S</math></b>									
Total	15.63	-0.40	–	–	–	10.26	1, 21	0.004	0.33
Arable land	20.13	-1.14	–	–	–	22.74	1, 21	0.0001	0.52
Forest ( woods & shrubs)	7.80	–	–	–	–	–	–	NS	–
Forest ( herbs & lich.)	4.24	-0.12	–	–	–	13.99	1, 21	0.001	0.40
Forest-steppe	7.03	-0.35	–	–	–	24.26	1, 21	<0.0001	0.54
Grassland	8.48	-0.26	–	–	-0.12	16.83	2, 20	<0.0001	0.63
Wetland	3.60	-0.46	–	–	–	64.00	1, 21	<0.0001	0.75
Generalists	3.23	0.19	–	–	–	34.51	1, 21	<0.0001	0.62
<b>Diversity <math>H</math></b>									
Total	1.73	–	-0.078	–	–	8.63	1, 21	0.008	0.29
Arable land	0.99	–	-0.089	–	–	13.93	1, 21	0.001	0.40
Forest ( woods & shrubs)	1.29	–	–	–	–	–	–	NS	–
Forest ( herbs & lich.)	0.99	–	–	–	–	–	–	NS	–
Forest-steppe	1.03	-0.06	–	–	–	6.99	1, 21	0.01	0.25
Grassland	1.21	–	–	–	–	–	–	NS	–
Wetland	0.82	-0.11	–	–	–	24.26	1, 21	<0.0001	0.54
Generalists	0.78	–	–	0.020	–	6.66	1, 21	0.02	0.24
<b>Evenness <math>J</math></b>									
Total	0.32	–	-0.015	–	–	9.22	1, 21	0.006	0.30
Arable land	0.33	–	-0.032	–	–	16.07	1, 21	0.0006	0.43
Forest ( woods & shrubs)	0.31	–	–	–	-0.017	9.83	1, 21	0.005	0.32
Forest ( herbs & lich.)	0.34	0.008	–	–	–	4.88	1, 21	0.04	0.19
Forest-steppe	0.26	–	–	–	–	–	–	NS	–
Grassland	0.28	–	–	–	–	–	–	NS	–
Wetland	0.32	–	–	–	–	–	–	NS	–
Generalists	0.33	-0.02	–	–	–	20.24	1, 21	0.0002	0.49

Diversity  $H$  of the other habitat guilds either significantly decreased in time, as in forest-steppe and more markedly so in wetland species, or did not change either in time or under the effect of the climate variables. Diversity  $H$  of generalists increased with growing mean annual temperature, in spite of their decreasing evenness  $J$  during the monitoring period. Evenness  $J$  slightly increased in time for forest species feeding on woodland herbs and lichens, and decreased for habitat generalists. Finally, evenness of forest species feeding on trees and shrubs decreased with increasing precipitation (Table 1).

## Discussion

### Methodological biases

The placement of the light trap differed from those of most other light traps that usually illuminate the vicinity circularly and draw insects from quite wide areas and mixtures of habitats. In our study, the catches originated from well defined environments, that of a dendrology park in front of the building, the surrounding arable land in the near vicinity, and the environments of originally seminatural vegetation beyond the arable land. While the park, the surrounding arable land and the grasslands changed only little during the whole

period of the monitoring, the originally seminatural environments changed markedly. Large areas within the range of the light trap were built-up during the study period. Light pollution increased accordingly, and it might have an effect, especially on some specific groups of moths, e.g., on sedentary habitat specialists, which could be attracted by closer sources of light, or those species with highest sensitivity to light spectra used in street lamps. These effects cannot be exactly specified, and we cannot exclude their influence on the moth catches.

### *Species richness and diversity indices measure environmental changes different way*

It appears that the distribution of abundance, briefly and clearly summarized by means of indices of diversity, may be a more sensitive indicator of a recent environmental disturbance than the number of species (Kempton and Taylor 1974, Taylor et al. 1978). The diversity index thus may appear more characteristic of the community at a site than is the number of species caught (Taylor et al. 1976, Taylor 1978, Bock et al. 2007). However, the use of diversity indices has often been criticised (e.g., Hurlbert 1971, Peet 1974, May 1975, Hubalek 2000), and the uncharitable view is that diver-

sity indices do not give any additional insight compared to species richness (Southwood and Henderson 2000).

Our results show that species diversity, expressed by the Shannon's  $H$  and evenness  $J$ , describes the relationship to habitat changes differently than species richness  $S$ . Using the standardized values of regression slopes (Table 1), diversity  $H$ , and even more so evenness  $J$ , appeared less sensitive to decrease in time than species richness  $S$ . On the other hand,  $H$  and  $J$  revealed several more subtle patterns to a mere decrease or increase in species richness in time. The effect of warming on generalists was apparent for  $H$  as an increase in diversity with increasing temperature, while species richness  $S$  indicated only increase in time (Table 1). In addition, diversity and evenness (Table 1 and Fig. 2) were able to reveal the domed relationship of arable species and species total, with the highest diversity in the middle of the monitoring period and a decrease both toward the beginning and the end of the period. This pattern was not apparent for species richness. The domed pattern is attributable to abandonment of small arable fields in the vicinity of grassland formations. A few years later, after initialisation of succession processes, diversity of arable species on these plots increased, as a lot of these species utilise larval host plants associated with early succession (Jongepierova et al. 2004, Kiehl and Pfadenhauer 2007). However, subsequent successional development of these fields again initiated their decrease.

#### *Habitat specialists and generalists react to environmental changes differently*

Our results support the hypothesis that habitat-specialised species will respond mainly to land use changes, whereas the diversity of generalists will reflect long-term climatic trends (Warren et al. 2001). The decrease of species richness in time for habitat specialist of arable land, wetlands, forest-steppes, grasslands and forest species feeding on woodland herbs and lichens (Table 1) can all be attributed to decreasing range of their habitats in the vicinity of the trap. Though difficult to assess quantitatively, the extent of the decreases, expressed by the strength of the negative slopes of the species richness  $S$  on years in Table 1, probably roughly corresponds to the extent of decrease of the individual habitats. Small arable fields were gradually abandoned and finally converted to build-up areas; wetlands were destroyed and the riverine carr scrubs diminished by the establishment of the pond; the forest-steppe habitats were also gradually converted into build-up areas, intervened by just small patches of mesic grasslands. The slowest decrease affected species associated with grasslands, and with herbs and lichens in forest understory (the latter accompanied by an increase in evenness, cf. Table 1), probably reflected relatively minor decrease of these habitats. Though tempting, it is not possible to express these declines by replacing the explanatory variable years of monitoring by the areas of the individual habitats in the individual years of monitoring. This is so because most of the habitat changes were so gradual that they can be hardly delimited by the individual years. Moreover, it

is not possible to determine the exact borders of light-attraction area.

The results also confirmed that species richness of those species whose habitats remained intact should not exhibit any particular trend. This was the case of forest species feeding on trees and shrubs, mostly coming from the dendrology park in front of the building. Species richness in this guild remained unchanged throughout the whole period of the monitoring, the only recorded change being a decrease in species evenness with increasing precipitation (Table 1). A likely reason is that moths that develop as larvae on shrubs and trees (and also grasses) tend to utilise a broader taxonomic range of host plants than moths that develop on herbs (Loder et al., 1998). This pattern is, in turn, attributable to the major difference between antiherbivory defences utilised by woody vs. non-woody plants, the former relying on macromolecular compounds that are difficult to digest (i.e., tanins) and the latter on low molecular weight compounds that are essentially poisonous and must be handled via specific biochemical pathways (i.e., alkaloids) (Feeny 1976, Cizek et al. 2006). It follows that many herb feeders are limited by presence of specific hosts, which may appear or disappear as a result of profound climate and/or habitat change, whereas many woody plants feeder are limited by host plant quality, which is a temporary trait, responding to such factor as precipitation.

Grasslands species also reacted to climate, as their numbers decreased with increasing precipitation (Table 1). This can be associated with various mechanisms, such as their survivorship being negatively affected by strong summer rainstorms, due to the dissolution of eggs and first larval instar, particularly of small species (Kobori and Amano 2003). Increase of precipitation may also cause excessive "greening" of grasslands habitats, which may lead, paradoxically, to lower temperatures being experienced by grassland immature stages, as had been demonstrated for a butterfly by Wallisdevries and Van Swaay (2006).

Most importantly, numbers and diversity of generalists increased in time. This, and the lack of response or even decreases of specialists, provide further evidence that prevailing response among generalist species of temperate regions will be increases of richness and diversity, contrary to specialised species (Warren et al. 2001). The underlying reasons seem to be that generalists tend to be polyphages inhabiting large geographical ranges, which provides them head start when temperature increases, as these species easily locate appropriate biotope and host plants during range expansions (Bale et al. 2002, Brachsler and Hill 2007). Increasing temperature shortens developmental time of pre-imaginal stages and thus mortality caused by predation and diseases (Hill and Gatehouse 1992, Dennis and Sparks 2007). In addition, many of the generalists are migrants, whose probability of arrival further depends on temperature: in hot summers, they have better chance for surviving in regions where temperature is normally insufficient (Sparks et al. 2005). However, hot and wet seasons may also have negative effects on sur-

vival of generalist and grassland species. This is so if caterpillars are the overwintering stage and the winter temperatures appear insufficiently low for dormancy (Conrad et al. 2002, Parajulee et al. 2004).

In summary, that the species richness of habitat-specialised species responded mainly to land use changes, whereas that of generalists reflected long-term meteorological trends suggests that for specialised moths, any climatic effects were probably overlaid by changes in habitat availability. Consequently, for long-term monitoring in environments with extensive changes in land use, non-specialised species appear more sensitive indicators of climate changes than habitat specialists.

**Acknowledgements:** Our research was supported by the Czech Ministry of Education (LC06073, MSM 600766 5801 and 21620828 to MAAMK, TK, MK and VJ), the Grant Agency of the Czech Republic (206/05/HO12 to TK), by doctoral grant (206/08/H049 to TK) and EC FP6 ALARM (GOCE-CT-2003-506675; see Settele et al. 2005 to VJ).

## References

- Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press, I. Symnioudis, A.D. Watt and J.B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8: 1-16.
- Bock, C.E., Z.F. Jones and J.H. Bock. 2007. Relationships between species richness, evenness, and abundance in a southwestern savanna. *Ecology* 88: 1322-1327.
- Braschler B. and J.K. Hill. 2007. Role of larval host plants in the climate-driven range expansion of the butterfly *Polygonia c-album*. *J. Anim. Ecol.* 76: 415-423.
- Cizek, L., Z. Fric and M. Konvicka. 2006. Host plant defences and voltinism in European butterflies. *Ecol. Entomol.* 31: 337-344.
- Conrad, K.F., M.S. Warren, R. Fox, M.S. Parsons and I.P. Woiwod. 2006a. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132: 279-291.
- Conrad, K.F., J.N. Perry, I.P. Woiwod and C.J. Alexander. 2006b. Large-scale temporal changes in spatial pattern during declines of abundance and occupancy in a common moth. *J. Insect Conserv.* 10: 53-64.
- Conrad, K.F., I.P. Woiwod and J.N. Perry. 2002. Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biol. Conserv.* 106: 329-337.
- Crawley, M.J. 1993. *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85: 231-241.
- Davies, Z.G., R.J. Wilson, S. Coles and C.D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *J. Anim. Ecol.* 75: 247-256.
- Dennis, R.L.H. and T.H. Sparks. 2007. Climate signals are reflected in an 89 year series of British Lepidoptera records. *Eur. J. Entomol.* 104: 763-767.
- Fajčik, J. 1998. Motýle strednej Európy: Noctuidae – určovanie, rozšírenie, stanovište a bionómia motýľa, II. zväzok. [Die Schmetterlinge Mitteleuropas: Bestimmung, Verbreitung, Flugstandort und Bionomie – Noctuidae, II. Band.] Polygrafia SAV, Bratislava.
- Fajčik, J. 2003. Motýle strednej a severnej Európy – určovanie, rozšírenie, stanovište a bionómia. [Die Schmetterlinge Mittel- und Nordeuropas - Bestimmung, Verbreitung, Flugstandort und Bionomie.] Er-print, Senica.
- Feeny, P. 1976. Plant apparency and chemical defense. *Recent Adv. Phytochem.* 10: 1-40.
- Franco, A.M.A., J.K. Hill, C. Kitschke, Y.C. Collingham, D.B. Roy, R. Fox, B. Huntley and C.D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Glob. Change Biol.* 12: 1545-1553.
- Gaston, K.J. and R.A. Fuller. 2007. Biodiversity and extinction: losing the common and the widespread. *Prog. Phys. Geog.* 31: 213-225.
- Harrington, R., I. Woiwod and T. Sparks. 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* 14: 146-150.
- Hassall, C., D.J. Thompson, G.C. French and I.F. Harvey. 2007. Historical changes in the phenology of British Odonata are related to climate. *Glob. Change Biol.* 13: 933-941.
- Hill, J.K. and A.G. Gatehouse. 1992. Effects of temperature and photoperiod on development and prereproductive period of the Silver Moth *Autographa gamma* (Lepidoptera, Noctuidae). *B. Entomol. Res.* 82: 335-341.
- Hubalek, Z. 2000. Measures of species diversity in ecology: an evaluation. *Folia Zool.* 49: 241-260.
- Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.
- Jepsen, J.U., S.B. Hagen, R.A. Ims and N.G. Yoccoz. 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *J. Anim. Ecol.* 77: 257-264.
- Jongepierova, I., J.W. Jongepier and L. Klimes. 2004. Restoring grassland on arable land: an example of a fast spontaneous succession without weed-dominated stages. *Preslia* 76: 361-369.
- Kempton, R.A. and L.R. Taylor. 1974. Log series and log normal parameters as diversity discriminants for the Lepidoptera. *J. Anim. Ecol.* 43: 381-399.
- Kiehl, K. and J. Pfadenhauer. 2007. Establishment and persistence of target species in newly created calcareous grasslands on former arable fields. *Plant Ecol.* 189: 31-48.
- Kobori, Y. and H. Amano. 2003. Effect of rainfall on a population of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Appl. Entomol. Zool.* 38: 249-253.
- Konvicka, M., Z. Fric and J. Benes. 2006. Butterfly extinctions in European states: do socioeconomic conditions matter more than physical geography? *Glob. Ecol. Biogeogr.* 15: 82-92.
- Konvicka, M., M. Maradova, J. Benes, Z. Fric and P. Kepka. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Glob. Ecol. Biogeogr.* 12: 403-410.
- Kristensen, N.P., M.J. Scoble and O. Karsholt. 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa* 1668: 699-747.
- La Sorte, F.A. and F.R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88: 1803-1812.
- Lastuvka, Z. 1998. *Checklist of Lepidoptera of Czech and Slovak Republics*. Konvoj, Brno.

- Loder, N., K.J. Gaston, P.H. Warren and H.R. Arnold. 1998. Body size and feeding specificity: macrolepidoptera in Britain. *Biol. J. Linn. Soc.* 63: 121-139.
- Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Chapman and Hall, London.
- May, R.M. 1975. Patterns of species abundance and diversity. In: M.L. Cody and J.M. Diamond (eds): *Ecology and Evolution of Communities*. Belknap, Harvard. pp. 81-120.
- McLaughlin, J.F., J.J. Hellmann, C.L. Boggs and P.R. Ehrlich. 2002. Climate change hastens population extinctions. *P. Natl. Acad. Sci. USA* 99: 6070-6074.
- Neter, J., M.H. Kutner, C.J. Nachtsheim and W. Wasserman. 1996. *Applied Linear Statistical Models*. 4th edition. Irwin, Illinois.
- Novák, I. 1983. An efficient light trap for catching insects. *Acta Entomol. Bohemoslov.* 80: 29-34.
- Parajulee, M.N., D.R. Rummel, M.D. Arnold and S.C. Carroll. 2004. Long-term seasonal abundance patterns of *Helicoverpa zea* and *Heliothis virescens* (Lepidoptera : Noctuidae) in the Texas high plains. *J. Econ. Entomol.* 97: 668-677.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.
- Peet, R.K. 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5: 285-307.
- Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13: 131-144.
- Pimm, S.L. 2008. Biodiversity: Climate change or habitat loss - Which will kill more species? *Curr. Biol.* 18: 117-119.
- Pyšek, P., T. Kučera and V. Jarošík. 2002. Plant species richness of nature reserves: the interplay of area, climate and habitat in a Central European landscape. *Glob. Ecol. Biogeogr.* 11: 279-289.
- Quinn, G.P. and M.J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Roy, D.B. and T.H. Sparks. 2000. Phenology of British butterflies and climate change. *Glob. Change Biol.* 6: 407-416.
- Settele, J., V. Hammen, P. Hulme, U. Karlson, S. Klotz, M. Kotarac, W. Kunin, G. Marion, M. O'Connor, T. Petanidou, K. Peterson, S. Potts, H. Pritchard, P. Pyšek, M. Rounsevell, J. Spangenberg, I. Steffan-Dewenter, M. Sykes, M. Vighi, M. Zobel and I. Kühn. 2005. ALARM: Assessing large-scale environmental risks for biodiversity with tested methods. *GAIA – Ecol. Persp. Sci. Soc.* 14: 69-72.
- Sokal, R. and F.J. Rohlf. 1995. *Biometry*. Ed. 3. Freeman, New York.
- Southwood, T.R.E. and P.A. Henderson. 2000. *Ecological Methods*. 3<sup>rd</sup> edition. Blackwell, Oxford.
- Sparks, T.H., D.B. Roy and R.L.H. Dennis. 2005. The influence of temperature on migration of Lepidoptera into Britain. *Glob. Change Biol.* 11: 507-514.
- Sparks, T.H., R.L.H. Dennis, P.J. Croxton and M. Cade. 2007. Increased migration of Lepidoptera linked to climate change. *Eur. J. Entom.* 104: 139-143.
- Taylor, L.R. 1978. Bates, Williams, Hutchinson – a variety of diversities. In: L.A. Mound, N. Waloff (eds.): *The Diversity of Insect Faunas*. Academic Press, London. pp 1-18.
- Taylor, L.R., R.A. French and I.P. Woiwod. 1978. The Rothamsted Insect Survey and the urbanization of land in Great Britain. In: G.W. Frankie, C.S. Koehler (eds): *Perspectives in Urban Entomology*. Academic Press, London. pp. 31-65.
- Taylor, L.R., R.A. Kempton and I.P. Woiwod. 1976. Diversity statistics and the log-series model. *J. Anim. Ecol.* 45: 255-272.
- Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.N.F. Erasmus, M.F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips and S.E. Williams. 2004. Extinction risk from climate change. *Nature* 427: 145-148.
- Wallisdevries, M.F. and C.A.M. Van Swaay. 2006. Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Glob. Change Biol.* 12: 1620-1626.
- Warren, M.S., J.K. Hill, J.A. Thomas, J. Asher, R. Fox, B. Huntley, D.B. Roy, M.G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S.G. Willis, J.N. Greatorex-Davies, D. Moss and C.D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.
- Wilson, R.J., D. Gutierrez, J. Gutierrez and V.J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Glob. Change Biol.* 13: 1873-1887.

Received January 14, 2009  
 Revised June 23, 2009  
 Accepted September 17, 2009

## Appendix

Checklist of moth species included in the study. The file may be downloaded from the publisher's web site at [www.akademiai.com](http://www.akademiai.com).