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The Use of Insects for Monitoring Global Changes

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PhD Thesis

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INTRODUCTION

We analysed two long-term sets of data on insect species, suitable for (1) evaluation of changes in species diversity and population dynamics, and (2) assessment of the effect of climate change on the distribution and abundance of insects. The first set of data is an assemblage of moth species at a suburb of Prague (50°5'11"N,14°18'06"E), which were monitored by a highly efficient mercury light trap for 23 years (1967-1976, 1980-1992) by Ivo Novák. The second set is data on the thermal requirements for development of 66 species from 8 orders of insects, which were obtained from the literature by Alois Honěk and his collaborators.

The thesis consists of Introduction, Literature Review, and three studies in the form of manuscripts. The first study (Effect of land use and climate on diversity of moth guilds with different habitat specialization) and the second (Effects of life history traits on the long-term population dynamics of moths) are unpublished manuscripts which are based on the data on moth species. The third study (Relationship between the minimum and maximum temperatures of the thermal tolerance range in insects) is based on the data on thermal requirements for insect development and will be published in *Functional Ecology*.

In our first study, 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 whose part remained unchanged for all the time, whereas the other part underwent substantial land use changes. The trap attracted both habitat specialists on several habitat types and habitat generalists, and 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 been losing habitats with those not losing them.

The unique setting, and concurrent recording of meteorological data, allows 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 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).

Our second study analyse a long-term, highly reliable set of data on 81 species of moths that were monitored for 26 years (Novák 1983, Holyoak et al. 1997). This large set of analysed species enables to compare their life-history traits with their population dynamics by detecting their density dependences, level of seasonal fluctuation, linear decreases/increases and concave/convex population dynamics over time. This approach enables to ask clear biological questions: (1) Are there groups of species that have a similar population dynamics based on their biology? (2) What are the common biological characteristics of the species with significant density dependence? (3) Do we recognise groups of species reacting in the same way to environmental changes and are they biologically related?

The objective of our third study is to determine whether in insects the difference between the temperatures when development proceeds at the minimum and maximum rates is about 20° C, whether the width of this thermal window can be modified by environmental and biological traits and species phylogeny, and whether the relationship between the minimum and maximum developmental rate temperatures is dependent on species relatedness. If our analysis indicates that each species of insect can only develop over a limited range of temperatures, independent of species traits, and that the relationship between the minimum and maximum developmental rate co-vary, independent of species phylogeny, it may help identify the precise nature of the biochemical adaptations underlying the seasonal development and distribution of ectotherms. This could be an important step in achieving a better understanding of how communities work and integrating physiology and ecology at the community scale. In addition, this concept might help when predicting the effect of climate change on the distribution and abundance of insects (e.g. Harrington & Stork 1995; Yamamura & Kiritani 1998; Dixon 2003; Kiritani 2006) and the spread of invasive species (e.g. Simberloff, Parker & Windle 2005; Baker et al. 2005; Hatherly et al. 2005).

LITERATURE REVIEW

1 Light traps sampling

1.1 History

The first primitive light traps operating with oil lantern were used by Roman beekeepers to protect against wax moths. Engravings, illustrating beekeepers or people with oil lamps or burning torches killing wax moths, are also recorded from the 17th and 18th centuries (Hoberg 1682). Hungarian forestry literature in the 19th-century advised that great fires must be lit at forest edges to suppress moth pests (like *Lymantria dispar*, *Operophtera brumata*, *Malacosoma neustria* or *Euproctis chrysorrhoea*) causing defoliation, because many of them would be attracted and burnt by the flames (Szentkiralyi 2002). At these times, a generally applied insect collecting method had become 'lamping' with the aid of a white sheet placed in front of a light source (Kov Acs 1958, Lbdl 1989).

In the second half of the 1910s, a wider availability of electricity made possible the development of several trap types with this light source that allowed automatic insect collection. From that time, an increasing number of studies were published annually throughout the world on light trapping, mostly in the international agricultural entomology literature (Szentkiralyi 2002). During trapping of different target pests, it was discovered that from nearly all winged insect orders, a huge number of species flies toward light, e.g. moths, beetles, leafhoppers, flies, mosquitoes, crickets, hymenopteran parasitoids, etc. (Szentkiralyi 2002). These experiments greatly contributed in the development of different trap types: several constructions were tested; furthermore, capture changes due to different spectral composition of light sources were also discovered and comparative studies were made on the light sensitivity of different insect orders.

In the 1910s and 1920s, Williams trapped several important economic pests (froghopper, cotton and pink bollworm) in tropical areas (Surinam, Trinidad and Egypt, respectively), and during this work he developed a new type of light trap design which he continuously kept modifying to increase its efficiency.

In the late 1940s and early 1950s, before the use of light traps, post-war Hungarian plant protection was faced with the countrywide outbreaks and heavy damage by serious insect pests (Szentkiralyi 2002). In that period, JERMY investigated both under field and

laboratory conditions the control of these pests. Also he studied the behavior and the ecological characteristics of these pests and he saw that the foundation of a forecasting system, with greater spatial scale and different temporal scales, was needed to prevent insect damage at the national or regional level, and he knew about the results of studies reporting that light traps are capable of collecting a high number of individuals, especially noctuid moths.

In 1952, JERMY constructed his light trap from very simple components, while taking into consideration practical point of view (as a part of the trap, there is a circular roof made of aluminum with a diameter of 1 meter fixed to a column at two meters above ground level). Jermy intended his light trap to forecasting of insect pests - his idea was to operate it in a long-term national network. His great technical talent, which he has proved many times with his experiments, helped him to make a very clever selection of all the materials and tools: all of them could be bought then and were expected to remain commercially available for decades. So, as a light source, he chose a 100 W incandescent, tungsten filament light bulb. (This bulb type is still available in Hungary.) The Hungarian network is still operating with the "JERMy-type" traps, being the best proof of the grandiosity of his conception. Although minor technical modifications on the trap have been made on experience while running the network (Benedek et al. 1974), its main structure, the arrangement of technical elements determining the way and level of catches has remained. Jermy's light trap type was tested mainly in the surrounding countries, e.g., in Austria (Maliczky 1965), but was also used in France (Gagnepain 1974), and it was thoroughly described and compared with other traps in Germany (Mesch 1965, Jermy 1961, 1974).

In former Czechoslovakia, IVO NOVÁK in sixties of the last century designed a light trap incorporating an electrified wire grid for stunning the insects (Figs. 1 and 2). The use of the stunning grid massively increased catches of Lepidoptera and other insects in comparison with other types of light traps commonly used (Minnesota, Rothamsted, Robinson, Mesch, Jermy, New Jersey, ESLU-2, Pennsylvania, etc.).

The light-trap is 2.50 m high and 1.00 m wide, with a slanting roof 1.40 m wide by 0.80 m deep. The light source is a Tesla RYL 250 VV mercury-vapor (MV) lamp commonly used for street lighting. It produces a white light with approximately 25% total energy radiation in the ultraviolet (UV) part of the spectrum. The MV lamp is located 0.20 m in front of a white wall measuring 1.00 m by 1.20 m. The white surface reflects the light thereby increasing the overall illumination of the surroundings. Placed at a 20° angle in front of the MV lamp and white light-reflecting wall is an electrified wire grid set in a frame measuring 1.00 m by 1.00

m. The grid is made of copper wires (0.3 mm in diameter) spaced 7 mm apart and attached alternately to the poles of a 220 '1/2000 V transformer (Figure 1). At the bottom each wire is held fast in a hole drilled in the screw fitted in a strip of insulation material and can be tightened by turning the screw.

Beneath the MV lamp and grid is a large collecting funnel made of thin metal sheet: It is rectangular at the top, where it measures 1.10 m by 0.60 m, and funnels to a circular hole 80 mm in diameter opening into the neck of a collecting vessel. The protective roof is only slightly larger than the collecting funnel and therefore partially shields the light-trap from rain. A larger roof would shade the light too much and thus reduce the number of insects attracted to the trap. The glass collecting vessel has a capacity of 5000 ml. A pad made of muslin or organdie filled with cotton wool is placed at the bottom. This proved to be better than mere cotton wool from which insects are often disentangled with difficulty. Below the pad is the small hole (10 mm in diameter) for drainage. Suspended on a wire about one-third of the way up the vessel is a small glass container with anaesthetic measuring 60 mm in diameter at the top (Figure 2). By using a container with a smaller neck opening, e.g. 20 mm in diameter, it is possible to decrease the amount of evaporation of the chloroform or other anaesthetic thereby merely stupefying the insects, which may then be revived and released or retained alive for breeding, etc. The opening is covered with organdie to prevent insects from falling into the liquid and attached to the wire above the container is a small flap to keep water out. For the more information about the light trap see Novák (1983).

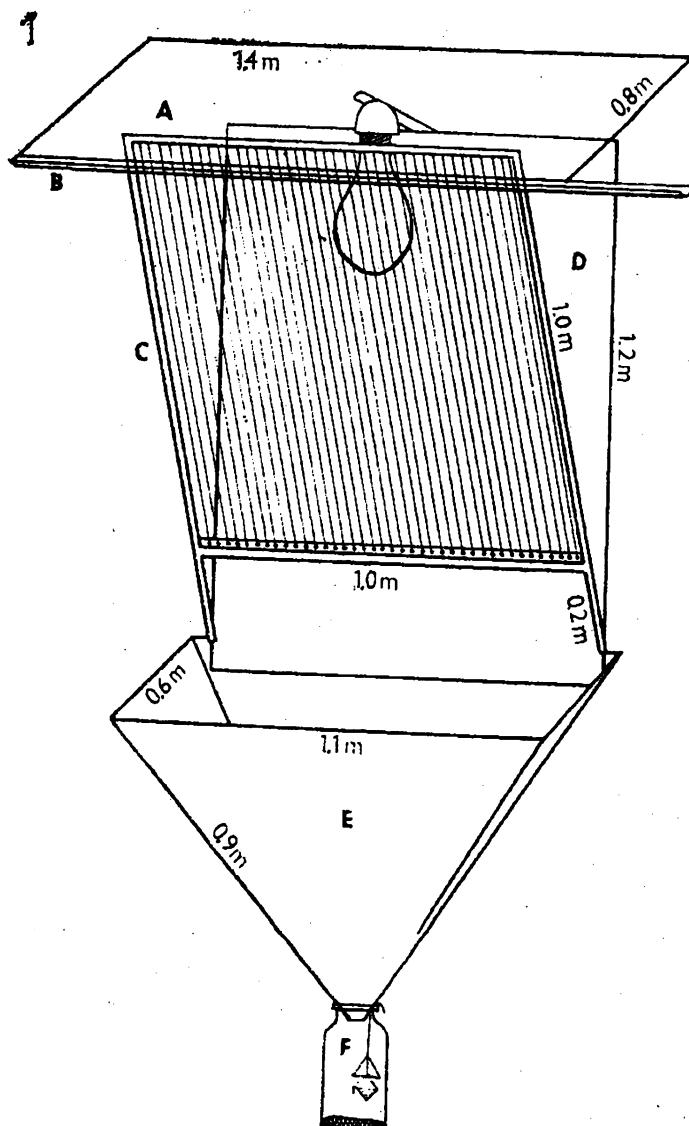
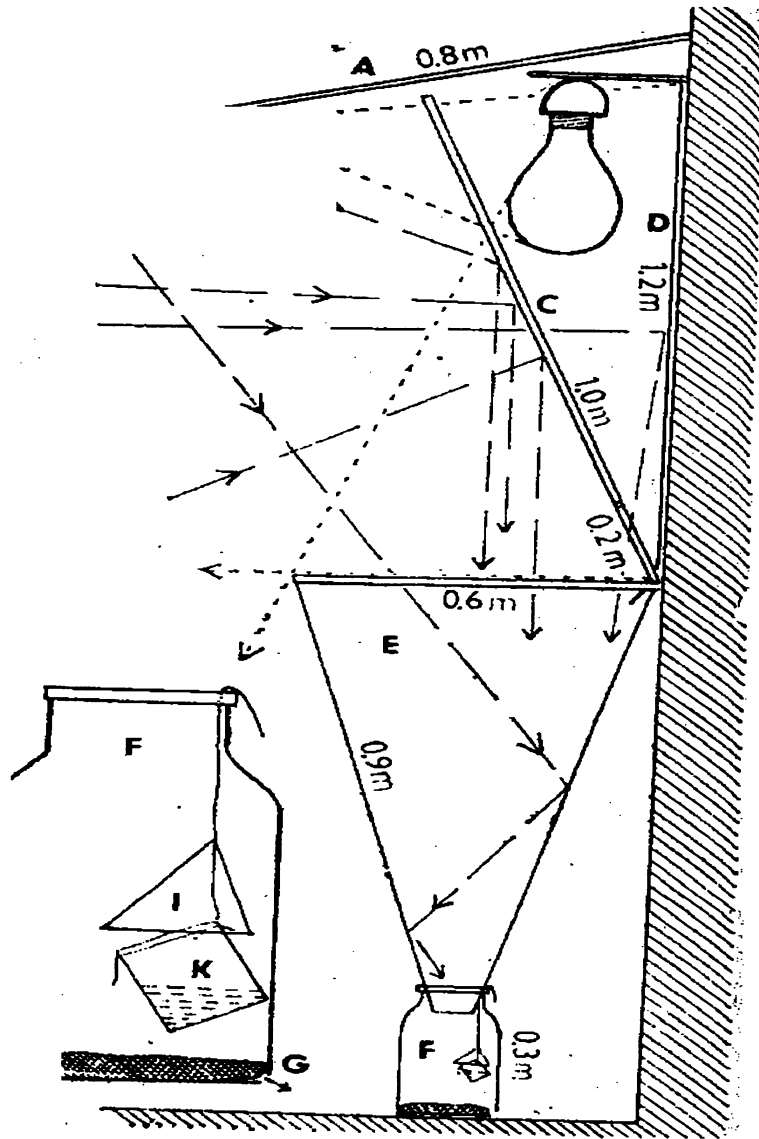


Fig.1. Front view of the light-trap designed by Ivo Novák (Novák 1983). A roof, B gutter, C electric grid, D white light-reflecting wall and baffle, E collecting funnel, and F collecting vessel.

Fig. 2 Side view of the light-trap designed by Ivo Novák (Novák 1983). A roof, B gutter, C electric grid, D white light-reflecting wall and baffle, E collecting funnel, F collecting vessel, G hole, H pad, I small flap, and K container with anesthetic, light , and insect.



1.2 Applications

Nowadays, hundreds of light traps are working around the world mainly to forecast

agricultural and forest pests. Forecasting results of light trapping concerning agricultural pests were summarized by Meszaros and Vojnits (1968, 1974) and Nowinszky (2000). These forecasting methods became part of the every day practice in plant protection (Benedek et al. 1974, Szentkiralyi 2002). Light trap catch data played an important role in the yearly forecast of forest pests (Lesko and Szaboky 1998). Those research results, which were based upon the simultaneous analyses of light trap and damage data series of forest defoliating moth pests, were built into the yearly published forecasting works (Szontagh 1974, 1976, 1980, 1987, Lesko et al. 1994, 1995, 1997, 1999, Szentkiralyi 2002).

Two countries are known worldwide where there is an existing national light trap network, >50 stations, that has been operating for decades. One of these is in UK (Rothmansted Insect Survey: R.I.S.), the other one is in Hungary (Hungarian Light-trap Network) (Szentkiralyi 2002). Samplings with the networks of light traps are carried out according to landscape, or even at a larger spatial scale to forecast insect pest densities. Transformation of the information from such networks to distribution maps is useful in the analysis of spreading and migration of species (Kov Acs 1971, Mezaros and Vojnits 1967, Vojnits 1966, 1968a). These networks are able to make synoptic monitoring dynamics of complete insect assemblages. Such as survey systems are fundamental not only for pest forecasting, but also to others modern research fields, e.g., the study of effects of climate change on habitats and communities, or for long-term monitoring of biodiversity changes and their trends.

The biological effects of climate change have an increasing importance since 1980s (Tracy 1992). There are numerous predictions for expected influences of the increasing temperature ("global warming") on abundance, life cycle and phenology of insects, interspecific relationships in food chains of insects, and geographical distribution of some pests (Watt et al. 1990, Harrington and Woiwod 1995, Szentkiralyi 2002). Various hypotheses regarding direct and indirect effects of arid, warm climate on insects (Plant Stress Hypothesis, Climate Release Hypothesis, Plant Vigour Hypothesis) exist that may explain the insects' outbreaks (Martinat 1987, Mattson and Haack 1987, Price 1991, Szentkiralyi 2002). Different climate elements and aridity indices were used in time series analysis of data sets of yearly moth catches by Lesko et al. (1994, 1995, 1997, 1999), Szentkiralyi et al. (1995, 1998) and Szentkiralyi (2002). Light trap network in Great Britain (Taylor 1986, Taylor et al. 1978) informed that the land-use changes (mechanization of agriculture, increase of intensity of farm practice, "hedging and ditching", forest clearing, intensive field margin management, widespread use of pesticides) reduced the total number of moths by about 60 percent between

1950 and 1960. In parallel, the diversity of the moth assemblages was also decreasing (Szentkiralyi 2002).

The possible uses of data on the identified species from light traps thus appear wide ranging. Apart from the forecasting of pests and monitoring of climatic and biodiversity changes mentioned above, they can serve the analyses of effect of light trap location and surrounding habitats on captures, taxonomic-faunistic, zoogeographic or insect-ecological studies, to name a few. Light traps have been also used widely in studies of community structure, population variability, incidence of density dependence and spatial synchrony (Wolda, 1978, Hanski and Woiwod, 1991, 1993a, b, Holyoak, 1993a, Yela & Hen'era, 1993, Holyoak et al. 1997).

Data coming from the method of light trapping can also aid in analyses of insect daily, seasonal and long-term year-to-year activities. The research on daily activity includes effects of weather elements on daily flight activity (Kadar and Szentkiralyi 1992, Nowtnszky 1994, 1997, 2000, 2001, Puskas et al. 1997, Lesko et al. 1998), effects of moonlight and moon phases, characteristics of night flight behavior, changes of male/female ratio, nocturnal flight distribution, relationship between egg-laying and flight to light (Williams 1935, 1936a, 1936b, 1939, 1940, 1948, 1951, 1953, 1964, Szentkiralyi 2002).

The most interesting research on daily activity concerns the moth response to light traps. This response differs between species, some flying directly to the light, others in a chaotic fashion and some seem completely unaffected by the light source and fly straight past (Brook and Conrad 2007). Two theories explaining this behavior have been advanced, but the first has been disregarded. Moths may be dazzled by a bright light. Once they enter a circle of light they are reluctant to leave it because they cannot see outside it. The second explanation which has more physiological backing is that moths are attracted to lights by what is more or less an optical illusion, known as a mach band caused by lateral inhibition in the moth's eye. This optical illusion means the moth sees a dark band adjacent to the strong light source and is, in fact, flying toward what it believes is the darkest spot in the sky (Brook and Conrad 2007).

Analyses of seasonal activity includes flight pattern of insects from catches summed e.g. weekly. These light trap data provided useful information for seasonality description of *Heteroptera* (Jaszatne and Benedek 1968, Benedek and Jaszal 1973, Erdelyi and Benedek 1974) cockchafers (Homonnay 1977), and certain leaf hopper species (*Macrosteles* spp., Jaszaine 1977). The long-term data series of light trappings can be implemented also in the

description or characterization of seasonal flight patterns of less abundant, rarer species (Szentkiralyi 2002). In this way sufficient number of data has been collected for seasonality analysis of some rare species (Kadar and Szentkiralyi 1998), Szentkiralyi 1992, 1997, 2002).

Analyses on long-term year-to-year activities concern fluctuations in population dynamics. Increase in the abundance of *Lygus* species caused by arid years could be proved by long-term light trapping (Racz and Bernath 1993). The spatial spreading of an invader moth pest (cotton bollworm) has been reported in dry and warm years (Szaboky and Szentkiralyi 1995). Kadar and Szentkiralyi (1997) demonstrated the emigration of hygrophilous species by flight from drying habitats in arid seasons.

1.3 Pitfalls

The use of light traps in sampling moth populations is an established technique used by entomologists and ecologists. However, trap data partly reflect the variable attractiveness of UV light to different moth species. An alternative method of recording moth populations is developed, using a modification of the transect count technique used for butterflies and recently applied to moths (Birkinshaw and Thomas 2004).

With moth sampling by light trap, it might be expected that the samples are taken from a community occupying a limited area. However, this depends on the mode of action of the now usually mercury vapor light trap (Cook and Graham 1996). Baker (1985) likens the process of recording moths to some of the traffic traveling in one direction along a motorway, rather than to sampling from a community. If this is the mechanism at work then the moths caught is not come from the vicinity of the trap, but come from other places further field, different species from different places. The differences in pattern between catches on grass and in woodland suggest that the communities in these habitat types in close proximity are different. However, this may be explained alternatively by arguing that different species have different favored flight paths (Majerus et al. 1994).

Another pitfall concerns the effects of weather. Temperature is obviously an important environmental factor, especially for ectothermic organisms like insects. Brehm et al. (2003b) and Brehm and Fiedler (2003) discussed possible physiological adaptation of geometrid moths (particularly Larentiinae) to low flight temperature. Geometrids clearly demonstrate that not all insects prefer the warmest climates, although richness of small ranged Ennomonae and Geometridae as a whole showed a significantly positive correlation with temperature (Brehm et al. 2007). The numbers of moths caught in light traps are thus generally higher on warmer nights and lower on windy or wet nights (Williams 1940, 1961, Persson 1976,

Bowden 1982, Dent and Pawar 1988). Consequently, daily changes in moth captures are more representative of changes in flight activity than changes in abundance (Muirhead - Thomson, 1991). Holyoak et al. (1997) say that this is supported by: (1) actograph experiments with tethered moths (Lance et al. 1988), (2) comparisons of activity of captive moths with light trap catches (Riley et al. 1992) and (3) comparisons between direct censuses of moths and light trap catches (Riley et al. 1992). The last two forms of evidence also suggest that daily changes in moth abundance are usually small by comparison to changes in numbers flying, and environmental conditions are also likely to influence light trap catches by altering trap efficiency (Holyoak et al. 1997). For example, winds might blow moths approaching a trap off course, and background illumination could reduce trap efficiency (e.g. Hardwick 1972).

Holyoak et al. (1997) and Morton et al. (1981) interpreted the effects of weather on light trap catches as sampling error that could be corrected for by estimating the size of weather effects on abundances and adjusting to constant conditions. However, Holyoak et al. (1997) concluded that they cannot separate meteorological effects on flight activity from those on trap efficiency without independent evidence. As a consequence, no study of population dynamics probably can exactly correct for the effects of weather on catches in multiply species assemblages, because effects vary between species (Morton et al. 1981, Gaydecki 1984, Muirhead- Thomson 1991, Holyoak et al. 1997).

Light- trap catches of many species are also affected by the moon. Observers have noted that catches are less at full moon and have attributed this to a reduction in the effectiveness of the trap because of competing moonlight (Williams, 1939, Bowden 1972). Differences in catch imply an effect of light illumination, because this is the only major difference in average conditions between moon phases, but few attempts have been made previously to estimate that effect of different amount of night illumination on catch (Bowden and Church 1973). Changes in light-trap catches associated with differences in night illumination may be caused by changes in insect activity (i.e. in the type and pattern of movement of individuals within a given distance of the trap when the light is switched off), by changes in population, and by changes in the range of effectiveness of the light-trap and the proportion of the population within this range which is trapped (Bowden and Church 1973).

Also humidity and rainfall can have direct or indirect effects, via the vegetation, on herbivorous insects. It remains to be shown whether or not ambient humidity levels could act as physiological constraint to certain moth species (Brehm et al. 2007).

Light traps used by naturalists to trap moths are however not believed to effect moth population sizes. In fact, light traps used to control pest moths have been largely unsuccessful. Car headlight's are also probably not a substantial form of light pollution as most of the moth deaths are likely to be the result of moths and cars coinciding in the same time and place. However, street lighting, floodlighting security lighting and other urban light sources are a serious cause of concern and might be the single biggest threat to urban moth population (Brook and Conrad 2007). An alternative suggestion is that modern street lighting is generally less attractive to moths. However this may not be a good thing, for example the widely used sodium lamps that do not attract moths and therefore might seem benign, may in fact be particularly pernicious as they stop moths flying altogether (Uffen 1994).

2 Population dynamic

The central task for ecologists studying biological populations is to develop an understanding of the dynamics of those populations. Such understanding can only be forged by combining a consideration of the dynamics themselves with a consideration of the underlying responses of individuals and the interactions between individuals (Bjornstad et al. 1998). Understanding population dynamics of insects has long been of interest for solving these general questions, as a consequence of both their economic and ecological significance (Nothnagle and Shultz 1987, Wallner 1987, Cappuccino et al. 1995, Nylin 2001).

Regarding the responses of individuals, insect researches (e.g. Dodge and Price 1991, Thompson and Pellmyr 1991, Larsson et al. 1993, Miller 1996, Ribeiro et al. 2003) have been focused on identification the life history differences between herbivorous insects with eruptive and latent population dynamics. Typically, eruptive species exhibit temporal population size fluctuations ranging from three to five orders of magnitude, whereas latent species fluctuate between only one to two orders of magnitude (Price et al. 1990, Velditman 2005). In general therefore, population size variability in eruptive species is considered to be far higher than that in latent species (Wallner 1987, Price et al. 1990, Price et al. 1995, Leyva et al. 2003).

A generality in the relationship between life history traits and population dynamics of the eruptive and latent species has potential application in both conservation and pest management (Velditman 2005). Nothnagle and Shultz (1987) found the difference between eruptive and latent species of Northern Hemisphere Macrolepidoptera. However, eruptive and latent species are extremes on a gradient of population size variability, and species with

moderate population size fluctuations may not have readily predictable life history traits (Price et al. 1990, Nylin 2001, Steinbauer et al. 2001). Even if different life history traits are associated with eruptive versus latent population dynamics, it does not necessarily follow that they are the cause of differences in population dynamics (Velditman 2005). Although insects may have life history traits typical of eruptive species, factors such as host plant distribution, predation pressure and other biotic factors can, either directly or indirectly, significantly alter the population dynamics observed (Larsson et al. 1993, Bjorkman et al. 2000, Azerefegne et al. 2001, Steinbauer et al. 2001). From the point of underlying responses of individuals, consideration of species interactions with their biotic (natural enemies) and abiotic environments (climate), in addition to life history traits, is thus clearly important for understanding population dynamics (Nylin 2001, Steinbauer et al. 2001).

Regarding the interactions among individuals, the most important trait for population dynamic is definitively the interaction between natural enemies and their prey (Wallner 1987, Price et al. 1990, Berryman 1996, Muzika and Liebhold 2000). These responses are defined as any relationship between the natural enemy and host (or prey) (Gaston et al. 1997, Frears et al. 1999, Gentry and Dyer 2002, Stireman and Singer 2003, Velditman 2005), including association between natural enemy responses and herbivore defensive traits (Larsson et al. 1993, Bowers 1993, Dyer and Gentry 1999, Louda et al. 2003).

Regarding the dynamics themselves, density dependence is central to understanding population persistence and fluctuations (Ginzburg et al. 1990, Royama 1992, Murdoch 1994). However, the measurements of persistence, fluctuation and a level of density dependence are difficult to interpret, because time series of animal abundances usually contain both sampling error and variation in population size due to real changes in abundance (Gaston and McArdle 1994, Link and Nichols 1994, Holyoak et al. 1997). As a consequence, one of the most persistent and challenging questions in population biology, which concerns the degree to which natural populations are characterized by complex or even chaotic dynamics due to inherent nonlinear relationships among key demographic variables (Schaffer and Kot 1986, Berryman and Millstein 1989, Turchin and Taylor 1992, Hanski et al. 1993, Ellner and Turchin 1995, Constantino et al. 1995, John et al. 1998), is difficult to answer. If deterministic chaos is common in natural populations, then predictability over long time scales is essentially impossible, even though short-term predictability can be enhanced by strong density dependence (Ellner and Turchin 1995). An alternate hypothesis is that complex population dynamics arise from stochastic environmental variation. This does not offer much improvement for short-term predictability unless we understand the sources and dynamics of

environmental variability, but at least stochastic effects will not propagate over time, as they do for chaotic systems (Ellner and Turchin 1995).

Disregarding environmental variability, fluctuations may be caused by either demographic stochasticity (disruptive forces) or delays in regulatory mechanisms (controlling forces). The delays may arise because of developmental time and/or interactions between individuals of different stages (age, stage, or size-structured dynamics) (Nisbet et al. 1983, Royama 1992). From a mechanistic point of view, fluctuations caused by regulatory delays in structured populations may be divided into two broad categories: (i) those driven by symmetric interactions between similar individuals, and (ii) the resulting from asymmetric interactions between individuals of different stages (Gurney et al. 1985, Nisbet et al. 1994). Sustained population cycles may result in either case if the interactions are highly nonlinear or if it is weakly nonlinear or linear dynamics are disrupted by stochastic forces (Stenseth et al. 1996a).

3 Diversity

The most simple and straightforward way of measuring species diversity is the number of species. However, as the total number of species depends on sample size, total species number usually does not enable the researcher to determine if one site is more, or less, diverse than another.

The second approach is species-abundance curves based on the rank of species abundance. Alpha statistic of Fisher et al. (1943) is often considered the "best" diversity measure for many communities of species of this type, including Lepidoptera (Southwood 1978, Taylor 1978, Wolda 1983, Barlow and Woiwod 1989, Wolda et al. 1994, Chey et al. 1997), and was the only diversity measure, apart from species richness, used by Intachat and Holloway (2000). Magurran (1985) tested three species abundance curves, log normal, log series, and broken stick, for goodness of fit to her light-trap data from forests in Northern Ireland. She found that the log normal model provided the best fit. Landau et al. (1999) studied moth diversity in Louisiana forests. They determined that the species distribution "roughly followed a log normal pattern". However, they were unable to give a number characterizing diversity because when compared different sites the lognormal species-abundance curve, similarly as log series and broken stick curves, unlike alpha cannot be

characterized by a single number, which makes comparisons among sites difficult.

Though alpha can be characterized numerically, which makes between-site comparisons easier, its disadvantage lies in its inability to discriminate between sites that have the same numbers of individuals and species. It is likely that such sites vary in the evenness of the frequencies of the constituent species. A site that has a greater evenness is usually considered more diverse than a site where a few species dominate, even though the alpha value may be higher in the site showing greater dominance (Rings and Metzler 1990). The use of alpha to describe a community's diversity thus confounds two factors, species richness and the evenness with which the individuals are apportioned among the species (Pielou 1975).

The disadvantage of alpha index is overcome by a third approach, a diversity index which summarizes the data on the number of species and their proportional abundances into a single numeric value (Hill 1973). There is no single index suitable for all situations and the choice of an index depends upon which criteria the researcher wishes to emphasize. These criteria may include how well the index discriminates between sites or samples that are not unduly different, to which extent the index is sensitive to sample size, to species richness, or to the evenness with which the individuals are apportioned among species (Rings and Metzler 1990). Examples include Margalef richness index (Dash and Mahanta 1993):

$$R = \frac{S-1}{\ln(n)}$$

where R is the richness index, S is the total number of species and n is the number of individuals observed; Shannon and Weiner diversity index (e.g. Magurran 1988):

$$H = -\sum p_i \ln p_i$$

where H is the diversity index, p_i is the frequency of the i 'th species and \ln natural logarithm; and evenness or equability index of the species (Pielou 1975, 1977):

$$J = H / \ln S$$

where J is the species evenness or equitability index, H is the Shannon and Weiner diversity index and S is the numbers of species recorded.

Excellent introductions to the measurement of diversity are to be found in Pielou (1975), Southwood (1978), Magurran (1988), Krebs (1989) and a relatively recent paper by Colwell and Coddington (1994). Practical examples on measurements of diversity from light trap data include Lesko et al. (2001), Szentkiralyi et al. (2000, 2001), Szentkiralyi (1992, 1998, 2002), Kadar and Szel (1999), Clay et al. (1998), Profant (1990), Butler et al. (1995, 1999), Landau and Prowell (1999a, 1999b), Landau et al. (1999), Barlow and Woiwod (1989, 1990), Robinson and Tuck (1993), Voss (1969, 1981, 1983, 1991), Sanders (1991), Grimble and Beckwith (1992), Chaundy (1999), Butler and Kondo (1991), Dirks (1937), Frost (1964), Moulding and Madenjian (1979), Rings et al. (1987), Rings and Metzler (1988, 1989, 1990) and Lang and Tbrbk (1997).

4 Thermal requirements for insect development

Temperature is an important component of an insect environment, as it significantly affects both its rate of development and survival. For each species, there is a range of temperatures over which it can survive, and within this range there is a more limited range over which it can grow and reproduce. Of particular concern is the latter, which is referred to as a species' ecologically relevant temperature range (Jarošík et al. 2002, 2004).

A simple way to describe the effect of temperature on insect development is the linear regression of development rate on temperature. This relationship is significant in a range of biologically favorable temperatures from about 2°C above the temperature at which the growth ceases to the upper temperature above which the development is negatively affected (Honek 1996b). Although the variation in development rate over the whole range of temperatures may be described by non linear relationships, use of linear regression is sufficient in most cases (Lamb 1992).

Linear regression enables calculation of the lower development threshold (LDT), a temperature at which development ceases, and sum of effective temperatures (SET), the number of heat units called day degrees above LDT required to complete development (Honek 1996b). From the linear relationship between development rate and temperature ($R = aT + b$, where R is development rate and T is temperature), the thermal characteristics of development may be calculated as $LDT = -b/a$ and $SET = 1/a$. Thermal constants LDT and SET are convenient for comparing requirements of insect populations since they provide a good prediction of development time over a wide range of biologically significant temperatures (Honek 1996b).

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

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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 seven guilds according to habitat specialisation, and analysed for yearly catches and effect of annual mean temperature and precipitation by Shannon's index of diversity, separately for all and abundant (≥ 5 individuals per year) species. Overall, 424 species was recorded: 25 early successional species of arable land (43% of all caught individuals), 116 forest species feeding on trees and shrubs, 33 forest species feeding on herbs and lichens, 92 forest-steppe species, 116 grassland species, 28 wetland species, and 14 non-specialized generalists. Species diversity of habitat specialist was mainly driven by changes of land use, independently on climate variables: diversity of arable land species followed a domed relationship with a peak in early succession stages after field abandonment, diversity of wetland and forest-steppe species decreased in time due to the destruction of their habitats, and diversity of grassland, and both groups of forest species, did not change in time as their habitats were not substantially changing. In contrast, the diversity of generalists increased with mean annual temperature. Abundant species were represented by 127 species and exhibited patterns similar to all species, plus some more subtle changes. Grassland species tended to increase with mean annual precipitation at low mean annual temperature. Non-specialized species in the first years of observation had the same tendency but simultaneously tended to decrease with increasing precipitation at high average temperature. It is concluded that for habitat specialist, the indication of climate changes by indices of diversity can be overlaid by changes in habitat use or buffered by availability of suitable habitats, and that selection of abundant species, by elimination of random catches, can precise the revealed patterns of diversity.

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 (Konvicka 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 of earth, particularly so in industrial countries (Konvicka et al. 2005, Pimm 2008). The losses no longer affect only rare and specialised organism, but apply to widely distributed species as well (Gaston and Fuller 2007). For instance, Britain's once common moths have declined in numbers by about one third of their abundance forty years ago (Conrad et al. 2006), likely affecting food supply of insectivorous vertebrates, and hence structuring of food chains. Overall, it has been estimated that 15-35% of Earth's species face 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 close 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 is 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 in California, eventually leading to population extinction (McLaughlin et al. 2002) and complex effects increasing extinction proneness have been observed elsewhere (Wallisdevries and Van Swaay 2006). It is increasingly clear that without disentangling the climate change and habitat loss effects, we cannot achieve predictive models of response to biotic communities to either of the two developments.

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 whose part remained unchanged for all the time, whereas the other part underwent substantial land use changes. The trap attracted both habitat specialists on several habitat types and habitat generalists, and 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 been losing habitats with those not losing them.

The unique setting, and concurrent recording of meteorological data, allows 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 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 a dendrological park with a collection of deciduous trees and shrubs (2.7 ha), further surrounded by arable land (77.5 ha). In a larger distance, 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 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 (Figure 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 IN. Yearly catches of all species belonging to families of traditional “macrolepidoptera” (i.e., the monophyletic Macrolepidopteran *sensu* Kristensen et al. 2007, plus primitive Hepialidae), which are available for 23 years, are analyzed here. Catches from 1977–1979, when only 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 with relationship to woodland herbs and lichens; forest species directly 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.

From *all species* sampled, we selected a group of *abundant species*, which had annual average catches five or more individuals (species in bold in Appendix 1). This selection should remove species with large occurrence of zeros in the data (Woiwod and Hanski, 1992), and eliminate the influence of random effects (scarce species and random catches stray individuals from distant habitats). In the following analyses, all sampled species and the abundant species are analysed separately.

Species diversity in each of 23 years was expressed, separately for all/abundant species and all/abundant species belonging to the specified guilds, as Shannon’s index of diversity

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

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). This index was chosen because it is largely independent of sample size (Pielou 1966, 1975, Kobayashi 1981) and summarises the number of species (i.e. species richness) and the pattern of distribution of the individuals between the species (i.e. equitability or evenness) with a single number, which can be easily expressed to non-biologists, such as planners (Southwood and Henderson 2000).

The diversity was then analysed by multiplicative regression models that included interactions between explanatory variables. The diversity index H was the response variable, 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. 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, we checked for collinearity with a matrix of correlation coefficients and by calculating tolerance values. To achieve the latter, we compared the regression of the explanatory variable in question against all the remaining explanatory variables in the model. The tolerance values for each explanatory variable were considered unacceptably low if their values in the expression $1-r^2$ (where r^2 is the variance explained by the remaining explanatory variables) were < 0.1 (Quinn and Keough 2002, p. 128). These low tolerance values, indicating a high correlation, can negatively affect the estimates of model parameters.

We sought to obtain the minimal adequate models where all explanatory variables and their interactions were significantly ($p < 0.05$) different from zero and from one another, and all non-significant terms were removed. 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). 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 observation (Neter et al. 1996), only the quadratic terms of explanatory variables which appeared significant in preliminary regressions of the response variable on the single individual 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.

Following Quinn and Keough (2002, p. 131-133), we analyzed interactions among the explanatory variables by using centered variables (i.e., variables rescaled by subtracting their mean from each observation). Significant interaction between two variables was examined with simple slopes of the multiplicative models at varying values of the interacted variables. We used simple slopes of one variable on another to arrive at three specific values of the changing variable: mean and mean plus and minus its sample standard deviation (Quinn and Keough 2002). All calculations were made in S-PLUS® v. 6.2.1 (Insightful Corp.).

Results

Overall, during 23 years, 424 macro-moth species and 800,690 individuals were recorded: 25 species of arable land (in 365,820 individuals), 116 forest species feeding on trees and shrubs (49,123 individuals), 33 forest species feeding on 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 generalists (75,558 individuals) (Table 1). Mean annual temperature and precipitation had an insignificant tendency for increase.

The diversity of *all species* followed a domed relationship, with the highest diversity about 1980, symmetrically decreasing both towards the beginning (1967) and the end (1992) of observation. This pattern was however caused just by the guild of arable land species (Figure 2A), which formed 43% of all caught individuals. Diversity of the other habitat guilds either significantly decreased in time, as in forest-steppe and more markedly in wetland

species (Figure 2B), or did not change neither in time nor under the effect of the climate variables (Table 1). Generalists increased with growing mean annual temperature (Fig. 2C).

Abundant species were represented by 127 species, i.e. by 30% of all sampled species, and 768,489 individuals. Comparing with all species, forest species feeding on herbs and lichens, arable land species and generalists were proportionally over-represented in this group, while forest-steppe species, forest species feeding on trees and shrubs, and particularly wetland species were under-represented (Table 1). The diversity of the total and arable land abundant species showed the same domed relationship (Figure 2D) as was the case for the all sampled species (Figure 2A), but explained more variance than for all species (Table 1). This was clearly due to the guild of arable land species that comprised 45% of abundant species individuals. The diversity of abundant species however also revealed some more subtle changes not apparent for the all sampled species, which appeared as significant interactions among predictors of species diversity (Table 1). Grassland species tended to increase with mean annual precipitation at low mean annual temperature, and generalists had the same tendency in the first years of observation, but also tended to decrease with increasing precipitation at high average temperature (Table 2).

Discussion

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). However, the use of diversity indices has often been criticised (Hurlbert 1971, Peet 1974, May 1975), and the uncharitable view is that diversity indices do not give any additional insight comparing to species number (Southwood and Henderson 2000). In spite of this view, diversity measures remain popular (Cairns 1974, Kempton and Taylor 1974, Kempton 1979, Lyons 1981, Magurran 1988, Purvis and Hector 2000), especially in empirical studies (Rosenberg 1972, Maurer 1974, Bakelaar and Odum 1978, Pyšek et al. 2004). We believe diversity indices can appear superior to the number of species, their abundance or biomass (Jarošík 1991), as well as diversity expressed as species-abundance relationships (Jarošík 1992). However, for their reliable use, the catches have to cover the whole period of the activity of the species (Jarošík 1991). The analysed moths have to work through a fixed reproductive program each year, by means of an almost constant total amount of activity which is realized step by step during spells of suitable weather during a season (Holyoak et al. 1997). The monitoring throughout the whole period of activity is thus crucial for the adequate use of diversity index, as short-term catches give unreliable estimates of diversity indices, due to inadequate assessments of relative abundances of individual species (Jarošík 1991, Holyoak 1994).

In light trap catches of macromoths from a suburban station in Prague, generalists increased their diversity in response to warming climate, whereas several guilds of habitat specialists did not increase at all. This suggests that for specialist moths, any climatic effects were probably overlaid by changes in habitat availability. That abundant grassland species also reacted to climatic variables does not contradict this assertion, as grassland habitats are created, comparing to the other habitats, by relatively non-specialised environments from trampled areas and mesic grasslands to house gardens. 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 specialist.

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 communities. Contrary, the catches from this trap came from well defined environments, that of a dendrology park in front of the building, the surrounding arable land, and the environments of originally seminatural vegetation behind the arable land. While the park, the surrounding arable land and grassland formations remained largely unchanged throughout the whole period of the monitoring, the originally seminatural environments changed markedly. The forest-steppe habitats were gradually converted into build up areas, intervened by just small patches of mesic grasslands. This likely decreased the diversity in all sampled forest-steppe species, and caused their proportional decrease in abundant species. Wetlands were destructed and the riverine carr fen scrubs strongly limited by the establishment of the pond. That was the cause of rapid decrease of diversity of wetland species in the sample of all species and an occurrence of only one abundant wetland species among the abundant species. The high proportional decrease of forest species feeding on woods and shrubs among abundant species had a similar cause, as many of these species could had been associated with car fen scrubs. Small arable fields in the vicinity of grassland formations were abandoned. A few years later, after initialization of succession processes, diversity of arable species on these plots increased, as a lot of these species belong to early successional (Jongepierova et al. 2004, Kiehl and Pfadenhauer 2007). However, subsequent successional development of these fields again initiated rapid decrease of these species. This pattern is responsible for the domed relationship of arable species, with the highest diversity in the mid of monitoring, and a decrease both to the start and the end of this period. Proportional increase in representation of arable land species, forest species feeding on herbs and lichens and non-specialized species can be attributed to unchained environment of the park and surrounding arable land, and the overall ruderalization of the whole area in the range of the light trap operation.

The increase of generalists and grassland species is caused by two interrelated processes. The first process is the change of habitat types and their proportional availability, manifested by the succession of the arable land to mesic biotopes, which compensates for the increase of overbuilding sites. This process supports particularly grassland species. Second, generalist and grassland species are those best able to face climate changes. As mostly generalists, they are mainly polyphagous and have large geographical ranges, which give them, in a case of temperature increase, better chance for finding an appropriate biotope and host plant (Bale et al. 2002, Brachslar 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, some of the generalist and grassland species are migrants and their probability of occurrence thus further depends on temperature; in hot summers, migrants 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 survival 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). Survivorship can also be negatively affected by strong summer rainstorms, due to the dissolution of eggs and first larval instar, particularly of small species (Kobori and Amano 2003). This could be the cause of the decrease of generalists with increasing precipitation at high average temperature.

The results suggest that the selection of abundant species eliminates effects of random catches and thus help to indicate relationships which appear vague in sample of all detected species. A disadvantage is that this selection can decrease the sample to a magnitude that does not enable to analyse diversity, as happened for wetland species (Table 1). On the other hand, the selection of abundant species enabled to reveal the interactions among the predictors of species diversity for grassland and generalist species and to explain more variance in the

domed relationship for arable land species. Even if the decrease in sample size prevents to determine significant changes in species diversity, as probably happened for forest-steppe species, comparison of proportional representation between all and abundant species still can indicate long term trends. This was shown as the proportional decrease between all and abundant species for the forest-steppe guild. Finally, proportional changes between all and abundant species can indicate changes that were not apparent by the use of the index of diversity, as appeared for forest species feeding on woods and shrubs, where the index of diversity did not reveal any trend, but the decline of forest species was clearly apparent in the decrease of the proportion of abundant species. A change in proportion can also indicate overall changes in land use, as suggested the proportional increase of abundant species for generalists, arable land species and forest species feeding on herbs and lichens.

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Table 1. Number of species (S) and individuals (N), intercepts, significant ($P < 0.05$) slopes and interactions (\cdot) of predictors (temp = temperature, prec = precipitation), and test statistics (F , df , P , R^2) for minimal adequate models of species diversity (Shannon's index H). Totals and numbers in individual habitats for all sampled species and abundant (yearly catches ≥ 5 individuals) species.

	S	N	Intercept	Slopes and interactions of predictors				Test statistics			R^2	
				year	year ²	temp	temp:prec	year:temp:prec	F	df		P
All species												
Total	424	800690	1.73	-	-0.078	-	-	-	8.63	1, 21	0.008	0.29
Arable land	25	365820	0.99	-	-0.089	-	-	-	13.93	1, 21	0.001	0.40
Forest – woods & shrubs	116	49123	1.29	-	-	-	-	-	-	-	NS	-
Forrest – herbs & lichens	33	33059	0.99	-	-	-	-	-	-	-	NS	-
Forest-steppe	92	88310	1.03	-0.055	-	-	-	-	6.99	1, 21	0.01	0.25
Grassland	116	184539	1.21	-	-	-	-	-	-	-	NS	-
Wetland	28	4281	0.82	-0.11	-	-	-	-	24.26	1, 21	<0.0001	0.54
Generalists	14	75558	0.78	-	-	0.020	-	-	6.66	1, 21	0.02	0.24
Abundant species												
Total	127	768489	1.65	-	-0.083	-	-	-	11.24	1, 21	0.003	0.35
Arable land	17	364677	0.98	-	-0.089	-	-	-	14.37	1, 21	0.001	0.41
Forest – woods & shrubs	31	60496	1.03	-	-	-	-	-	-	-	NS	-
Forrest – herbs & lichens	16	33544	1.00	-	-	-	-	-	-	-	NS	-
Forest-steppe	17	62447	0.83	-	-	-	-	-	-	-	NS	-
Grassland	37	171480	1.08	-	-	-	-0.046	-	4.59	1, 21	0.04	0.18
Wetland	1	1411	not analyzed	-	-	-	-	-	-	-	-	-
Generalists	8	74434	0.75	-	-	-	-	-0.030	12.75	4, 18	<0.0001	0.74

Table 2. Simple slopes (estimates, standard errors *SE*, t-tests *t*, degrees of freedom *df* and significances *P*) of species diversity (Shannon's index *H*) on mean annual precipitation for different values of mean annual temperature for abundant (yearly catches ≥ 5 individuals) grassland species, and for different values of mean annual temperature and year of observation for abundant generalists (only combinations for marginally significant values, i.e. slopes with $0.05 \leq P \leq 0.1$, are shown).

Interacting variables	Estimate	<i>SE</i>	<i>t</i>	<i>df</i>	<i>P</i>
Grassland species					
Mean annual temperature 6.1 °C	0.0062	0.0032	1.91	19	0.07
Mean annual temperature 7.7 °C	0.0025	0.0029	0.84	19	0.41
Mean annual temperature 9.4 °C	-0.0013	0.0052	-0.24	19	0.81
Generalists					
Mean annual temperature 6.1 °C in 1985	0.017	0.0082	2.10	16	0.05
Mean annual temperature 9.4 °C in 1985	-0.019	0.0098	-1.94	16	0.07

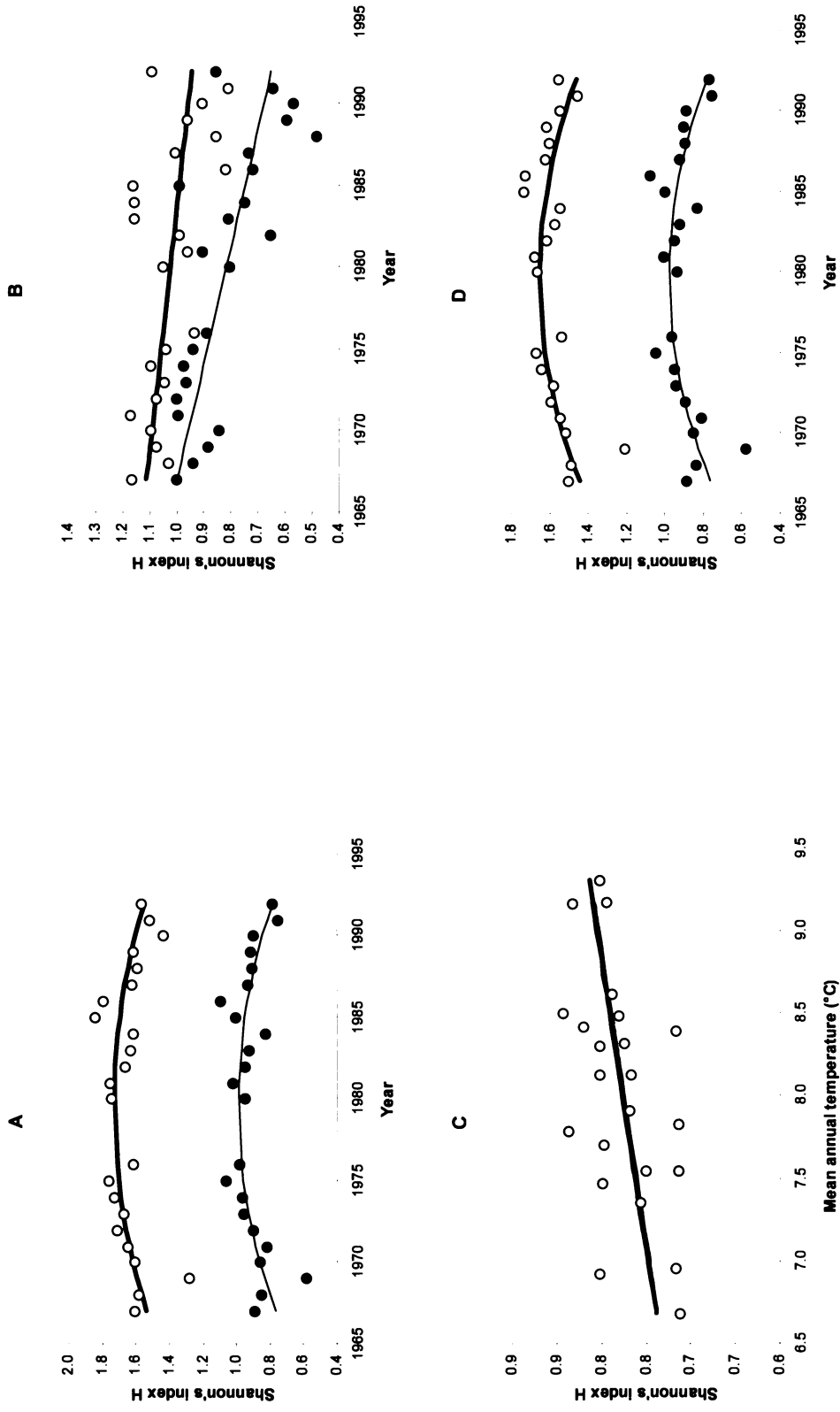


Figure 1: Proportional distribution of main habitat types and components in monitored region, a) situation in 1967, b) in 1992. Black concentric cycles shows approximate position of light-trap.

Legend of map:



Figure 2. Species diversity (Shannon's index H) plotted against significant predictors for all (A – C) and abundant (yearly catches ≥ 5 individuals) species (D). (A) Species diversity plotted against the years of observation for species total (empty circles and thick line) and arable land species (full circles and thin line); (B) Species diversity for species inhabiting forest-steppe (empty circles and thick line) and wetland (full circles and thin line) habitats; (C) Species diversity plotted against the mean annual temperature for generalist; (D) against the years for total (empty circles and thick line) and arable land species (full circles and thin line). Statistics are given in Table 1.



Appendix 1: Check-list of moth species obtained to this study. Marked species (**bold**) are chosen as abundant (yearly catches ≥ 5 individuals). Nomenclature of species follows Laštůvka and Liška (2005).

Genus	Species	Author and year of description	Family	Guild
<i>Abraxas</i>	<i>sylvata</i>	(Scopoli, 1763)	Geometridae	forest species feeding on trees/ shrubs
<i>Abrostola</i>	<i>tripartita</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Abrostola</i>	<i>triplasia</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
<i>Acronicta</i>	<i>acensis</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Acronicta</i>	<i>alni</i>	(Linnaeus, 1767)	Noctuidae	forest species feeding on trees/ shrubs
<i>Acronicta</i>	<i>auricoma</i>	(Denis et Schiffmueller, [1775])	Noctuidae	forest-steppe species
<i>Acronicta</i>	<i>leporina</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Acronicta</i>	<i>megacephala</i>	(Denis et Schiffmueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Acronicta</i>	<i>psi</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Acronicta</i>	<i>rumicis</i>	(Linnaeus, 1758)	Noctuidae	non-specialized (ubiquistic) species
<i>Actinotia</i>	<i>polyodon</i>	(Clerck, 1759)	Noctuidae	grassland (steppe and meadow) species
<i>Agriopis</i>	<i>aurantiaria</i>	(Huebner, [1799])	Geometridae	forest species feeding on trees/ shrubs
<i>Agriopis</i>	<i>leucophaearia</i>	(Denis et Schiffmueller, [1775])	Geometridae	forest species feeding on trees/ shrubs
<i>Agriopis</i>	<i>marginaria</i>	(Fabricius, 1776)	Geometridae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>circellaris</i>	(Hufnagel, 1766)	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>helvola</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Agrochola</i>	<i>humilis</i>	(Denis et Schiffmueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Agrochola</i>	<i>laevis</i>	(Huebner, [1803])	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>litura</i>	(Linnaeus, 1761)	Noctuidae	forest-steppe species
<i>Agrochola</i>	<i>lota</i>	(Clerck, 1759)	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>lychnidis</i>	(Denis et Schiffmueller, [1775])	Noctuidae	non-specialized (ubiquistic) species
<i>Agrochola</i>	<i>macilenta</i>	(Huebner, [1809])	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>nitida</i>	(Denis et Schiffmueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Agrotis</i>	<i>cinerea</i>	(Denis et Schiffmueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Agrotis</i>	<i>clavis</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Agrotis</i>	<i>exclamationis</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Agrotis</i>	<i>ipsilon</i>	(Hufnagel, 1766)	Noctuidae	early successional arable land species
<i>Agrotis</i>	<i>segetum</i>	(Denis et Schiffmueller, [1775])	Noctuidae	early successional arable land species
<i>Allophyes</i>	<i>oxyacanthae</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Ammonoquia</i>	<i>caecimacula</i>	(Denis et Schiffmueller, [1775])	Noctuidae	forest-steppe species
<i>Amphipoea</i>	<i>fucosa</i>	(Freyer, 1830)	Noctuidae	grassland (steppe and meadow) species
<i>Amphipoea</i>	<i>oculea</i>	(Linnaeus, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Amphipyra</i>	<i>berbera</i>	Rungs, 1949	Noctuidae	forest species feeding on trees/ shrubs

<i>Amphipyra</i>	<i>pyramidea</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Amphipyra</i>	<i>tragopoginis</i>	(Clerck, 1759)	Noctuidae	grassland (steppe and meadow) species
<i>Anaplectoides</i>	<i>prasinus</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Anticlea</i>	<i>derivata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Apamea</i>	<i>crenata</i>	(Hufnagel, 1766)	Noctuidae	forest-steppe species
<i>Apamea</i>	<i>ophiogramma</i>	(Esper, [1794])	Noctuidae	wetland (and wet meadow) species
<i>Apamea</i>	<i>remissa</i>	(Huebner, [1809])	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>scolopacina</i>	(Esper, [1788])	Noctuidae	wetland (and wet meadow) species
<i>Apamea</i>	<i>sublustris</i>	(Esper, [1788])	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>unanimis</i>	(Huebner, [1813])	Noctuidae	wetland (and wet meadow) species
<i>Apamea</i>	<i>anceps</i>	(Denis et Schiffermueller, [1775])	Noctuidae	early successional arable land species
<i>Apamea</i>	<i>lateritia</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>lithoxyloea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>monoglypha</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>sordens</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Aplocera</i>	<i>plagiata</i>	(Linnaeus, 1758)	Geometridae	early successional arable land species
<i>Arctia</i>	<i>caja</i>	(Linnaeus, 1758)	Arctiidae	forest-steppe species
<i>Arctornis</i>	<i>l-nigrum</i>	(Mueller, 1764)	Lymantriidae	forest species feeding on trees/ shrubs
<i>Archanara</i>	<i>dissoluta</i>	(Treitschke, 1825)	Noctuidae	grassland (steppe and meadow) species
<i>Archanara</i>	<i>geminipuncta</i>	(Haworth, [1809])	Noctuidae	wetland (and wet meadow) species
<i>Archanara</i>	<i>sparganii</i>	(Esper, [1790])	Noctuidae	wetland (and wet meadow) species
<i>Asthera</i>	<i>albula</i>	(Hufnagel, 1767)	Geometridae	forest-steppe species
<i>Atethmia</i>	<i>ambusta</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Athetis</i>	<i>pallustris</i>	(Huebner, 1808)	Noctuidae	wetland (and wet meadow) species
<i>Atypha</i>	<i>pulmonaris</i>	(Esper, 1790)	Noctuidae	forest-steppe species
<i>Auchmis</i>	<i>detersa</i>	(Esper, [1787])	Noctuidae	grassland (steppe and meadow) species
<i>Autographa</i>	<i>bractea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Autographa</i>	<i>gamma</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Autographa</i>	<i>pulchrina</i>	(Haworth, [1809])	Noctuidae	forest-steppe species
<i>Axylla</i>	<i>putris</i>	(Linnaeus, 1761)	Noctuidae	forest-steppe species
<i>Bena</i>	<i>bicolorana</i>	(Fuessly, 1775)	Nolidae	forest species feeding on trees/ shrubs
<i>Biston</i>	<i>betularius</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Biston</i>	<i>stratarius</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Brachyloemia</i>	<i>viminalis</i>	(Fabricius, 1776)	Noctuidae	wetland (and wet meadow) species
<i>Bupalus</i>	<i>pinarius</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Cabera</i>	<i>pusaria</i>	(Linnaeus, 1758)	Geometridae	forest species with relationship to woodland herbs and lichens

<i>Calamia</i>	<i>tridens</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Calliteara</i>	<i>pudibunda</i>	(Linnaeus, 1758)	Lymantriidae	forest species feeding on trees/ shrubs
<i>Campaea</i>	<i>margaritaria</i>	(Linnaeus, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Campogramma</i>	<i>bilineatum</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Caradrina</i>	<i>morpheus</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Cataclypeme</i>	<i>riguata</i>	(Huebner, [1813])	Geometridae	grassland (steppe and meadow) species
<i>Catarhoe</i>	<i>cuculata</i>	(Hufnagel, 1767)	Geometridae	grassland (steppe and meadow) species
<i>Catarhoe</i>	<i>rubidata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Catocala</i>	<i>elocata</i>	(Esper, 1787)	Noctuidae	forest species feeding on trees/ shrubs
<i>Catocala</i>	<i>fraxini</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Catocala</i>	<i>fulminea</i>	(Scopoli, 1763)	Noctuidae	forest-steppe species
<i>Catocala</i>	<i>nupta</i>	(Linnaeus, 1767)	Noctuidae	forest species feeding on trees/ shrubs
<i>Celaena</i>	<i>leucostigma</i>	(Huebner, [1808])	Noctuidae	wetland (and wet meadow) species
<i>Cepphis</i>	<i>advenaria</i>	(Huebner, [1790])	Geometridae	forest-steppe species
<i>Ceramica</i>	<i>pisi</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Cerapteryx</i>	<i>graminis</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
<i>Cerastis</i>	<i>leucographa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Cerastis</i>	<i>rubricosa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Cidaria</i>	<i>fulvata</i>	(Forster, 1771)	Geometridae	grassland (steppe and meadow) species
<i>Cilix</i>	<i>glaucata</i>	(Scopoli, 1763)	Drepanidae	forest-steppe species
<i>Cleora</i>	<i>cinctaria</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Clostera</i>	<i>curtula</i>	(Linnaeus, 1758)	Notodontidae	forest-steppe species
<i>Colobochyla</i>	<i>salicalis</i>	(Denis et Schiffermueller, [1775])	Noctuidae	wetland (and wet meadow) species
<i>Colocasia</i>	<i>coryli</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Colostygia</i>	<i>pectinataria</i>	(Knock, 1781)	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Colotois</i>	<i>pennaria</i>	(Linnaeus, 1761)	Geometridae	forest species feeding on trees/ shrubs
<i>Conisania</i>	<i>luteago</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Conistra</i>	<i>erythrocephala</i>	(Denis et Schiffermueller, [1775])	Noctuidae	non-specialized (ubiquistic) species
<i>Conistra</i>	<i>rubiginea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Conistra</i>	<i>rubiginosa</i>	(Scopoli, 1763)	Noctuidae	forest-steppe species
<i>Conistra</i>	<i>vaccinii</i>	(Linnaeus, 1761)	Noctuidae	forest-steppe species
<i>Cosmia</i>	<i>pyralina</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Cosmia</i>	<i>trapezina</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Cosmorhoe</i>	<i>ocellata</i>	(Linnaeus, 1758)	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Craniophora</i>	<i>ligustri</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Crocallis</i>	<i>elinguaria</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs

<i>Cucullia</i>	<i>absinthii</i>	(Linnaeus, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Cucullia</i>	<i>artemisiae</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Cucullia</i>	<i>fraudatrix</i>	Eversmann, 1837	Noctuidae	grassland (steppe and meadow) species
<i>Cucullia</i>	<i>chamomillae</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Cucullia</i>	<i>umbratica</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
<i>Cyclophora</i>	<i>albipunctata</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Cyclophora</i>	<i>annularia</i>	(Fabricius, 1775)	Geometridae	forest species feeding on trees/ shrubs
<i>Cyclophora</i>	<i>linearia</i>	(Huebner, [1799])	Geometridae	forest species feeding on trees/ shrubs
<i>Cyclophora</i>	<i>punctaria</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Deilephila</i>	<i>elipenor</i>	(Linnaeus, 1758)	Sphingidae	forest-steppe species
<i>Deilephila</i>	<i>porcellus</i>	(Linnaeus, 1758)	Sphingidae	grassland (steppe and meadow) species
<i>Deileptenia</i>	<i>ribeata</i>	(Clerck, 1759)	Geometridae	forest species feeding on trees/ shrubs
<i>Diacrisia</i>	<i>sannio</i>	(Linnaeus, 1758)	Arctiidae	forest-steppe species
<i>Diachrysa</i>	<i>chrysitis</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Diaphora</i>	<i>mendica</i>	(Clerck, 1759)	Arctiidae	forest-steppe species
<i>Diarsia</i>	<i>brunnea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Diarsia</i>	<i>rubi</i>	(Vieweg, 1790)	Noctuidae	forest-steppe species
<i>Dichonia</i>	<i>convergens</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Diloba</i>	<i>caeruleocephala</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Drepana</i>	<i>falcataria</i>	(Linnaeus, 1758)	Drepanidae	forest species feeding on trees/ shrubs
<i>Drymonia</i>	<i>dodonaea</i>	(Denis et Schiffermueller, [1775])	Notodontidae	forest species feeding on trees/ shrubs
<i>Dypterygia</i>	<i>scabriuscula</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Dysstroma</i>	<i>citrata</i>	(Linnaeus, 1761)	Geometridae	forest species feeding on trees/ shrubs
<i>Dysstroma</i>	<i>truncata</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Earias</i>	<i>clorana</i>	(Linnaeus, 1761)	Nolidae	wetland (and wet meadow) species
<i>Earias</i>	<i>vernana</i>	(Fabricius, 1787)	Nolidae	wetland (and wet meadow) species
<i>Earophila</i>	<i>badlata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Ecliptopera</i>	<i>silaceata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Ectropis</i>	<i>crepuscularia</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Egira</i>	<i>conspicillaris</i>	(Linnaeus, 1758)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Eilema</i>	<i>complana</i>	(Linnaeus, 1758)	Arctiidae	forest species feeding on trees/ shrubs
<i>Eilema</i>	<i>depressum</i>	(Esper, 1787)	Arctiidae	forest species with relationship to woodland herbs and lichens
<i>Eilema</i>	<i>lurideola</i>	(Zincken), 1817	Arctiidae	forest-steppe species
<i>Eilema</i>	<i>lutarella</i>	(Linnaeus, 1758)	Arctiidae	grassland (steppe and meadow) species
<i>Eilema</i>	<i>sororcula</i>	(Hufnagel, 1766)	Arctiidae	forest species with relationship to woodland herbs and lichens
<i>Ematurga</i>	<i>atomaria</i>	(Linnaeus, 1758)	Geometridae	non-specialized (ubiquistic) species

<i>Enargia</i>	paleacea	(Esper, [1788])	Noctuidae	forest species feeding on trees/ shrubs
Ennomos	autumnarius	(Werneburg, 1859)	Geometridae	forest species feeding on trees/ shrubs
<i>Ennomos</i>	<i>erosarius</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest species feeding on trees/ shrubs
Ennomos	fuscantarius	(Haworth, 1809)	Geometridae	forest species feeding on trees/ shrubs
<i>Ennomos</i>	<i>quercinarius</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
Ennomos	alniarius	(Linnaeus, 1758)	Geometridae	forest-steppe species
Epirrhoe	alternata	(Mueller, 1764)	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Epirrhoe</i>	<i>rivata</i>	(Huebner, [1813])	Geometridae	forest-steppe species
<i>Epirrhoe</i>	<i>tristata</i>	(Linnaeus, 1758)	Geometridae	grassland (steppe and meadow) species
<i>Erannis</i>	<i>defoliaria</i>	(Clerck, 1759)	Geometridae	forest species feeding on trees/ shrubs
<i>Euchoeca</i>	<i>nebulata</i>	(Scopoli, 1763)	Geometridae	forest-steppe species
<i>Eulithis</i>	<i>mellinata</i>	(Fabricius, 1787)	Geometridae	forest species feeding on trees/ shrubs
<i>Eulithis</i>	<i>populata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
Eulithis	pyraliata	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Eulithis</i>	<i>testata</i>	(Linnaeus, 1761)	Geometridae	forest-steppe species
Eulithis	prunata	(Linnaeus, 1758)	Geometridae	forest-steppe species
<i>Euphyia</i>	<i>unangulata</i>	(Haworth, [1809])	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Eupithecia</i>	<i>abietaria</i>	(Goeze, 1781)	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>absinthiata</i>	(Clerck, 1759)	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>analoga</i>	Diakonoff, 1926	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>assimilata</i>	Doubleday, 1856	Geometridae	forest species with relationship to woodland herbs and lichens
Eupithecia	centaureata	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>denotata</i>	(Huebner, 1813)	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>dodoneata</i>	Guenee, 1857	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>egenaria</i>	Herrich-Schaeffer, 1848	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>extraversaria</i>	Herrich-Schaeffer, 1852	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>goossensata</i>	Mabille, 1869	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Eupithecia</i>	<i>haworthiata</i>	Doubleday, 1856	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>icterata</i>	(Villers, 1789)	Geometridae	grassland (steppe and meadow) species
Eupithecia	innodata	(Hufnagel, 1767)	Geometridae	non-specialized (ubiquitous) species
Eupithecia	intricata	(Zetterstedt, [1839])	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>inturbata</i>	(Huebner, [1817])	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>lanceata</i>	(Huebner, [1825])	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>lariciata</i>	(Freyer, 1842)	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>linariata</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>millefoliata</i>	Roessler, 1866	Geometridae	grassland (steppe and meadow) species

<i>Eupithecia</i>	<i>nanata</i>	(Huebner, [1813])	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>pimpinellata</i>	(Huebner, [1813])	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>plumbeolata</i>	(Haworth, 1809)	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>pusillata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>sinuosaria</i>	(Eversmann, 1848)	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>subfuscata</i>	(Haworth, [1809])	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>subumbrata</i>	(Denis et Schiffermueller, [1775])	Geometridae	non-specialized (ubiquistic) species
<i>Eupithecia</i>	<i>succenturiata</i>	(Linnaeus, 1758)	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>tantillaria</i>	Boisduval, 1840	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>tenuiata</i>	(Huebner, 1813)	Geometridae	forest-steppe species
<i>Eupithecia</i>	<i>tripunctaria</i>	Herrich-Schaeffer, [1852]	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Eupithecia</i>	<i>venosata</i>	(Fabricius, 1787)	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>virgaureata</i>	Doubleday, 1861	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>vulgata</i>	(Haworth, [1809])	Geometridae	forest-steppe species
<i>Euplexia</i>	<i>lucipara</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Euxoa</i>	<i>aquilina</i>	(Denis et Schiffermueller, [1775])	Noctuidae	early successional arable land species
<i>Euxoa</i>	<i>obelisca</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Euxoa</i>	<i>tritici</i>	(Linnaeus, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Euxoa</i>	<i>nigricans</i>	(Linnaeus, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Falcaria</i>	<i>lacertinaria</i>	(Linnaeus, 1758)	Drepanidae	forest species feeding on trees/ shrubs
<i>Gortyna</i>	<i>flavago</i>	(Denis et Schiffermueller, [1775])	Noctuidae	wetland (and wet meadow) species
<i>Graphiphora</i>	<i>augur</i>	(Fabricius, 1775)	Noctuidae	forest-steppe species
<i>Gymnoscelis</i>	<i>ruffasciata</i>	(Haworth, [1809])	Geometridae	grassland (steppe and meadow) species
<i>Habrosyne</i>	<i>pyritoides</i>	(Hufnagel, 1766)	Drepanidae	forest species with relationship to woodland herbs and lichens
<i>Hada</i>	<i>plebeja</i>	(Linnaeus, 1761)	Noctuidae	forest-steppe species
<i>Hadena</i>	<i>bicruris</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Hadena</i>	<i>compta</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Hadena</i>	<i>confusa</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Hadena</i>	<i>perplexa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Hadula</i>	<i>trifolii</i>	(Hufnagel, 1766)	Noctuidae	early successional arable land species
<i>Hecatera</i>	<i>bicolorata</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Hecatera</i>	<i>dysodea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Hemithoa</i>	<i>aestivaria</i>	(Huebner, [1799])	Geometridae	forest species feeding on trees/ shrubs
<i>Hepialus</i>	<i>hecta</i>	(Linnaeus, 1758)	Hepialidae	grassland (steppe and meadow) species
<i>Hepialus</i>	<i>humuli</i>	(Linnaeus, 1758)	Hepialidae	grassland (steppe and meadow) species
<i>Hepialus</i>	<i>lupulinis</i>	(Linnaeus, 1758)	Hepialidae	grassland (steppe and meadow) species

<i>Herminia</i>	<i>grisealis</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Herminia</i>	<i>farsicrinalis</i>	(Knoch, 1782)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Hoplodrina</i>	<i>ambigua</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Hoplodrina</i>	<i>respersa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Hoplodrina</i>	<i>blanda</i>	(Denis et Schiffermueller, [1775])	Noctuidae	non-specialized (ubiquistic) species
<i>Hoplodrina</i>	<i>octogenaria</i>	(Goeze, 1781)	Noctuidae	non-specialized (ubiquistic) species
<i>Horisme</i>	<i>corticata</i>	(Treitschke, 1835)	Geometridae	grassland (steppe and meadow) species
<i>Hydraecia</i>	<i>petasitis</i>	Doubleday, 1847	Noctuidae	wetland (and wet meadow) species
<i>Hydraecia</i>	<i>micacea</i>	(Esper, [1789])	Noctuidae	wetland (and wet meadow) species
<i>Hydrelia</i>	<i>flammeolaria</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Hydria</i>	<i>cervinalis</i>	(Scopoli, 1763)	Geometridae	grassland (steppe and meadow) species
<i>Hydria</i>	<i>undulata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Hydriomena</i>	<i>furcata</i>	(Thunberg, 1784)	Geometridae	forest-steppe species
<i>Hydriomena</i>	<i>impluviata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Hypena</i>	<i>proboscidalis</i>	(Linnaeus, 1758)	Noctuidae	non-specialized (ubiquistic) species
<i>Hypena</i>	<i>rostralis</i>	(Linnaeus, 1758)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Charanyca</i>	<i>trigrammica</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species
<i>Charissa</i>	<i>obscurata</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Chesias</i>	<i>legatella</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Chiasmia</i>	<i>ciathrata</i>	(Linnaeus, 1758)	Geometridae	early successional arable land species
<i>Chilodes</i>	<i>maritimus</i>	(Tauscher, 1806)	Noctuidae	wetland (and wet meadow) species
<i>Chloantha</i>	<i>hyperici</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Chortodes</i>	<i>fluxa</i>	(Huebner, [1809])	Noctuidae	wetland (and wet meadow) species
<i>Chortodes</i>	<i>minima</i>	(Haworth, 1809)	Noctuidae	wetland (and wet meadow) species
<i>Idaea</i>	<i>biselata</i>	(Hufnagel, 1767)	Geometridae	forest-steppe species
<i>Idaea</i>	<i>deversaria</i>	(Herrich-Schaeffer, [1847])	Geometridae	grassland (steppe and meadow) species
<i>Idaea</i>	<i>dilutaria</i>	(Huebner, 1799)	Geometridae	grassland (steppe and meadow) species
<i>Idaea</i>	<i>dimidiata</i>	(Hufnagel, 1767)	Geometridae	early successional arable land species
<i>Idaea</i>	<i>fuscovenosa</i>	(Goeze, 1781)	Geometridae	grassland (steppe and meadow) species
<i>Idaea</i>	<i>humiliata</i>	(Hufnagel, 1767)	Geometridae	grassland (steppe and meadow) species
<i>Idaea</i>	<i>inquinata</i>	(Scopoli, 1763)	Geometridae	early successional arable land species
<i>Idaea</i>	<i>laevigata</i>	(Scopoli, 1763)	Geometridae	early successional arable land species
<i>Idaea</i>	<i>seriata</i>	(Schrank, 1802)	Geometridae	early successional arable land species
<i>Idaea</i>	<i>sylvestriaria</i>	(Huebner, 1799)	Geometridae	early successional arable land species
<i>Idaea</i>	<i>aversata</i>	(Linnaeus, 1758)	Geometridae	grassland (steppe and meadow) species
<i>Idia</i>	<i>calvaria</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
				forest species with relationship to woodland herbs and lichens

<i>Ipimorpha</i>	<i>retusa</i>	(Linnaeus, 1761)	Noctuidae	wetland (and wet meadow) species
<i>Ipimorpha</i>	<i>subtusa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Isturgia</i>	<i>murinaria</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Lacanobia</i>	<i>aliena</i>	(Huebner, 1809)	Noctuidae	grassland (steppe and meadow) species
<i>Lacanobia</i>	<i>contigua</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Lacanobia</i>	<i>oleracea</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Lacanobia</i>	<i>suasa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	early successional arable land species
<i>Lacanobia</i>	<i>thalassina</i>	(Hufnagel, 1766)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Lacanobia</i>	<i>w-latinum</i>	(Hufnagel, 1766)	Noctuidae	early successional arable land species
<i>Laothe</i>	<i>populi</i>	(Linnaeus, 1758)	Sphingidae	forest species feeding on trees/ shrubs
<i>Laspeyria</i>	<i>flexula</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Leucania</i>	<i>comma</i>	(Linnaeus, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Leucania</i>	<i>obsoleta</i>	(Huebner, [1803])	Noctuidae	wetland (and wet meadow) species
<i>Leucodonta</i>	<i>bicoloria</i>	(Denis et Schiffermueller, [1775])	Notodontidae	forest species feeding on trees/ shrubs
<i>Leucoma</i>	<i>salicis</i>	(Linnaeus, 1758)	Lymantriidae	forest species feeding on trees/ shrubs
<i>Ligia</i>	<i>adustata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Lithophane</i>	<i>furcifera</i>	(Hufnagel, 1766)	Noctuidae	forest species feeding on trees/ shrubs
<i>Lithophane</i>	<i>ornitopus</i>	(Hufnagel, 1766)	Noctuidae	forest species feeding on trees/ shrubs
<i>Lithophane</i>	<i>socia</i>	(Hufnagel, 1766)	Noctuidae	forest species feeding on trees/ shrubs
<i>Lobophora</i>	<i>halterata</i>	(Hufnagel, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Lomaspilis</i>	<i>marginata</i>	(Linnaeus, 1758)	Geometridae	forest-steppe species
<i>Luperina</i>	<i>testacea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Lycia</i>	<i>hirtaria</i>	(Clerck, 1759)	Geometridae	forest species feeding on trees/ shrubs
<i>Lycophotia</i>	<i>porphyrea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Lygephila</i>	<i>cracca</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Lygephila</i>	<i>pastinum</i>	(Treitschke, 1826)	Noctuidae	grassland (steppe and meadow) species
<i>Lymantria</i>	<i>dispar</i>	(Linnaeus, 1758)	Lymantriidae	forest species feeding on trees/ shrubs
<i>Lymantria</i>	<i>monacha</i>	(Linnaeus, 1758)	Lymantriidae	forest species feeding on trees/ shrubs
<i>Macaria</i>	<i>alternata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest species feeding on trees/ shrubs
<i>Macaria</i>	<i>liturata</i>	(Clerck, 1759)	Geometridae	forest species feeding on trees/ shrubs
<i>Macaria</i>	<i>notata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Macaria</i>	<i>wauaria</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Macedunnoughia</i>	<i>confusa</i>	(Stephens, 1850)	Noctuidae	early successional arable land species
<i>Macrothylacia</i>	<i>rubi</i>	(Linnaeus, 1758)	Lasiocampidae	forest-steppe species
<i>Malacosoma</i>	<i>neustria</i>	(Linnaeus, 1758)	Lasiocampidae	forest-steppe species
<i>Mamestra</i>	<i>brassicae</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species

Melanchnra	<i>persicariae</i>	(Linnaeus, 1761)	Noctuidae	early successional arable land species
Mesoligia	<i>furuncula</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
Mitochrista	<i>miniata</i>	(Forster, 1771)	Arctiidae	wetland (and wet meadow) species
Mimas	<i>tiliae</i>	(Linnaeus, 1758)	Sphingidae	forest species feeding on trees/ shrubs
Mniotype	<i>satura</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
Mythimna	<i>albipuncta</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
Mythimna	<i>l-album</i>	(Linnaeus, 1767)	Noctuidae	forest-steppe species
Mythimna	<i>conigera</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
Mythimna	<i>ferrago</i>	(Fabricius, 1787)	Noctuidae	forest-steppe species
Mythimna	<i>impura</i>	(Huebner, [1808])	Noctuidae	grassland (steppe and meadow) species
Mythimna	<i>pallens</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
Mythimna	<i>pudorina</i>	(Denis et Schiffermueller, [1775])	Noctuidae	wetland (and wet meadow) species
Mythimna	<i>sicula</i>	(Treitschke, 1835)	Noctuidae	grassland (and wet meadow) species
Mythimna	<i>straminea</i>	(Treitschke, 1825)	Noctuidae	wetland (and wet meadow) species
Mythimna	<i>turca</i>	(Linnaeus, 1761)	Noctuidae	forest-steppe species
Naenia	<i>typica</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
Noctua	<i>interposita</i>	(Huebner, [1790])	Noctuidae	forest-steppe species
Noctua	<i>orbona</i>	(Hufnagel, 1766)	Noctuidae	forest species with relationship to woodland herbs and lichens
Noctua	<i>comes</i>	Huebner, [1813]	Noctuidae	forest-steppe species
Noctua	<i>fimbriata</i>	(Schreber, 1759)	Noctuidae	forest-steppe species
Noctua	<i>janthina</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
Noctua	<i>pronuba</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
Nola	<i>cucullatella</i>	(Linnaeus, 1758)	Nolidae	forest-steppe species
Nonagria	<i>typhae</i>	(Thunberg, 1784)	Noctuidae	wetland (and wet meadow) species
Notodonta	<i>dromedarius</i>	(Linnaeus, 1767)	Notodontidae	forest species feeding on trees/ shrubs
Notodonta	<i>ziczac</i>	(Linnaeus, 1758)	Notodontidae	forest species feeding on trees/ shrubs
Nycteola	<i>asiatica</i>	(Krulikowski, 1904)	Nolidae	forest species feeding on trees/ shrubs
Nycteola	<i>revayana</i>	(Scopoli, 1772)	Nolidae	forest species feeding on trees/ shrubs
Nycterosea	<i>obstipata</i>	(Fabricius, 1794)	Geometridae	grassland (steppe and meadow) species
Ochropacha	<i>duplaris</i>	(Linnaeus, 1761)	Drepanidae	non-specialized (ubiquistic) species
Ochroleura	<i>plecta</i>	(Linnaeus, 1761)	Noctuidae	early successional arable land species
Oligia	<i>fasciuncula</i>	(Haworth, [1809])	Noctuidae	wetland (and wet meadow) species
Oligia	<i>latruncula</i>	(Denis et Schiffermueller, [1775])	Noctuidae	non-specialized (ubiquistic) species
Oligia	<i>strigilis</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
Opigena	<i>polygona</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
Opisthograptis	<i>luteolata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs

<i>Oria</i>	<i>musculosa</i>	(Huebner, [1808])	Noctuidae	grassland (steppe and meadow) species
<i>Orthosia</i>	<i>cerasi</i>	(Fabricius, 1775)	Noctuidae	forest species feeding on trees/ shrubs
<i>Orthosia</i>	<i>gothica</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Orthosia</i>	<i>gracilis</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Orthosia</i>	<i>incerta</i>	(Hufnagel, 1766)	Noctuidae	forest species feeding on trees/ shrubs
<i>Orthosia</i>	<i>miniosa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species
<i>Orthosia</i>	<i>populeti</i>	(Fabricius, 1781)	Noctuidae	forest species feeding on trees/ shrubs
<i>Ourapteryx</i>	<i>sambucaria</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Pachetra</i>	<i>sagittigera</i>	(Hufnagel, 1766)	Noctuidae	forest-steppe species
<i>Pachycnemia</i>	<i>hippocastanaria</i>	(Huebner, [1799])	Geometridae	forest species feeding on trees/ shrubs
<i>Panolis</i>	<i>flammea</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Paradrina</i>	<i>clavipalpis</i>	(Scopoli, 1763)	Noctuidae	grassland (steppe and meadow) species
<i>Paradrina</i>	<i>selini</i>	(Boisduval, 1840)	Noctuidae	grassland (steppe and meadow) species
<i>Parascotia</i>	<i>fuliginaria</i>	(Linnaeus, 1761)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Parastichtis</i>	<i>suspecta</i>	(Huebner, [1817])	Noctuidae	wetland (and wet meadow) species
<i>Parastichtis</i>	<i>ypsillon</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Pareulype</i>	<i>berberata</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Pasiphila</i>	<i>chloerata</i>	(Mabille, 1870)	Geometridae	forest-steppe species
	<i>Pasiphila</i>			
	<i>rectangulata</i>			
<i>Pelurga</i>	<i>comitata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Peribatodes</i>	<i>rhomboidearius</i>	(Linnaeus, 1758)	Geometridae	grassland (steppe and meadow) species
<i>Perigrappa</i>	<i>munda</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Perizoma</i>	<i>alchemillatum</i>	(Linnaeus, 1758)	Geometridae	forest-steppe species
<i>Perizoma</i>	<i>bifaciatum</i>	(Haworth, [1809])	Geometridae	grassland (steppe and meadow) species
<i>Perizoma</i>	<i>blandiatum</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Perizoma</i>	<i>flavofasciatum</i>	(Thunberg, 1792)	Geometridae	forest-steppe species
<i>Phalera</i>	<i>bucephala</i>	(Linnaeus, 1758)	Notodontidae	forest species feeding on trees/ shrubs
<i>Pheosia</i>	<i>gnoma</i>	(Fabricius, 1776)	Notodontidae	forest species feeding on trees/ shrubs
<i>Pheosia</i>	<i>tremula</i>	(Clerck, 1759)	Notodontidae	forest species feeding on trees/ shrubs
<i>Philereme</i>	<i>transversata</i>	(Hufnagel, 1767)	Geometridae	forest-steppe species
<i>Philereme</i>	<i>vetulata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Phlogophora</i>	<i>meticulosa</i>	(Linnaeus, 1758)	Noctuidae	forest-steppe species
<i>Phragmatobia</i>	<i>fuliginosa</i>	(Linnaeus, 1758)	Arctiidae	forest species with relationship to woodland herbs and lichens
<i>Phytometra</i>	<i>viridaria</i>	(Clerck, 1759)	Noctuidae	grassland (steppe and meadow) species
<i>Plagodis</i>	<i>dolabraria</i>	(Linnaeus, 1767)	Geometridae	forest species feeding on trees/ shrubs
<i>Plemyria</i>	<i>rubiginata</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest species feeding on trees/ shrubs

<i>Plusia</i>	<i>festucae</i>	(Linnaeus, 1758)	Noctuidae	wetland (and wet meadow) species
<i>Poecilocampa</i>	<i>populi</i>	(Linnaeus, 1758)	Lasiocampidae	forest species feeding on trees/ shrubs
<i>Polia</i>	<i>nebulosa</i>	(Hufnagel, 1766)	Noctuidae	forest-steppe species
<i>Polia</i>	<i>bombycina</i>	(Hufnagel, 1766)	Noctuidae	forest-steppe species
<i>Polymixis</i>	<i>xanthomista</i>	(Huebner, [1819])	Noctuidae	grassland (steppe and meadow) species
<i>Polyponon</i>	<i>tentacularius</i>	(Linnaeus, 1758)	Noctuidae	grassland (steppe and meadow) species
<i>Proserpina</i>	<i>proserpina</i>	(Pallas, 1772)	Sphingidae	grassland (steppe and meadow) species
<i>Pseudoips</i>	<i>prasinana</i>	(Linnaeus, 1758)	Nolidae	forest species feeding on trees/ shrubs
<i>Pterostoma</i>	<i>palpina</i>	(Clerck, 1759)	Notodontidae	forest species feeding on trees/ shrubs
<i>Ptilodon</i>	<i>capucina</i>	(Linnaeus, 1758)	Notodontidae	forest species feeding on trees/ shrubs
<i>Pyrrhia</i>	<i>umbra</i>	(Hufnagel, 1766)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Rhizedra</i>	<i>lutosa</i>	(Huebner, [1803])	Noctuidae	wetland (and wet meadow) species
<i>Rhodostrophia</i>	<i>vibicaria</i>	(Clerck, 1759)	Geometridae	grassland (steppe and meadow) species
<i>Rivula</i>	<i>sericealis</i>	(Scopoli, 1763)	Noctuidae	grassland (steppe and meadow) species
<i>Rusina</i>	<i>ferruginea</i>	(Esper, [1785])	Noctuidae	forest-steppe species
<i>Scoliopteryx</i>	<i>libatrix</i>	(Linnaeus, 1758)	Noctuidae	wetland (and wet meadow) species
<i>Scopula</i>	<i>marginepunctata</i>	(Goeze, 1781)	Geometridae	grassland (steppe and meadow) species
<i>Scopula</i>	<i>ornata</i>	(Scopoli, 1763)	Geometridae	grassland (steppe and meadow) species
<i>Scopula</i>	<i>rubiginata</i>	(Hufnagel, 1767)	Geometridae	grassland (steppe and meadow) species
<i>Selenia</i>	<i>dentaria</i>	(Fabricius, 1775)	Geometridae	forest-steppe species
<i>Selenia</i>	<i>lunularia</i>	(Huebner, [1788])	Geometridae	forest-steppe species
<i>Selenia</i>	<i>tetralunaria</i>	(Hufnagel, 1767)	Geometridae	forest-steppe species
<i>Shargacucullia</i>	<i>verbasci</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Sideridis</i>	<i>reticulatus</i>	(Goeze, 1781)	Noctuidae	grassland (steppe and meadow) species
<i>Sideridis</i>	<i>rivularis</i>	(Fabricius, 1775)	Noctuidae	forest-steppe species
<i>Sideridis</i>	<i>turbida</i>	(Esper, 1790)	Noctuidae	grassland (steppe and meadow) species
<i>Siona</i>	<i>lineata</i>	(Scopoli, 1763)	Geometridae	non-specialized (ubiquistic) species
<i>Smerinthus</i>	<i>ocellatus</i>	(Linnaeus, 1758)	Sphingidae	forest species feeding on trees/ shrubs
<i>Sphinx</i>	<i>ligustri</i>	Linnaeus, 1758	Sphingidae	forest-steppe species
<i>Sphinx</i>	<i>pinastri</i>	Linnaeus, 1758	Sphingidae	forest species feeding on trees/ shrubs
<i>Spilosoma</i>	<i>lubricipeda</i>	(Linnaeus, 1758)	Arctiidae	grassland (steppe and meadow) species
<i>Spilosoma</i>	<i>luteum</i>	(Hufnagel, 1766)	Arctiidae	grassland (steppe and meadow) species
<i>Spilosoma</i>	<i>urticae</i>	(Esper, 1789)	Arctiidae	grassland (steppe and meadow) species
<i>Tetheella</i>	<i>fluctuosa</i>	(Huebner, [1803])	Drepanidae	forest species feeding on trees/ shrubs
<i>Thalera</i>	<i>fimbrialis</i>	(Scopoli, 1763)	Geometridae	grassland (steppe and meadow) species
<i>Thalpophila</i>	<i>matura</i>	(Hufnagel, 1766)	Noctuidae	grassland (steppe and meadow) species

<i>Thera</i>	<i>firmata</i>	(Huebner, [1822])	Geometridae	forest species feeding on trees/ shrubs
<i>Thera</i>	<i>obeliscata</i>	(Huebner, [1787])	Geometridae	forest species feeding on trees/ shrubs
<i>Thera</i>	<i>juniperata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Tholera</i>	<i>cespitis</i>	(Denis et Schiffermueller, [1775])	Noctuidae	grassland (steppe and meadow) species
<i>Tholera</i>	<i>decimalis</i>	(Poda, 1761)	Noctuidae	grassland (steppe and meadow) species
<i>Thyatira</i>	<i>batis</i>	(Linnaeus, 1758)	Drepanidae	forest species with relationship to woodland herbs and lichens
<i>Tiliacea</i>	<i>aurago</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species feeding on trees/ shrubs
<i>Tiliacea</i>	<i>citrago</i>	(Linnaeus, 1758)	Noctuidae	forest species feeding on trees/ shrubs
<i>Timandra</i>	<i>comae</i>	Schmidt, 1931	Geometridae	grassland (steppe and meadow) species
<i>Trichopteryx</i>	<i>carpinata</i>	(Borkhausen, 1794)	Geometridae	forest species feeding on trees/ shrubs
<i>Triphosa</i>	<i>dubitata</i>	(Linnaeus, 1758)	Geometridae	forest-steppe species
<i>Tyta</i>	<i>luctuosa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	early successional arable land species
<i>Watsonalla</i>	<i>binaria</i>	(Hufnagel, 1767)	Drepanidae	forest species feeding on trees/ shrubs
<i>Watsonalla</i>	<i>culturaria</i>	(Fabricius, 1775)	Drepanidae	forest species feeding on trees/ shrubs
<i>Xanthia</i>	<i>icteritia</i>	(Hufnagel, 1766)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Xanthia</i>	<i>ocellaris</i>	(Borkhausen, 1792)	Noctuidae	forest species feeding on trees/ shrubs
<i>Xanthia</i>	<i>togata</i>	(Esper, [1788])	Noctuidae	forest-steppe species
<i>Xanthorhoe</i>	<i>birviata</i>	(Borkhausen, 1794)	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Xanthorhoe</i>	<i>designata</i>	(Hufnagel, 1767)	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Xanthorhoe</i>	<i>ferrugata</i>	(Clerck, 1759)	Geometridae	non-specialized (ubiquistic) species
<i>Xanthorhoe</i>	<i>fluctuata</i>	(Linnaeus, 1758)	Geometridae	forest species feeding on trees/ shrubs
<i>Xanthorhoe</i>	<i>montanata</i>	(Denis et Schiffermueller, [1775])	Geometridae	grassland (steppe and meadow) species
<i>Xanthorhoe</i>	<i>quadrifasciata</i>	(Clerck, 1759)	Geometridae	forest-steppe species
<i>Xanthorhoe</i>	<i>spadicearia</i>	(Denis et Schiffermueller, [1775])	Geometridae	forest-steppe species
<i>Xestia</i>	<i>baja</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Xestia</i>	<i>c-nigrum</i>	(Linnaeus, 1758)	Noctuidae	early successional arable land species
<i>Xestia</i>	<i>rhomboidea</i>	(Esper, 1790)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Xestia</i>	<i>sexstrigata</i>	(Haworth, [1809])	Noctuidae	grassland (steppe and meadow) species
<i>Xestia</i>	<i>triangulum</i>	(Hufnagel, 1766)	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Xestia</i>	<i>ditrapezium</i>	(Denis et Schiffermueller, [1775])	Noctuidae	non-specialized (ubiquistic) species
<i>Xestia</i>	<i>xanthographa</i>	(Denis et Schiffermueller, [1775])	Noctuidae	forest-steppe species

Effects of life history traits on long-term population dynamics of moths

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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). A group of 81 abundant monovoltine species which had annual average catches five or more individuals was selected, and their density dependences, early fluctuations, linear decreases/increases, and concave/convex population dynamics were examined. Results were related to life histories of the moths. Eighty-three percent of the species was significantly density dependent. The probability of detection of density dependence increased with decreasing population fluctuation, independently of life histories of the individual species. Eleven species significantly decreased and was mostly prone to high population fluctuation, while only six species significantly increased. It is concluded that density dependence, at least to some extent, most probably influences population dynamic of all species, and that the highly fluctuating species are most liable to local extinctions.

Introduction

Important questions in population ecology are why and how much a population fluctuates, how much is the population regulated and which is a trend of its population dynamic. Since Nicholson (1933), Solomon (1949), Andrewartha & Birch (1954) and Morris (1959) first studied population dynamics there have been two trends in interpretation. The first stresses the disturbing influence of density independent environmental factors (Andrewartha 1957, Birch 1957, Dempster 1983, Den Boer 1988, 1990, Den Boer & Reddingius 1989) the second the stabilising influence of density dependent mechanisms (Varley et al. 1973, Hassell 1975, Bellows 1981, Royama 1984, Latto & Hassell 1987, Latto & Bernstein 1990, Turchin 1990), and there is an ongoing discussion between representatives of both opinions (e.g. Berryman 1987, 1991, 1998, Wolda 1989, 1991, Sinclair 1989, Wolda & Dennis 1993, Holyoak & Lawton 1993, Jarošík & Dixon 1999).

Three problems confound a real understanding of population dynamics: (1) a paucity of high-quality, long-term population data (Hassell et al. 1989, Woiwod & Hanski 1992, Holyoak & Lawton 1993), (2) absence of a reliable method of detecting density dependence, in spite of the effort of many authors (Varley & Gradwell 1960, Solomon 1964, Maelzer 1970, St Amant 1970, Bulmer 1975, Slade 1977, Vickery & Nudds 1984, Bernstein 1985, Gaston & Lawton 1987, Pollard et al. 1987, Reddingius & den Boer 1989, Turchin 1990, Vickery 1991, Turchin & Taylor 1992, Crowley 1992, Holyoak 1993, 1994, Holyoak & Crowley 1993, Dennis & Taper 1994, Shenk et al. 1998, Lele 2006), and (3) a preoccupation with extracting deterministic dynamics from the data, which may obscure the ultimate aim: to identify the nature of real-world dynamic processes (Kindlmann & Dixon 1995, Dixon et al. 1996, Sequeira & Dixon, 1997).

Most studies in which populations have been monitored over several generations show fluctuations in population size, but around some characteristic level of abundance. Clearly, some kind of negative density dependent feedback process must be involved in the dynamics of such populations, i.e. there must be some actions of repressive environmental factors which intensify as the population density increases and relax as this density falls (Huffaker & Messenger 1964). Identifying these feedback process by teasing out the density dependent signal from the environmental noise, and explaining just how they operate, is of fundamental importance. Only then can such practical applications as harvesting of renewable resources, epidemiology, conservation of species and pest control be properly addressed on a truly scientific basis (Hassell et al. 1989).

This study analyse a long-term, highly reliable set of data on 81 species of moths that were monitored for 26 years (Novák 1983, Holyoak et al. 1997). This large set of analysed species enables to compare their life-history traits with their population dynamics by detecting their density dependences, level of seasonal fluctuation, linear decreases/increases and concave/convex population dynamics over time. This approach then enables to ask clear biological questions: (1) Are there groups of species that have a similar population dynamics based on their biology? (2) What are the common biological characteristics of the species with significant density dependence? (3) Do we recognise groups of species reacting in the same way to environmental changes and are they biologically related?

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 a dendrological park with a collection of deciduous trees and shrubs (2.7 ha), further surrounded by arable land (77.5 ha). In a larger distance, 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 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.

The trap has been operating consistently throughout the growing seasons (March-November), from 1967 to 1992, and the catches were sorted to species by IN. Yearly catches of all species belonging to families of traditional “macrolepidoptera” (i.e., the monophyletic Macrolepidopteran *sensu* Kristensen et al. 2007, plus primitive Hepialidae), which are available for 23 years, are analyzed here. Catches from 1977-1979, when only 19 most abundant species were monitored, are excluded from this analysis. For further analyses, we selected a group of 81 monovoltine (i.e. having one generation per year) abundant species, which had annual average catches five or more individuals (Table 1). The selection of abundant species should remove those with large occurrence of zeros in the data (Woiwod and Hanski, 1992), and eliminate the influence of random effects (scarce species and random catches stray individuals from distant habitats). The selection of monovoltine species was done for correct testing of density dependence, as species tested for density dependence should be monovoltine and semelparous (Murdoch & Walde 1989).

The Bulmer’s (1975) test statistic of density dependence, based on the first-order serial correlation, was used for testing density dependence. Its value, for natural *log* of population density, $\ln N_t = X_t$, in census data N_1, N_2, \dots, N_n where N are population densities in 1, 2, ... n seasons, is

$$R = \frac{V}{U} \quad (1), \text{ where}$$

$$U = \sum_{i=1}^{n-1} (X_{i+1} - X_i)^2$$

$$V = \sum_{i=1}^n (X_i - X^*)^2 \text{ and}$$

$$X^* = \sum_{i=1}^n \frac{X_i}{n}$$

The null hypothesis on density independence is rejected for small values of R ; critical P -values are listed in Bulmer (1975). For correct use of the test, 62 species from the group of 81 monovoltine species, which had no population trends, was chosen, as testing density dependence by Bulmer’s (1975) test is inefficient for data with trends (Slade 1977, Vickery and Nudds 1984). The trends were tested by linear and quadratic regression in S-Plus v. 6 (Insightful Corp. 2003).

Results for density dependence and trends were related to the following life-history traits of individual species:

- level of population fluctuation: measured as standard deviation of natural *log* +1 of population abundance in individual years of monitoring;
- abundance: measured as mean for natural *log* +1 of population abundance in individual years, and as a dichotomous categorical variable (yes/no) for categories low/ intermediate/high abundance;
- habitat associations: dichotomous variable for habitat categories steppe/meadow/marsh/floodplain forest/oak forest/ coniferous forest/arable land/orchard/park/generalist;
- taxonomy: Noctuidae/Geometridae;
- size: wingspan and egg size (mm);

- fecundity (yes/no): tens/hundreds/thousands of eggs;
- flight period: dichotomous variable with selected months when the species on wings;
- altitude: dichotomous variable lowland (up to 400 m a.s.l.)/mountain (800-1000 m a.s.l.)/both lowland and mountain species;
- food specialization: dichotomous variable specifying whether imago takes/does not take food; caterpillar is endophagous/exophagous; caterpillar eats leaf/stems/flowers/flowers and buds/fruits/wood/roots, tubers and bulbs; caterpillar is monophagous on herbs/monophagous on shrubs and trees/oligophagous on herbs/oligophagous on shrubs and trees/oligophagous on wetland plants/polyphagous on herbs/polyphagous on shrubs and trees/polyphagous on vascular plants; caterpillar eats mosses and lichens/withered and decomposed plants/animals;
- migrant: no/yes/occasional;
- dormancy: diapause in egg/caterpillar/pupa/imago stage; hibernation in egg/caterpillar/pupa/imago stage; aestivation in egg/caterpillar/pupa/imago stage
- life-history according to population dynamic: r/K/K-r
- eggs laid: separately/in small (< 20 eggs)/large loads;
- tendency to outbreaks: yes/no
- caterpillars' aggregation: solitary/aggregated in nests.

The relationships of population trends and density dependence to the life history traits were analysed by classification trees. Density dependence (yes/no), linear (positive/none/negative) and quadratic (convex/concave/none) trends were the response variables, and the life-history traits explanatory variables. The trees were constructed by binary recursive partitioning in CART v. 6.0 (Breiman et al. 1984, Steinberg & Colla 1995), which uses the most reliable pruning strategy of over-growing trees, ensuring that any important tree structure is not overlooked. To find the optimal tree, a sequence of nested trees of decreasing size, each of them being the best of all trees of its size, were constructed, and their resubstitution relative errors were estimated. A random subset of the data (a test subset), comprising approximately 20% of all the data, was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the minimum cost tree was selected as the optimal tree (Steinberg & Colla 1995). Following De'ath & Fabricius (2000), a series of 50 cross-validations were run, and the modal (most likely) single tree was chosen for description. The quality of the best single classification tree was evaluated by its misclassification rate, i.e. by comparing the misclassification rate of this best model with misclassification rate of the null model (De'ath & Fabricius 2000). The best trees were represented graphically, with the root Node 1 standing for undivided data at the top, and the terminal nodes, describing the homogeneous groups of data, at the bottom of the hierarchy. To prevent missing explanatory variables to have an advantage as splitters, the explanatory variables were penalized in proportion to the degree to which they were missing, and treated by back-up rules that closely mimicked the action of the primary splitters.

Classification trees appeared ideally suited for these analyses, due to their flexibility and robustness, invariance to monotonic transformations of predictor variables, their ability to use combinations of explanatory variables that are categorical and/or numeric, to deal with nonlinear relationships, high order interactions and missing values that appeared for some of the explanatory variables and, despite all these analytical difficulties, their capability to give easily understandable and interpretable results, providing a highly intuitive insight into the kinds of interactions between the explanatory variables (De'ath & Fabricius 2000, Chytrý et al. 2008).

Results

Eighty-three percent of 62 species without trends, which were analysed by Bulmer's test of density dependence, appeared to have significant density dependence in their population dynamics (Table 1). None of the life history traits was able to explain which traits are responsible for the density dependence, except that the strength of density dependence was indirectly related to population fluctuation (Fig. 1). All significantly density dependent species had a standard deviation of log transformed population dynamic less than 0.74. This means that density dependent species fluctuated less than density independent species.

Of eighty-one abundant monovoltine species, eleven species significantly decreased and only six significantly increased over the monitoring period (Table 1). The decreasing species *Agrochloa circellaris*, *A. lychnidis*, *Agrotis ipsilon*, *Cidaria fulvata*, *Ennomos autumnarius*, *Eulithis prunata*, *E. pyraliata*, *Hydraecia micacea* and *Lacanobia w-latinum* highly fluctuated in time, and the two remaining species with decreasing trend *Apamea sordens* and *Oligia latruncula* were characterised by hibernating caterpillars. The increasing species *Euxoa aquilina*, *Hoplodrina octogenaria*, *Mythimna comma*, *M. ferrago*, *Opisthoptis luteolata* and *Thalpophila matura* were characterized by hibernating caterpillars (Figure 2).

Of the six species with concave population dynamic (Table 1), suggesting the highest abundance at the mid of the monitoring period, four (*Euxoa nigricans*, *E. aquilina*, *Mythimna comma* and *Opisthoptis luteolata*) laid small load eggs; the remaining two either little fluctuated (*Hoplodrina alsines*) or were little abundant (*Thalpophila matura*). The nine species with convex population dynamic (*Agrochloa lychnidis*, *Agrotis ipsilon*, *Apamea sordens*, *Ennomos autumnarius*, *Hydraecia micacea*, *Lacanobia w-latinum*, *Luperina testacea*, *Oligia latruncula* and *O. strigilis*, Table 1) had a tendency to a large population fluctuation and a large abundance (Figure 3).

Discussion

The fact that the probability of detection of density dependence increases with decreasing population fluctuation is not surprising. This is so because density dependence is responsible for population regulation, which, in turn, is manifested by dumping population fluctuation. The relationship between increasing density dependence and decreasing population fluctuation is directly incorporated in the structure of the Bulmer's (1975) test of density dependence: in Bulmer's test statistic (1), small value of R , for which the null hypothesis on density independence is rejected, means that numerator V in the equation (1), which describe average fluctuation around characteristic level of abundance X^* , is proportionally small comparing to the denominator U , which describe fluctuation between population densities in X_{i+1} and X_i season. In other words, in case of density dependence the fluctuation around some characteristic level of abundance X^* is small because of small values of X_{i+1} in the denominator U are followed by large values of X_i and vice versa, which is a consequence of a regulatory process.

More interesting is thus the fact that significant density dependence in population dynamic appeared rather a rule than exception, independently on population trends and all the other life histories of the individual species than is the level of population fluctuation. This result strongly suggests that density dependence, at least to some extent, influences population dynamic of all the examined species. It is consistent with the previous results on population dynamics of moths from light traps. Woiwod and Hanski (1992) detected significant density dependence in 79% of moth species by Bulmer's (1975) test. However, unlike our study, in noctuids the average degree of density dependence increased with body size.

That the density dependence was not detected in all species is affected by the fact that there is not a method which is reliably able to detect density dependence in census data,

independently on sample size and a type of population dynamic (e.g. Gaston & Lawton 1987, Pollard et al. 1987, Hassell et al. 1989, Turchin 1990, Shenk et al. 1998, Lele 2006). For instance, Dempster (1983) argued that density dependence was not detected in one third of life-table studies of butterflies and moths, but additional studies were able to detect density dependence in many of these studies (Sinclair 1989). Strong et al. (1984) were unable to detect density dependence in 11 of 31 studies on phytophagous insects, but a detail later study (Southwood et al. 1989) revealed density dependence in one of these cases. Stilling (1988), in review of life-table studies of insects, found density dependence for only about a half of cases, but Hassell et al. (1989) were able to find density dependence for most of these studies.

Similarly to density dependence, also the population trends were largely independent on life history traits of the individual species. Only the level of population fluctuation, average abundance, hibernating stage and egg load appeared significant determinants of population trends in time.

The percentage of decreasing species was about double that of displaying increases, similarly to results on population dynamics of moths from light traps in Great Britain (Conrad et al. 2004). All but two species with significantly decreasing trend highly fluctuated. This result suggests that decreasing species are more prone to high population fluctuation than other species, which in turn may increase their chance to local extinction. This is so because species with high population fluctuations are less regulated than species with low fluctuations, and these unregulated populations are more prone to extinctions than those which are strictly regulated (Reddingius 1971, Strong 1984). In case of a local decrease of a highly fluctuated species, its fluctuation thus can largely increase its extinction chance.

All significantly increasing species, but also two decreasing species, had hibernating caterpillars. Species with concave population dynamic often laid small egg loads and species with convex dynamic tended to fluctuate and be abundant. These traits however could hardly play an important role in the population dynamics per se. More important are probably interactions with habitat changes, which are related mainly to species' habitat associations (Table 1).

Some of the forest-steppe species can have a tendency to population increase due to gradual changes of grasslands into forest-steppe habitats (Kadlec et al. 2008). This can be the case for increase of *Mythimna ferrago*, feeding on grasses but living mainly in forest-steppe habitats. Conversely, the decrease of grassland habitats can be the cause of decline in grassland species *Cidaria fulvata*, *Eulithis pyraliata* and *E. prunata*. The decrease of *Hydraecia micacea*, and probably also of *Agrochloa circellaris* and *Ennomos autumnarius*, is related to the destruction of wetland habitats. The revealed concave and convex trends in species abundance concern mainly non-specialized ruderal species. Their peaks or troughs in population dynamics in the mid of the monitoring period thus can be attributed mainly to successional changes in availability of their food plants after abundance of small patches of arable land in the vicinity of the light trap at the beginning of the monitoring period.

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Table 1. Population trends, and density-dependence tests for monovoltine moth species without trends (Bulmer's P) which had annual average catches five or more individuals. P-values of Bulmer's (1975) test smaller than 0.05 indicate significant density dependence. Guilds describe habitat specialization of the species following Fajčík (1998, 2003). Nomenclature of species follows Laštůvka and Liška (2005).

Genus	Species	Author and year of description	Bulmer's		Polynomial trend	Family	Guild
			P	trend			
<i>Agrochola</i>	<i>circellaris</i>	(Hufnagel, 1766)		negative	none	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>litura</i>	(Linnaeus, 1761)	0.021	none	none	Noctuidae	forest-steppe species
<i>Agrochola</i>	<i>lychnidis</i>	(Denis et Schiffermueller, [1775])		negative	convex	Noctuidae	non-specialized (ubiquistic) species
<i>Agrochola</i>	<i>macilenta</i>	(Huebner, [1809])	0.032	none	None	Noctuidae	forest species feeding on trees/ shrubs
<i>Agrochola</i>	<i>nitida</i>	(Denis et Schiffermueller, [1775])	0.208	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Agrotis</i>	<i>clavis</i>	(Hufnagel, 1766)	0.032	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Agrotis</i>	<i>exclamationis</i>	(Linnaeus, 1758)	0.011	none	none	Noctuidae	early successional arable land species
<i>Agrotis</i>	<i>ipsilon</i>	(Hufnagel, 1766)		negative	convex	Noctuidae	early successional arable land species
<i>Agrotis</i>	<i>segetum</i>	(Denis et Schiffermueller, [1775])	0.020	none	none	Noctuidae	early successional arable land species
<i>Amphipoea</i>	<i>fucosa</i>	(Freyer, 1830)	0.019	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>anceps</i>	(Denis et Schiffermueller, [1775])	0.031	none	none	Noctuidae	early successional arable land species
<i>Apamea</i>	<i>lateritia</i>	(Hufnagel, 1766)	0.063	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>lithoxyloa</i>	(Denis et Schiffermueller, [1775])	0.028	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>monoglypha</i>	(Hufnagel, 1766)	0.011	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Apamea</i>	<i>sordens</i>	(Hufnagel, 1766)		negative	convex	Noctuidae	early successional arable land species
<i>Axylla</i>	<i>putris</i>	(Linnaeus, 1761)	0.021	none	none	Noctuidae	forest-steppe species
<i>Biston</i>	<i>betularius</i>	(Linnaeus, 1758)	0.015	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Cabera</i>	<i>pusaria</i>	(Linnaeus, 1758)		none	none	Geometridae	forest species with relationship to woodland herbs and lichens
<i>Camptogramma</i>	<i>bilineatum</i>	(Linnaeus, 1758)	0.032	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Caradrina</i>	<i>morpheus</i>	(Hufnagel, 1766)	0.019	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Cerastis</i>	<i>rubricosa</i>	(Denis et Schiffermueller, [1775])	0.026	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Cidaria</i>	<i>fulvata</i>	(Forster, 1771)		negative	none	Geometridae	grassland (steppe and meadow) species
<i>Cleora</i>	<i>cinctaria</i>	(Denis et Schiffermueller, [1775])	0.026	none	none	Geometridae	grassland (steppe and meadow) species
<i>Colotois</i>	<i>pennaria</i>	(Linnaeus, 1761)	0.027	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Osmia</i>	<i>trapezina</i>	(Linnaeus, 1758)	0.082	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Cucullia</i>	<i>fraudatrix</i>	Eversmann, 1837	0.075	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Cucullia</i>	<i>umbratica</i>	(Linnaeus, 1758)	0.012	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Egira</i>	<i>conspicillaris</i>	(Linnaeus, 1758)	0.026	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens

<i>Ennomos</i>	<i>aliniarius</i>	(Linnaeus, 1758)	0.036	none	none	Geometridae	forest-steppe species
<i>Ennomos</i>	<i>autumnarius</i>	(Werneburg, 1859)		negative	convex	Geometridae	forest species feeding on trees/ shrubs
<i>Ennomos</i>	<i>fuscanitarius</i>	(Haworth, 1809)	0.055	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Eulithis</i>	<i>prunata</i>	(Linnaeus, 1758)		negative	none	Geometridae	forest-steppe species
<i>Eulithis</i>	<i>pyraliata</i>	(Denis et Schiffermueller, [1775])	0.043	negative	none	Geometridae	grassland (steppe and meadow) species
<i>Eupithecia</i>	<i>intricata</i>	(Zetterstedt, [1839])	0.029	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Eupithecia</i>	<i>succenturiata</i>	(Linnaeus, 1758)		none	none	Geometridae	grassland (steppe and meadow) species
<i>Euxoa</i>	<i>aquilina</i>	(Denis et Schiffermueller, [1775])	0.032	positive	concave	Noctuidae	early successional arable land species
<i>Euxoa</i>	<i>nigricans</i>	(Linnaeus, 1761)	0.019	none	concave	Noctuidae	grassland (steppe and meadow) species
<i>Graphiphora</i>	<i>augur</i>	(Fabricius, 1775)	0.047	none	none	Noctuidae	forest-steppe species
<i>Heliothobus</i>	<i>reticulatus</i>	(Goeze, 1781)		none	none	Noctuidae	grassland (steppe and meadow) species
<i>Hoplodrina</i>	<i>octogenaria</i>	(Goeze, 1781)		positive	concave	Noctuidae	non-specialized (ubiquistic) species
<i>Hoplodrina</i>	<i>blanda</i>	(Denis et Schiffermueller, [1775])	0.030	none	concave	Noctuidae	non-specialized (ubiquistic) species
<i>Hydraecia</i>	<i>micacea</i>	(Esper, [1789])		negative	convex	Noctuidae	wetland (and wet meadow) species
<i>Charanyca</i>	<i>trigrammica</i>	(Hufnagel, 1766)	0.113	none	none	Noctuidae	grassland (steppe and meadow) species
<i>Chloroclystis</i>	<i>rectangulata</i>	(Linnaeus, 1758)	0.021	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Idea</i>	<i>aversata</i>	(Linnaeus, 1758)	0.044	none	none	Geometridae	forest-steppe species
<i>Ipirorpha</i>	<i>subtusa</i>	(Denis et Schiffermueller, [1775])	0.018	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Lacanobia</i>	<i>thalassina</i>	(Hufnagel, 1766)	0.039	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Lacanobia</i>	<i>w-latinum</i>	(Hufnagel, 1766)		negative	convex	Noctuidae	early successional arable land species
<i>Luperina</i>	<i>testacea</i>	(Denis et Schiffermueller, [1775])		none	convex	Noctuidae	grassland (steppe and meadow) species
<i>Macaria</i>	<i>liturata</i>	(Clerck, 1759)	0.033	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Macaria</i>	<i>wauaria</i>	(Linnaeus, 1758)	0.018	none	none	Geometridae	forest species feeding on trees/ shrubs
<i>Melanchnra</i>	<i>persicariae</i>	(Linnaeus, 1761)	0.042	none	none	Noctuidae	early successional arable land species
<i>Mythimna</i>	<i>comma</i>	(Linnaeus, 1761)		positive	concave	Noctuidae	grassland (steppe and meadow) species
<i>Mythimna</i>	<i>conigera</i>	(Denis et Schiffermueller, [1775])	0.022	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens
<i>Mythimna</i>	<i>ferrago</i>	(Fabricius, 1787)		positive	none	Noctuidae	forest-steppe species
<i>Noctua</i>	<i>comes</i>	Huebner, [1813]	0.201	none	none	Noctuidae	forest-steppe species
<i>Noctua</i>	<i>fimbriata</i>	(Schreber, 1759)	0.017	none	none	Noctuidae	forest-steppe species
<i>Noctua</i>	<i>janthina</i>	(Denis et Schiffermueller, [1775])	0.018	none	none	Noctuidae	forest-steppe species
<i>Noctua</i>	<i>pronuba</i>	(Linnaeus, 1758)	0.016	none	none	Noctuidae	early successional arable land species
<i>Oligia</i>	<i>furuncula</i>	(Denis et Schiffermueller, [1775])	0.029	none	none	Noctuidae	grassland (steppe and meadow) species

<i>Oligia</i>	<i>latruncula</i>	(Denis et Schiffermueller, [1775])		negative	convex	Noctuidae	non-specialized (ubiquistic) species				
<i>Oligia</i>	<i>strigilis</i>	(Linnaeus, 1758)	0.029	none	convex	Noctuidae	grassland (steppe and meadow) species				
<i>Opisthographpis</i>	<i>luteolata</i>	(Linnaeus, 1758)	0.068	positive	concave	Geometridae	forest species feeding on trees/ shrubs				
<i>Orthosia</i>	<i>cerasi</i>	(Fabricius, 1775)	0.02	none	none	Noctuidae	forest species feeding on trees/ shrubs				
<i>Orthosia</i>	<i>gothica</i>	(Linnaeus, 1758)	0.017	none	none	Noctuidae	forest species feeding on trees/ shrubs				
<i>Orthosia</i>	<i>gracilis</i>	(Denis et Schiffermueller, [1775])	0.041	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens				
<i>Orthosia</i>	<i>incerta</i>	(Hufnagel, 1766)	0.030	none	none	Noctuidae	forest species feeding on trees/ shrubs				
<i>Ourapteryx</i>	<i>sambucaria</i>	(Linnaeus, 1758)	0.024	none	none	Geometridae	forest species feeding on trees/ shrubs				
<i>Pelurga</i>	<i>comitata</i>	(Linnaeus, 1758)	0.108	none	none	Geometridae	grassland (steppe and meadow) species				
<i>Polia</i>	<i>bombycina</i>	(Hufnagel, 1766)	0.010	none	none	Noctuidae	forest-steppe species				
<i>Pyrrhia</i>	<i>umbra</i>	(Hufnagel, 1766)	0.026	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens				
<i>Rheumaptera</i>	<i>cervinalis</i>	(Scopoli, 1763)		none	none	Geometridae	grassland (steppe and meadow) species				
<i>Thalpophila</i>	<i>matura</i>	(Hufnagel, 1766)		positive	concave	Noctuidae	grassland (steppe and meadow) species				
<i>Thera</i>	<i>juniperata</i>	(Linnaeus, 1758)	0.027	none	none	Noctuidae	forest species feeding on trees/ shrubs				
<i>Tholera</i>	<i>decimalis</i>	(Poda, 1761)	0.022	none	none	Geometridae	forest species feeding on trees/ shrubs				
<i>Xanthia</i>	<i>icteritia</i>	(Hufnagel, 1766)	0.008	none	none	Noctuidae	grassland (steppe and meadow) species				
<i>Xanthia</i>	<i>ocellaris</i>	(Borkhausen, 1792)	0.014	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens				
<i>Xestia</i>	<i>baja</i>	(Denis et Schiffermueller, [1775])	0.029	none	none	Noctuidae	forest species feeding on trees/ shrubs				
<i>Xestia</i>	<i>ditrapezium</i>	(Denis et Schiffermueller, [1775])	0.045	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens				
<i>Xestia</i>	<i>triangulum</i>	(Hufnagel, 1766)	0.015	none	none	Noctuidae	non-specialized (ubiquistic) species				
<i>Xestia</i>	<i>xanthographa</i>	(Denis et Schiffermueller, [1775])	0.065	none	none	Noctuidae	forest species with relationship to woodland herbs and lichens				

Figures

Figure 1. Index of the strength of density dependence plotted against index of population fluctuation. The index of the strength of density dependence is expressed as -1 times the logit transformed probability of detection of density dependence by Bulmer's (1975) test, and the index of population fluctuation as a standard deviation of log-transformed $+1$ yearly catches of individual species. Larger indices mean, respectively, more likely detection of density dependence and larger population fluctuation. Density dependence = $4.82 - 1.90$ population fluctuation. $F = 33.33$; $df = 1, 58$; $P < 0.001$; $R^2 = 0.36$.

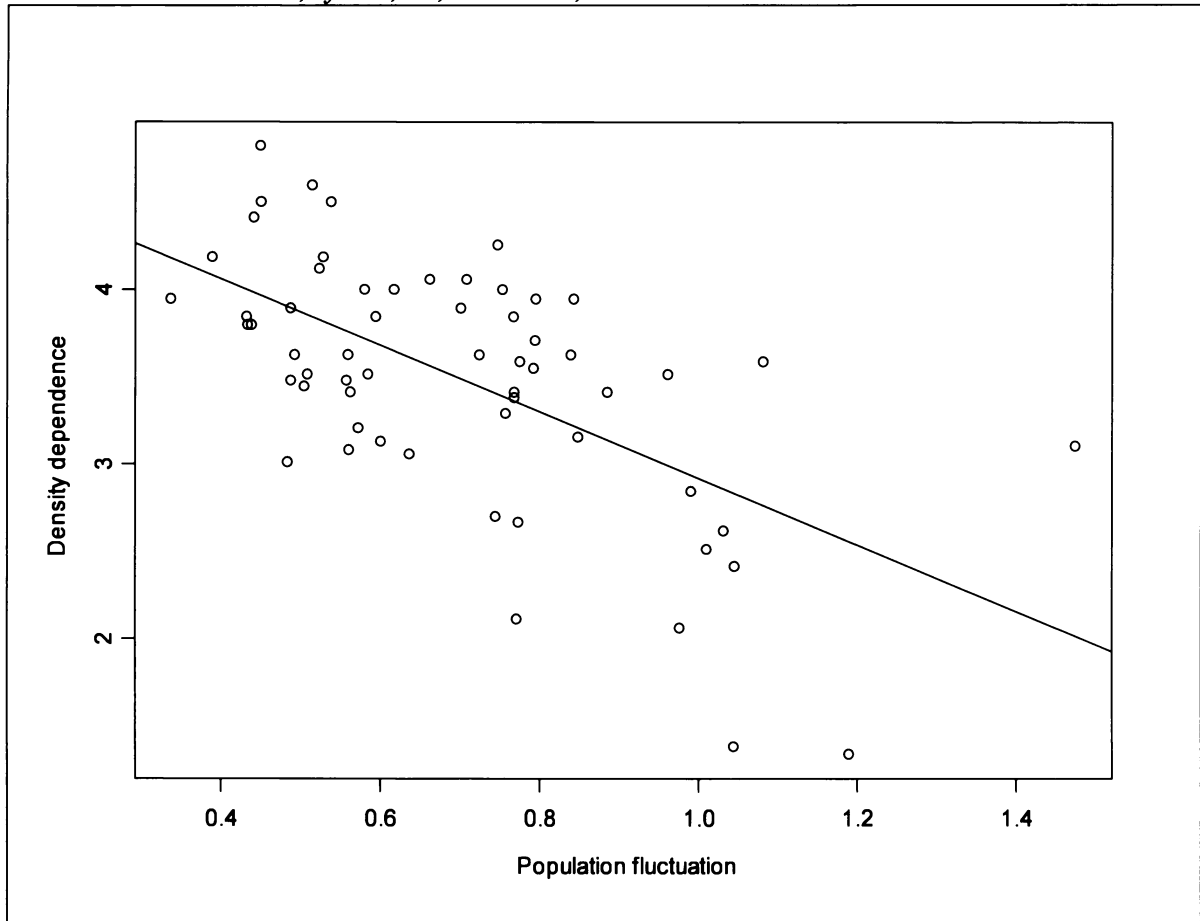


Figure 2. Classification tree analysis of the negative (red Class -1), positive (green Class 1) and no (blue Class 0) linear trend in population dynamic of 81 monovoltine moth species. Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion and number of cases of negative, none and positive trends. Code (0) of a splitting variable means no, code (1) yes. The splitting variable STANDARD_DEVIATION characterize population fluctuation – large values mean large population fluctuation. The misclassification rate for the negative trend is 18.1% (two misclass cases of eleven) and zero for the positive trend (no misclass cases of six), compared to misclassification rate 33.3% for the null model (guessing the probabilities of the negative, positive and none trend being equal, i.e. 33.3%).

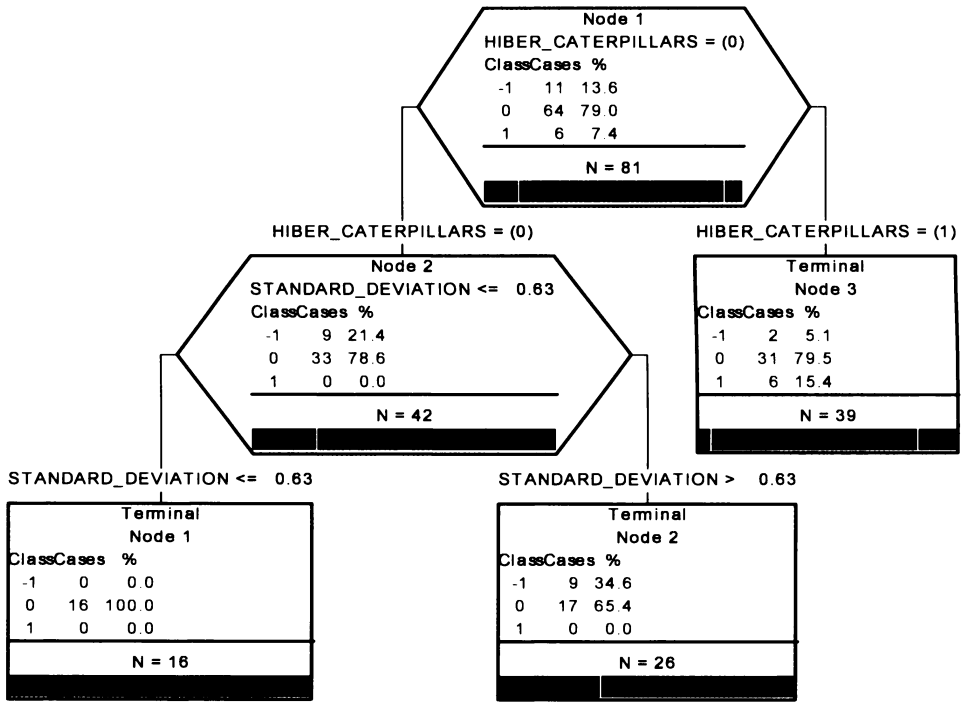
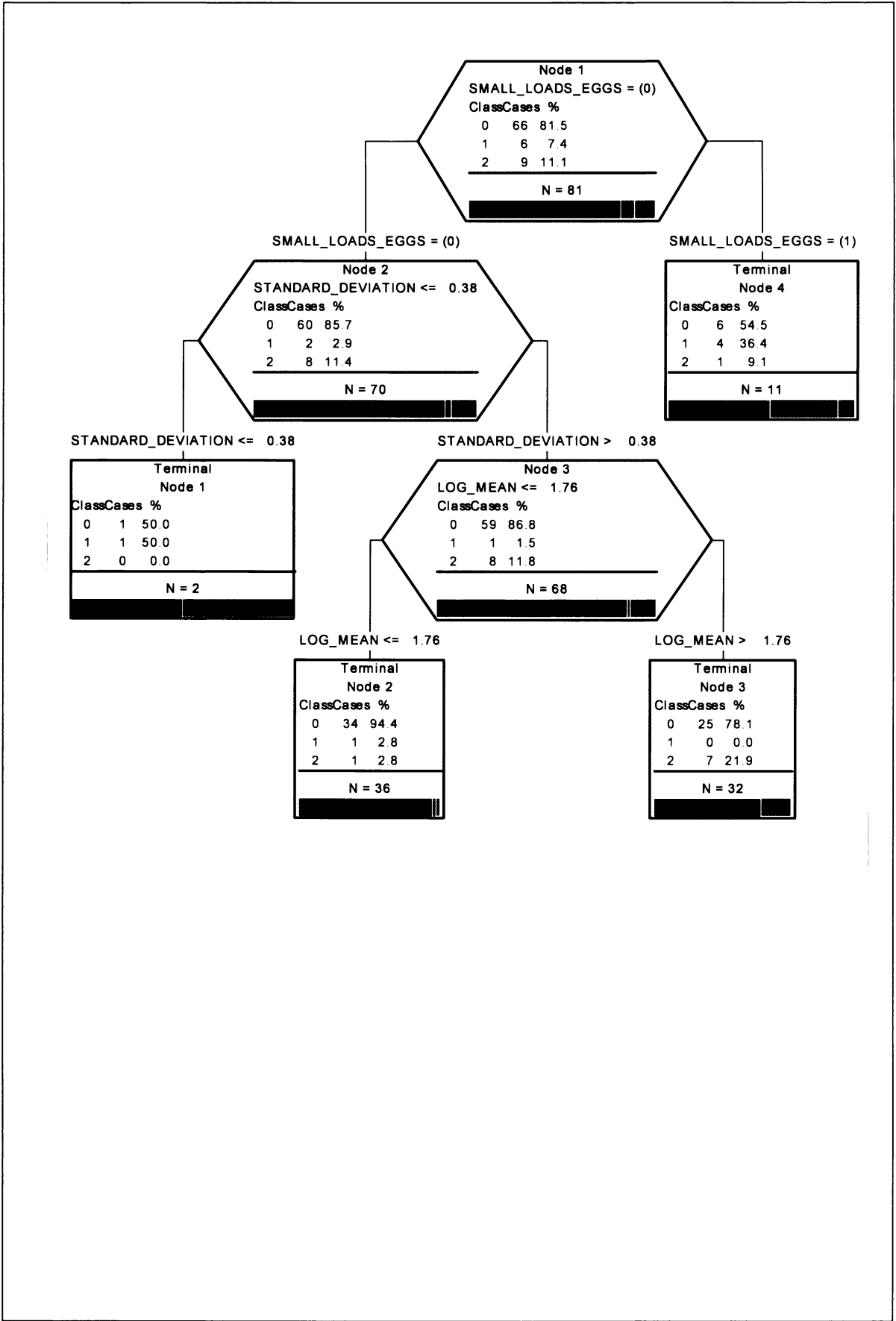


Figure 3. Classification tree analysis of the concave (blue Class 1), convex (green Class 2) and no (red Class 0) quadratic trends in population dynamic of 81 monovoltine moth species. Each node (polygonal table) and terminal node (rectangular table) shows node number, splitting variable name, split criterion and number of cases of negative, none and positive trends. Code (0) of a splitting variable means no, code (1) yes. The splitting variable STANDARD_DEVIATION characterize population fluctuation – large values mean large population fluctuation, and LOG_MEAN (average of log-transformed+1 yearly catches of individual species) characterize population abundance. The misclassification rate for the concave trend is 16.7% (one misclass case of six) and 22.2% for the convex trend (two misclass cases of nine), compared to misclassification rate 33.3% for the null model (guessing the probabilities of the concave, convex and none trend being equal, i.e. 33.3%).



Relationship between the minimum and maximum temperatures of the thermal tolerance range in insects

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Running headline: Thermal tolerance range in insects

Summary:

1. The objective of this study was to test the theoretical prediction that the thermal tolerance range for development in insects should be about 20° C.
2. The data on the thermal requirements for development of 66 species from 8 orders of insects was obtained from the literature. The temperatures at which the developmental rates are at their minimum and maximum was obtained for each population by defining the relationship between developmental rate (1/D) and temperature, using either Lactin *et al.*'s (1995) or Brière *et al.*'s (1999) model.
3. Thermal windows, i.e. the range in temperature between the minimum and maximum rate of development for individual species, and the relationship between the minimum and maximum temperatures, were examined.
4. The mean thermal window, 19.8° C with 95% confidence interval 19.1 – 20.5 and range 13.3 – 28.6, was influenced by species phylogeny, with the windows narrower for species having a true pupal stage, but not by ecological traits thought to affect species thermal requirements. The relationship between the minimum and maximum temperatures was highly significant and independent of species phylogeny.
5. The facts that theory and this analysis of empirical data indicate that each species of insect can only develop over a limited range of temperatures independently of species traits, and that the relationship between the minimum and maximum developmental rate co-vary independently of species phylogeny may help identify the precise nature of the physiological mechanism underlying the seasonal development and distribution of insects, and possibly other ectotherms.

Key words: distribution, insects, thermal requirements for development, thermal window, thermal tolerance range, ectotherms.

Introduction

The effect of temperature on the development and growth of ectotherms has been well studied over a very long period and is extremely well reported. Nearly three hundred years ago Réaumur (1735, 1736) was already aware that there were temperatures below which organisms cannot develop and appreciated that the temperature sum required for complete growth of an organism is a constant. That is, nearly three hundred years ago the basic aspect of the relationship between ectothermic species and their thermal environment, namely the constancy of the temperature sum required by each organism for development, now usually measured in day degrees (D°), had been identified. Current physiologically based theoretical studies are mainly concerned with the effect of temperature and body size on the rates of biological processes (Gillooly *et al.* 2002; Charnov & Gillooly 2003; Brown *et al.* 2004). It is appreciated that the lower developmental thresholds of tropical species are higher than those of temperate species (Honek 1996a) and for each species there is an ecologically relevant range of temperatures over which it can grow and reproduce, its thermal window (van der Have 2002; Jarošík, Honek & Dixon 2002; Jarošík *et al.* 2004). However, neither the relationship between the temperatures at which development proceeds at the minimum and maximum rates has been studied, or the prediction that the width of the thermal window is about 20°C been tested.

Theoretical studies (Charnov & Gillooly 2003; Gillooly *et al.* 2002) suggest that the width of the thermal window for each species should be about 20°C . This can be derived from Charnov & Gillooly's (2003) assertion that for ectotherms the lower developmental threshold is about ten centigrade below the mean developmental temperature in nature (10°C rule), that the rate of development is a linear approximation to a universal exponential function reflecting underlying biochemical kinetics of metabolism, and that this exponential function causes the estimated lower developmental threshold to increase with the mean developmental temperature in nature. The consequences of the 10°C rule are that the lower developmental threshold and the temperature at which the development is fastest should be correlated, and as the mean temperature for development should be the midpoint between the temperatures for the minimum and maximum developmental rates, the expected width of the thermal window should be about 20°C , with the exact value depending on a reference middle temperature for development rate. Finally, as both these predictions are based on a thermodynamic model of development in ectotherms then the mechanism is more likely to be physiological than ecological, and might be independent of phylogenetic relationships.

The objective of this study is to determine whether in insects the difference between the temperatures when development proceeds at the minimum and maximum rates is about 20°C , whether the width of the thermal window can be modified by environmental and biological traits and species phylogeny, and whether the relationship between the minimum and maximum developmental rate temperatures is dependent on species relatedness.

Material and Methods

In ectothermic organisms, development rate increases with temperature following a sigmoidal curve when measured over the ecologically relevant range of temperatures (e.g. Wagner *et al.* 1984, Wagner, Olson & Willers 1991). A surrogate value for the lower developmental threshold, which has been widely adopted, is to use the value obtained by extrapolating the linear portion of the relationship between rate of development and temperature back to intercept the X-axis. This virtual value is referred to in the literature as LDT or basal temperature (t_b) (e.g. Jarošík, Honek & Dixon 2002, Trudgill, Honek & Van Straalen 2005). At the higher temperatures the slope of the curve decreases, reaches a maximum and then decreases. The point of the maximum development rate is referred to as the optimum temperature (t_o) (Trudgill, Honek & Van Straalen 2005) or maximum temperature (t_{dmax}) (Birkemoe & Leinaas 2000). Although at temperatures

greater than that at which the maximum development rate is recorded some individuals can still develop they take longer to reach maturity and many die. That is, the thermal window can be defined in terms of the temperatures at which the minimum and maximum developmental rates occur. We favour the use of t_{dmax} over t_{dopt} because optimum implies this temperature is the most favourable for the organism concerned. However, in nature organisms are subject to fluctuations in temperature and are unlikely to be adapted to doing best at one particular temperature but to optimize their performance over the range of temperatures they most frequently experience in the field. For the same reasons and conformity, we prefer t_{dmin} to t_b .

Several models are proposed, which describe the non-linear relationship between developmental rate and temperature (e.g. Stinner, Gutierrez & Butler 1974; Logan *et al.* 1976; Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Harcourt & Yee 1982). Nevertheless, only two, relatively recent models (Lactin *et al.* 1995, their equation 1; Brière *et al.* 1999, their modified 2nd model) are biologically realistic and simple, and enable a simultaneous fitting of a non-linear developmental response to temperature and assessment of the value of t_{dmin} . These models are used in this study to determine t_{dmin} and t_{dmax} and the width of the thermal window, the difference between these two values.

The data on the thermal requirements for development of insects used in this study mainly comes from papers published by Alois Honek and his colleagues (Honek & Kocourek 1990; Honek 1996; Jarošík, Honek & Dixon 2002; Jarošík & Honek 2007). Developmental times for at least four different constant temperatures (°C) were obtained mainly from this literature for seventy-four non-dormant (i.e. not in diapause) populations of sixty-six species, belonging to eight orders of insects. To avoid pseudo-replication of the species for which the studies were done on different morphs or genetic strains, or in different atmospheric conditions or on different host plant cultivars, the values of the temperatures for the minimum and maximum developmental rates for the morphs, strains, atmospheric conditions or cultivars were calculated separately for each population of these species, and to obtain one independent data point for each species, the average value for these populations then established. The averages for these species were not calculated directly by first pooling the results for all their populations, because temperature dependent responses usually differed among the populations of each of these species. The species analysed and their estimated lower and upper temperatures for development are listed (before calculating average t_{dmin} and t_{dmax} for those species for which several populations were analyzed) in Appendix S1 in Supplementary Material.

With a few exceptions, for which only data for one developmental stage (egg, larva or pupa) or part of the total development (e.g. larva + pupa) are available, the total pre-imaginal development (egg to adult) for each population of a species was analysed. In those cases where data is available for more than one stage but the developmental time for these stages could not be pooled (usually, data available for egg and pupa, but not for larva), the developmental stages were analyzed separately, but only the result for the stage giving the better overall fit was chosen for analysis. This selection was based on a comparison of the residual sums of squares, total explained variance (r^2) and an inspection of fitted plots of the models. That data for total development is not available for all species should not bias these analyses, as all the developmental stages of an ectotherm species have the same lower developmental threshold (Jarošík, Honek & Dixon 2002; Jarošík *et al.* 2004).

To establish the minimum and maximum temperature for development of each population, the relationship between the developmental rates and temperature, with the rate expressed as the reciprocal values of the developmental times in days (1/d), was defined using the Lactin *et al.*'s (1995) or Brière *et al.*'s (1999) model. Brière *et al.*'s model for the rate of development, r , which is a positive function of temperature, T (°C), needs only three parameters:

$$r(T) = aT(T - T_0)\sqrt{T_L - T} \quad (1)$$

where a is an empirical constant, T_0 is the lower temperature developmental threshold, i.e. the minimum temperature t_{dmin} , and T_L lethal temperature. On the other hand, Lactin *et al.*'s model needs four parameters:

$$r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} + \lambda \quad (2)$$

where ρ is the developmental rate to the maximum temperature t_{dmax} , T_{max} lethal temperature (T_L in Brière *et al.*'s model above), Δ is the width of the high temperature boundary layer (the width of the high temperature decline in developmental rate, over which thermal breakdown becomes the overriding influence), and λ is the intersection of the fitted model curve with abscissa at the lower temperatures, which is used to estimate the minimum temperature t_{dmin} .

As a consequence of the difference in the number of parameters, to have at least one degree of freedom for the parameter estimates of a fitted model all the populations for which data for only four constant temperatures were available were fitted by Brière *et al.*'s three-parameter model. For the remaining populations, Lactin *et al.*'s model was preferred, because this model gives a better overall fit than that of Brière *et al.* (Kontodimas *et al.* 2004). Both the models were fitted using the least-square non-linear Levenberg-Marquardt iterative regression method in Statistica 6.0 for Windows (StatSoft, Tulsa), with convergence criterion set to 0.00001. Values for the maximum temperatures for development were calculated analytically from the fitted models; for Brière *et al.*'s model as:

$$t_{dmax} = \frac{2mT_L + (m+1)T_0 + \sqrt{4m^2T_L^2 + (m+1)^2T_0^2 - 4m^2T_0T_L}}{4m+2} \quad (3)$$

for $m = 2$ (Brière *et al.* 1999), and for Lactin *et al.*'s model as:

$$t_{dmax} = \frac{(\rho - 1/\Delta)T_{max} - \ln(\rho\Delta)}{\rho - 1/\Delta} \quad (4)$$

(Appendix S2). Values of the minimum temperatures t_{dmin} were estimated as the intersections of the fitted curves with abscissa (Fig. 1), but can be also solved numerically, as described in Appendix S2. Parameters of the fitted models are available in Appendices S3 (Lactin *et al.*'s model) and S4 (Brière *et al.*'s model).

The widths of the thermal windows, the differences between t_{dmax} and t_{dmin} for individual species (Fig. 1), were calculated, their distribution presented in a frequency histogram, and the mean value with 95% confidence interval (CI) determined. To reveal how the thermal windows are influenced by species phylogeny and ecological traits, the variation in thermal windows was partitioned into phylogenetic and non-phylogenetic components. First, for all 66 species, a patristic distance matrix (i.e. the sum of branch lengths on a path between a pair of taxa) was derived from the tree of life web site <http://tolweb.org/tree/phylogeny.html> [except for Diptera, for which phylogenetic relationships were extracted from Yeates & Wiegman (1999), Sæther (2000) and Yeates (2002)], considering each branch length to be equal to one unit (e.g. Prinzing *et al.* 2001). A principal coordinate analysis was then performed on this matrix, using the function *cmdscale* in R Package version 2.3.1 (R Development Core Team, 2006). Each principal coordinate (called PC hereafter) of the matrix represents the relative amount of phylogenetic variance, which is proportional to the associated eigenvalue (Diniz-Filho, De Sant'ana & Bini 1998). The PCs were listed in decreasing order of explained variance, from PC1 to PC65. Their order describes decreasing phylogenetic scales, but do not distinguish the exact hierarchical contribution of the individual PCs to the phylogeny.

We then incorporated phylogenetic information encompassed in the PCs into the statistical analysis that simultaneously included ecological traits, following Desdevides *et al.* (2003; Appendix S5). The included ecological traits were (i) species dry body mass in mg (\ln transformed), calculated as $\text{mass} = (\text{body length})^{2.62}$ (Rogers, Hinds & Buschbom 1976), (ii) latitude ($^{\circ}\text{N}$ or S) from which the experimental populations originated (a surrogate for the effect

of climate; Honek 1996a) and (iii) food specialization according to Honek (1999): (a) predators, which feed on living animals, i.e. true predators and parasitoids; (b) herbivores, which feed on living plants, i.e. grazers and sap feeders; and (c) “seed eaters”, feeding on dry seeds and dead plant and animal remains, represented mostly by store product pests. All these traits are known to affect the species thermal requirements, namely lower developmental thresholds and sum of effective temperatures necessary for the completion of development of a species (Honek 1996a, b, 1999, Honek & Kocourek 1990), and the effect of latitude on the lower developmental thresholds that differ in tropical (at $\leq 23^\circ\text{N}$ or S) and subtropical or temperate zones (Honek 1996a). Body mass (Honek 1996b, Honek 1999) and food specialization (Honek 1999) are known to affect the thermal requirements of insect orders differently, and the effect of food specialization to interact with temperature data for the locations from which the tested species originated (Honek 1996a).

Incorporation of these traits enabled the partitioning of the variance in thermal windows into a part strictly due to (1) ecological traits (i.e., body size, climate and food), (2) phylogeny, (3) joint influence of phylogenetic and ecological traits (i.e., phylogenetically structured variation of ecological traits) and (4) unexplained variation (see Appendix S5 for details).

The relationship between t_{dmax} and t_{dmin} for individual species was examined by regressing t_{dmax} on t_{dmin} . Because t_{dmax} and t_{dmin} were both estimated with error, and on the same scale ($^\circ\text{C}$), major axis (MA = model II) was used instead of least square (LS = model I) regression (Sokal & Rohlf 1995); however, for comparison and generality, a LS regression and its statistics (equation, F, df, and explained variance r^2) were also calculated. For MA the regression slope, which is always greater than the LS slope, and its 95% confidence intervals (CI) were calculated, following the method of Sokal & Rohlf (1995, p. 586-593). After the analysis of the original data, the same analysis was repeated with the variation due to phylogenetic relatedness removed, in which independent contrasts (Felsenstein 1985) for incompletely resolved phylogenies (Harvey & Pagel 1991) were used on the same phylogeny as for the thermal windows. If the slope of the regression for the independent contrasts, forced through the origin, remains significant, it is evidence that the evolutionary independent comparisons yield the same overall pattern between t_{dmax} and t_{dmin} as the cross-species comparison. That is, the variation in the relationship between t_{dmax} and t_{dmin} is, in fact, independent of differences associated with phylogeny (Harvey & Pagel 1991).

Results

RANGE IN THERMAL WINDOWS

The average range of the thermal window between t_{dmin} and t_{dmax} of individual species was 19.8°C , with 95% CI $19.1 - 20.5$ and the frequency for individual species concentrated around the predicted value of 20°C (Fig. 2). The range of values was $13 - 29^\circ\text{C}$ with the extremes 13.3 [*Feltiella acarisuga* (Vallot): Diptera], 13.7 [*Chilocorus bipustulatus* (L.): Coleoptera] and 28.6 [*Aphis spiraecola* (Patch): Hemiptera] $^\circ\text{C}$ (Appendix S1).

The fraction of variation in thermal windows related to ecological traits (i.e. body mass, geographical origin, and food specialization), which include the embedded parts of phylogenetically structured variation (fractions [a+b] in Fig. 3), were significant only if geographical origin is expressed as a geographical zone, i.e. tropical vs. subtropical or temperate species origin ($F = 4.067$; $df = 1, 64$; $P = 0.048$); when the origin of the populations is expressed as latitude in $^\circ\text{N}$ or S, the whole model with all the ecological traits and their possible interactions appeared insignificant ($F = 1.673$; $df = 11, 54$; $P = 0.105$). In the former model, the effect of body mass and its interactions with zones and food specializations were insignificant (deletion test: $F = 1.239$; $df = 4, 62$; $P = 0.305$), and that of geographical zone only marginally significant ($F =$

3.123; $df = 1, 63$; $P = 0.082$), suggesting narrower windows by 2.2 °C (standard error $SE = 1.767$, $df = 62$) for species originating from the tropics compared to subtropical or temperate species. Herbivores feeding on living plants and “seed eaters” did not differ significantly in thermal windows (deletion test on factor level reduction: $F = 1.585$; $df = 1, 64$; $P = 0.213$); the only significant effect of ecological traits thus indicated that true predators and parasitoids (deletion test: $F = 4.067$; $df = 1, 64$; $P = 0.048$) have narrower windows by 1.5 °C ($SE = 0.744$, $df = 64$) than grazers, sap feeders and “seed eaters”.

However, the net effect of ecological traits (part [a] in Fig. 3) appeared insignificant ($F = 1.457$; $df = 1, 64$; $P = 0.232$), containing only a negligible portion of the variation ($r^2 = 0.6\%$; part [a] in Fig. 3); this suggests that any effect of ecological traits have to be attributed to a joint influence of phylogenetic and ecological traits (part [b] in Fig. 3 which cannot be statistically tested). That is, though there is a small but significant contribution of ecological traits to the range of thermal windows, explaining 6.0% of variance (part [a+b] in Fig. 3), this has to be attributed to phylogenetically structured variation of ecological traits. That is, the thermal windows are independent of strictly ecological traits.

When ascertaining phylogenetically related fractions of variation in thermal windows that included the embedded parts of phylogenetically structured variation in ecological traits (fractions [b+c] in Fig. 3), only the first principal coordinate (PC) appeared significant and was retained in the model ($F = 9.863$; $df = 1, 64$; $P = 0.002$). Its eigenvalue represented 36.9% of the total variance of the patristic distance matrix and explained 13.4% of the variation in thermal windows (fractions [b+c] in Fig. 3). Because the order of PCs describes decreasing phylogenetic scales, this means that only differences at the largest phylogenetic scales were important; this is further supported by the fact that only the second PC still appeared marginally significant ($t = 1.786$; $df = 64$; $P = 0.079$). The sum of the eigenvalues of the first two PCs represented 68.3% of the total variance of the patristic distance matrix. The difference between the average thermal window among the highest phylogenetic clades, the Hemipteroid complex vs. Endopterygota, was highly significant (t-test: $t = 2.865$; $df = 64$; $P = 0.006$), with the average range 2.4 °C wider for the Hemipteroids (insect orders Psocoptera, Thysanoptera and Hemiptera) than for the Endopterygota (Neuroptera, Coleoptera, Diptera, Hymenoptera and Lepidoptera). That is, the widths of thermal windows are non-randomly distributed between these two taxonomic groups of insects.

The part of the variation strictly due to phylogeny (fraction [c] in Fig. 3) explained the largest percentage of variance (8.0%; $F = 6.950$; $df = 1, 64$; $P = 0.010$) and together with the phylogenetically structured variation of ecological traits (fraction [b] in Fig. 3) contributed 13.4 % to the variation in width of thermal windows (fractions [b] and [c] in Fig. 3). Because in total the fractions of variation simultaneously related to both ecological traits and phylogeny (fractions [a+b+c] in Fig. 3) account for 14% of the variation ($F = 5.698$; $df = 2, 63$; $P = 0.005$), the overwhelming amount of variation in thermal windows was clearly attributed to phylogeny. However, in spite of these phylogenetic effects, most of the variation (86.0%; part [d] in Fig. 3) remains unexplained.

THE RELATIONSHIP BETWEEN THE MINIMUM AND MAXIMUM DEVELOPMENTAL TEMPERATURES

The relationship between td_{min} and td_{max} for the individual species was highly significant (least square regression LS: $td_{max} = 24.78 + 0.50td_{min}$; $F = 32.45$; $df = 1, 64$; $P < 0.001$) and explained 33.6% of the variance ($r^2 = 0.336$); very similar results were obtained for phylogenetically independent contrasts (LS: $td_{max} = 0.54td_{min}$; $F = 14.24$; $df = 1, 34$; $P < 0.001$; $r^2 = 0.29$). The slope of the major axis (MA) for individual species suggested an increase in td_{max} of 1.3 °C ($td_{max} = -28.0 + 1.27td_{min}$) for each one degree centigrade increase in td_{min} , and the 95% confidence interval (CI) of this slope ($CI = 0.90 - 1.85$) broadly overlapped the

significant MA slope for phylogenetically independent contrasts ($b = 1.00$; $CI = 0.56 - 1.78$) (Fig. 4). This means that there is a strong relationship between t_{dmin} and t_{dmax} among species, and this relationship is independent of the phylogeny of the species.

Discussion

The analysis of empirical results on thermal requirements showed that the thermal window between t_{dmin} and t_{dmax} is similar among insect species. This is in accord with Charnov & Gillooly's (2003) theoretical predictions. A similar prediction can be derived from a linear approximation of the slope of the derivative of the Sharpe-Schoolfield developmental rate model at the middle of the temperature range (Schoolfield, Sharpe & Magnuson 1981). Both models predict thermal windows of about 20 °C, with ranges narrower than 10 or wider than 25 °C requiring a rather extreme combination of physiological parameters. This accords with our empirical results for insects (Fig. 2), and strengthens the theoretical premise that this phenomenon is physiologically rather than ecologically based. In addition, there are indications that ectothermic animals other than insects have thermal windows of similar widths (Moore 1942, 1949), and that the thermal window for plant development is also about 20° C (Bonhomme 2000). Thus, it is likely that this is a general feature of all ectothermic organisms.

Biochemists at the end of the 19th century developed temperature-coefficient equations, based on thermodynamic reasoning for simple inorganic systems, to account for the effect of temperature on the rate of biological processes (Arrhenius 1889; van't Hoff 1894). It was also appreciated that these relationships do not apply to the entire temperature range, but only narrow segments, depending on the species of animal, or in particular the enzyme(s) that control development. As the temperature rises, the enzymes begin to denature, with the effect that the accelerating effect of temperature on the speed of development may be counteracted by the inactivating effect on the limiting enzyme(s) (Chick & Martin 1910). It is possible limiting enzymes are similarly affected by temperatures at the lower end of the ecologically relevant range. These physiological constraints could delimit the widths of thermal windows in ectotherms in general.

The analysis of empirical results on thermal requirements for insects further showed that species that have a low t_{dmin} have a low t_{dmax} and vice versa, as predicted by Charnov and Gillooly (2003). Bodenheimer (1927), after studying two species of weevil that infest stored grain, *Sitophilus granarius* and *S. oryzae*, which in the field have a northern and southern distribution, respectively, argued their distributions could be attributed to *S. granarius* doing better at low temperatures than *S. oryzae* and vice versa at high temperatures. The trade-off between t_{dmin} and t_{dmax} , manifested by the observation that northern and southern insect species differ in their performance at high and low temperatures, with the northern species doing better at low temperatures than the southern species and vice versa at high temperatures, was thus appreciated nearly a hundred years ago. More recently, it has been suggested that the trade off between t_{dmin} and the D° required for development has a basis in the thermal adaptation of enzymes (van Straalen 1994; van der Have & de Jong 1996; van der Have 2002; Trudgill *et al.*, 2005), and that the same reasoning as for northern vs. southern species can be applied to closely related early spring vs. summer species in the temperate zone (Dixon & Hopkins, unpublished). In addition, there are indications that the t_{dmin} of C3 plants is lower than that for C4 plants, which accords with their respective predominantly temperate and tropical distributions (Bonhomme 2000). Thus, it is likely that, as with the widths of thermal windows, the trade-off between t_{dmin} and t_{dmax} is a general and physiologically based feature of all ectothermic organisms.

Fitness is often viewed in terms of potential rate of population increase. If it is a major component of fitness, and development rate and population rate of increase are correlated, as they are in related insect species (Dixon 1998, 2000), then it would appear to be generally advantageous for tropical species and those temperate species that develop in summer to have a lower t_{min} , as they would then be able to develop even faster at the high temperatures. However, this assumes there are no constraints to developing even faster at the temperatures prevailing in the tropics and high summer in temperate regions. Theory and this study indicate that the constraint is that each species can only develop over a narrow range of temperatures. That is, fitness is constrained by physiology, with the optimization of fitness in a variable thermal environment the central issue. Or put another way fitness is maximized by optimizing thermal reaction norms (Angilletta et al. 2003). Viewed in this way seasonal development and distribution are very similar in that they both involve adaptation to development over a particular temperature range. Northern species and those temperate species that start developing early in a year, have to be able to tolerate relatively low temperatures, those temperate species that develop in summer and tropical species, relatively high temperatures.

This study indicates that the widths of thermal windows are non-randomly distributed within the highest taxonomic groups of insect, slightly affected by phylogenetically structured variation of ecological traits, but not by ecological traits. Notably, there is no effect of body mass on the range of thermal windows, though body mass is the most important single trait related to many ecological and life-history traits (e.g. Peters 1983, Honek 1993, Brown 1995) and is known to have a significant phylogenetic component shared by related species (e.g. Cheverud, Dow & Leutenegger 1985, Gittleman & Kot 1990, Geffen *et al.* 1996, Pignata & Diniz-Filho 1996). The marginally significant effect of climatic zones, suggesting narrower windows for tropical compared to more cold-tolerant species, could be attributed to temperate species being exposed to a wider temperature range if development proceeds through spring and summer, whereas tropical species might develop in narrower temperature ranges. However, this interpretation must be verified with a larger data set. The same holds for the narrower windows of true predators and parasitoids compared to grazers, sap feeders and species feeding on dry seeds and dead plants and animals. This is so because though this pattern is significant, the overwhelming portion of variance in this relationship must be attributed to phylogenetically structured variation, which cannot be tested statistically.

The broader windows of the species in the Hemipteroid complex (orders Psocoptera, Thysanoptera and Hemiptera) compared to the Endopterygota (Neuroptera, Coleoptera, Diptera, Hymenoptera and Lepidoptera) may be attributed to differences in their postembryonic development. The Hemipteroids lack a true pupal stage (though Thysanoptera have quiescent stages, ecologically similar to true pupae) and their larvae become gradually more like the adults and live in the same environment as the adults. On the other hand, in the Endopterygota larvae and adults often live in completely different environments, and the species undergo a complete histolysis of larval tissues during pupation. These innovations in the latter group may have enabled the evolution of narrower thermal ranges for development. These narrow ranges, in turn, might have contributed to the greater ecological radiation of the Endopterygota, due to the more efficient niche differentiation among species along thermal gradients. That is, as argued by Angilletta et al. (2003) a unified theory that includes all classes of trade-offs is more likely to provide a better understanding of the mechanisms that drive the evolution of thermal reaction norms. However, the ecological significance of these differences in the width of their thermal, if confirmed, needs to be determined.

That most of the variation in the range of thermal windows remained unexplained, and the relationship between t_{max} and t_{min} , though highly significant accounts for only 34% of the variance, may in part be due to the quality of the original data. There has been a tendency to monitor the development of organisms at a fixed interval, usually a day, irrespective of the

temperature. This can lead to errors in the estimates of the duration of development, especially at higher temperatures (van Rijn, Mollema & Steenhuis-Broers 1995; Jarošík, Honek & Dixon 2002). In addition, mortality during development at each of the temperatures is very rarely recorded. This can lead to errors in the estimates of the duration of development especially at low temperatures, at which the individuals with the fastest development complete their development early while the rest succumb to adverse conditions (Jarošík, Honek & Dixon 2002). If the data had been specifically collected to determine the value of t_{dmax} and t_{dmin} then it is likely the estimates of these values would have been more accurate. Another factor that could have affected the results is food quality, which will be extremely difficult to standardize for insects and especially for ectotherms in general.

The facts that theory and this analysis of empirical data indicate that each species of insect can only develop over a limited range of temperatures, independent of species traits, and that the relationship between the minimum and maximum developmental rate co-vary, independent of species phylogeny, may help identify the precise nature of the biochemical adaptations underlying the seasonal development and distribution of ectotherms. This could be an important step in achieving a better understanding of how communities work and integrating physiology and ecology at the community scale. In addition, this concept might help when predicting the effect of climate change on the distribution and abundance of insects (e.g. Harrington & Stork 1995; Yamamura & Kiritani 1998; Dixon 2003; Kiritani 2006) and the spread of invasive species (e.g. Simberloff, Parker & Windle 2005; Baker *et al.* 2005; Hatherly *et al.* 2005).

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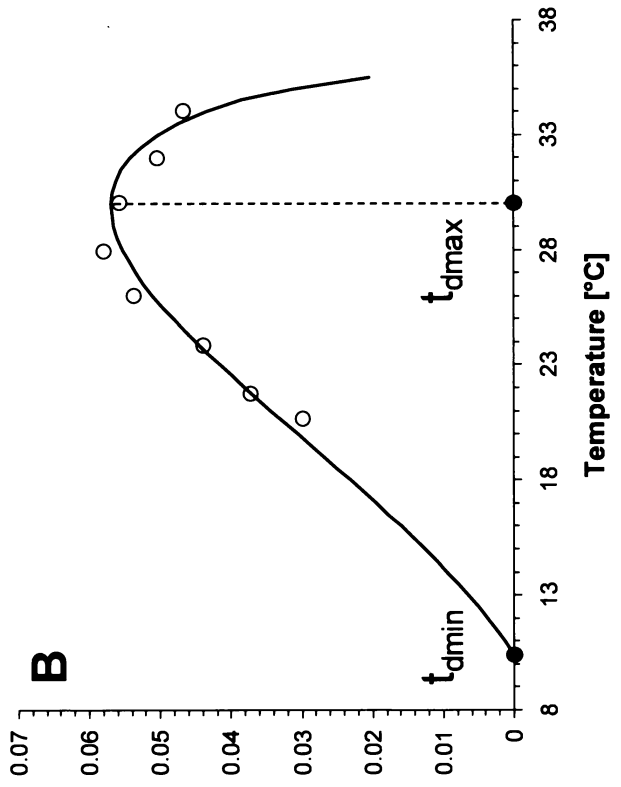
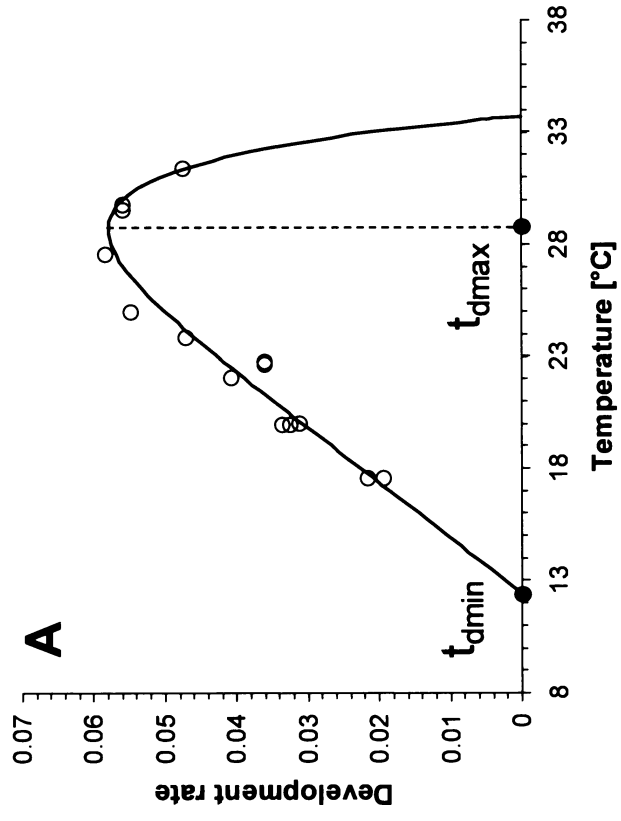
FIGURE LEGENDS

Figure 1. Least-square non-linear Levenberg-Marquardt iterative regression fit (A) of Lactin et al.'s model (equation 2) to results for *Bemisia tabaci*, biotype "B" reared on "DES119" cotton (Wagner 1995), parameters in Appendix S2, and (B) of Brière et al.'s model (equation 1) to results for *B. tabaci*, biotype "B" reared on "Pima S-6" cotton (Wagner 1995), parameters in Appendix S3. Values of td_{max} , calculated analytically (equation 4 for Lactin et al.'s model A, equation 3 for Brière et al.'s model B) and td_{min} , assessed as the intersections of the fitted curves with abscissa, are shown. Thermal window is the difference between the td_{max} and td_{min} values.

Figure 2. Frequency histogram of the thermal tolerance ranges (i.e. thermal windows) of the individual species.

Figure 3. Partitioning of the variation in thermal windows among ecological traits (ET, parts [a+b] of the Venn diagram), phylogeny (PH, parts [b+c]) and phylogenetically structured variation of ecological traits (PSVET, the intersection [b]). The rectangle represents 100% of the variation, of which [d] is the unexplained part. Values do not add up exactly due to rounding errors.

Figure 4. The relationship between the temperatures at which the developmental rates are at the minimum (td_{min}) and maximum (td_{max}) for individual species (A) and that of the phylogenetically independent contrasts (B). Statistics for least square (LS: equation, F, df, see text).



1
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Figure 1

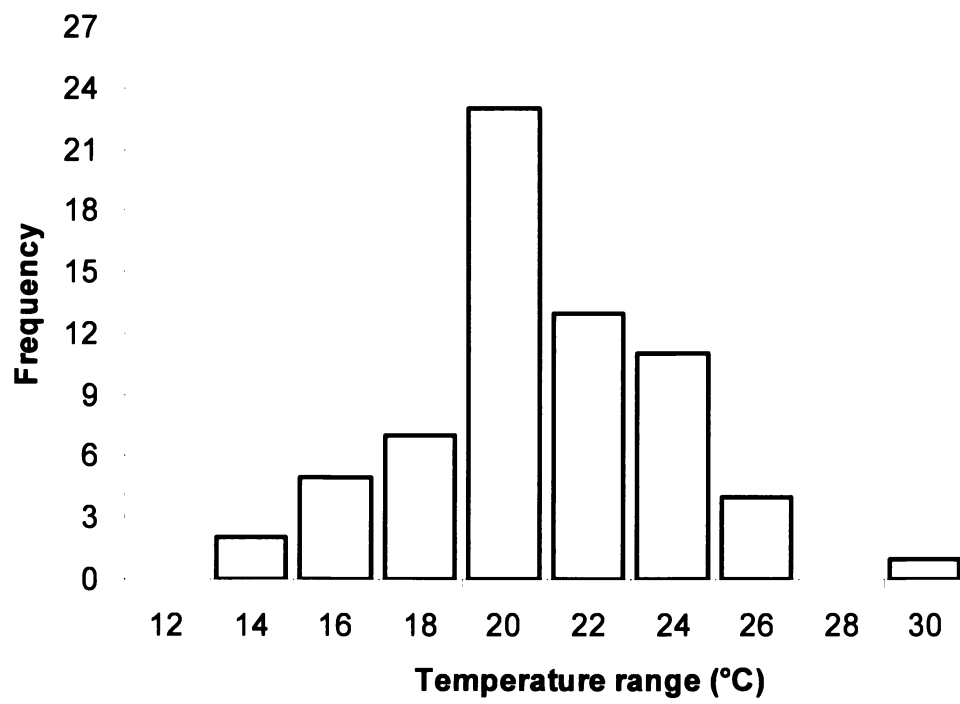


Figure 2

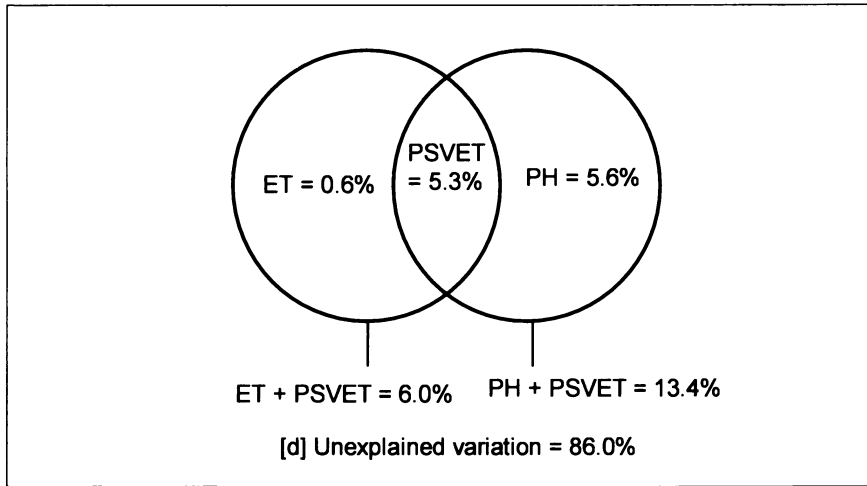


Figure 3

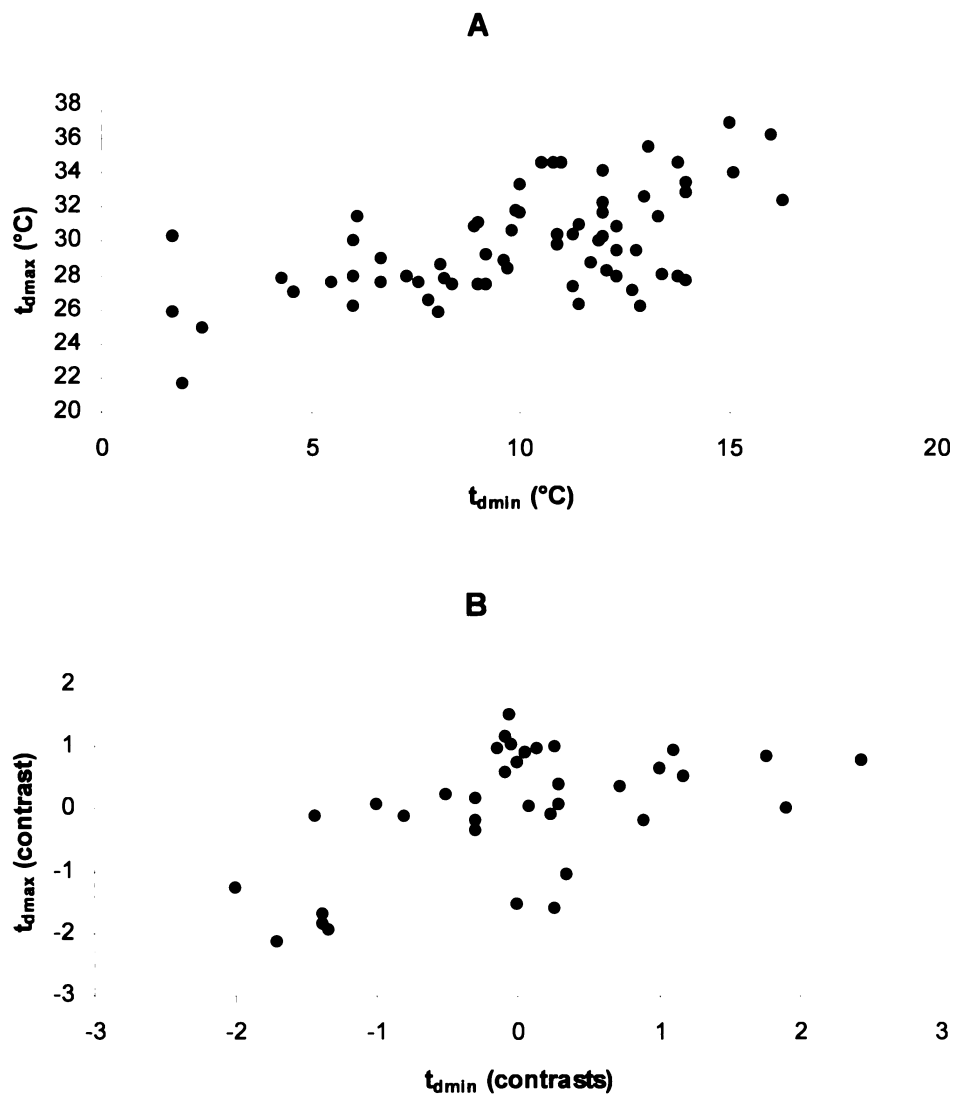


Figure 4

Appendix S1. List of the species included in the analysis classified by insect order, with the number of temperature points (N), stages, populations evaluated (footnotes), estimated values of t_{dmin} and t_{dmax} , and references to the sources of the data. Orders, and species within orders, are arranged alphabetically.

Order	Species	N	Stage	Reference	t_{dmin}	t_{dmax}
Coleoptera	<i>Agasicles hygrophila</i> (Selman & Vogt)	7	Egg to adult	Stewart <i>et al.</i> (1999)	12,8	29,5
Coleoptera	<i>Baris coerulescens</i> (Scopoli)	6	Larva	Lerin & Koubati (1998)	12	34,2
Coleoptera	<i>Carpophilus hemipterus</i> (L.)	8	Egg to adult	James & Volgele (2000)	15	36,9
Coleoptera	<i>Carpophilus humeralis</i> (F.)	8	Egg	James & Volgele (2000)	13,1	35,5
Coleoptera	<i>Carpophilus mutilatus</i> (Erickson)	8	Larva	James & Volgele (2000)	16	36,2
Coleoptera	<i>Chilocorus bipustulatus</i> (L.)	5	Egg	Podoler & Henen (1983)	14	27,7
Coleoptera	<i>Chilocorus kuwanae</i> (Silvestri)	5	Larva	Podoler & Henen (1983)	12,7	27,1
Coleoptera	<i>Cylas puncticollis</i> (Boehman)	5	Egg to adult	Niteletsana, Schoeman & McGeoch (2001)	15,1	34,0
Coleoptera	<i>Euhrychiopsis lecontei</i> (Dietz)	7	Larva	Mazzei <i>et al.</i> (1999)	11,7	28,8
Coleoptera	<i>Hippodamia sinuata</i> (Mulsant)	5	Egg	Michels & Behle (1991)	9,2	29,2
Coleoptera	<i>Hylobius pales</i> (Herbst)	6	Larva	Salom, Stephen & Thompson (1987)	7,6	27,6
Coleoptera	<i>Leptinotarsa decimlineata</i> (Say)	5	Egg	Ferro <i>et al.</i> (1985)	9	27,5
Coleoptera	<i>Nephus bisignatus</i> (Boehman)	5	Egg to adult	Kontodimas <i>et al.</i> (2004)	9,8	30,6
Coleoptera	<i>Nephus includens</i> (Kirsch)	6	Egg to adult	Kontodimas <i>et al.</i> (2004)	11	34,6
Coleoptera	<i>Prostephanus truncatus</i> (Horn)	5	Larva	Bell & Watters (1982)	12,3	28,0
Coleoptera	<i>Pterostichus nigrita</i> (F.)	11	Larva + pupa	Ferenz (1975)	6,7	29,0
Coleoptera	<i>Silophilus oryzae</i> (L.)	4	Larva	Ryoo & Cho (1988)	13,8	28,0
Diptera	<i>Anopheles gambia</i> (Giles)	8	Egg to adult	Bayoh & Lindsay (2003)	11,3	30,4
Diptera	<i>Bactocera zonata</i> (Sanders)	5	Egg to adult	Duyck, Sterlin & Quilici (2004)	13	32,6
Diptera	<i>Chironomus crassicaudatus</i> (Malloch)	14	Egg to adult	Frouz, Ali & Lobinske(2002)	11,3	27,4
Diptera	<i>Chrysomya rufifacies</i> (Macquart)	4	Egg	Byrd & Butler (1997)	7,3	27,9
Diptera	<i>Culiseta melanura</i> (Coquillett)	5	Larva	Mahmood & Crans (1998)	10	31,7
Diptera	<i>Dacus cucubritae</i> (Coquillett)	10	Pupa	Nakamori, Soemori & Kakinohana (1978)	8,2	27,8
Diptera	<i>Dacus oleae</i> (Gmelin)	5	Egg to adult	Crovetti <i>et al.</i> (1982)	12,1	28,3
Diptera	<i>Drosophila funebris</i> (Fabricius)	6	Egg to adult	Gibert & De Jong (2001)	8,05	25,9

Diptera	<i>Drosophila melanogaster</i> (Meigen)	21	Egg to adult	Frazier <i>et al.</i> (2001)	4,3	27,8
Diptera	<i>Drosophila willistoni</i> (Sturtevant)	5	Egg to adult	Gibert & De Jong (2001)	9,7	28,4
Diptera	<i>Feltiella acarissuga</i> (Vallot)	4	Egg to adult	Gillespie, Opit & Roitberg (2000)	12,9	26,2
Diptera	<i>Lydeella jalisco</i> (Woodley)	4	Pupa	Lauziere <i>et al.</i> (2002)	14	32,8
Diptera	<i>Stomoxys calcitrans</i> (L.)	5	Egg to adult	Lysyk (1998)	12	31,7
Hemiptera	<i>Abgallaspis cyanophylli</i> (Signoret)	6	Egg to adult	Ponsonby & Copland (2000)	12,3	29,5
Hemiptera	<i>Acrosternum hilare</i> (Say)	5	Larva	Simmons & Yeargan (1988)	9,2	27,5
Hemiptera	<i>Acyrtosiphon pisum</i> (Harris) ¹	5	Egg to adult	Morgan, Walters & Aegerter (2001)	4,8	23,7
Hemiptera	<i>Acyrtosiphon pisum</i> (Harris) ²	5	Egg to adult	Morgan, Walters & Aegerter (2001)	0	26,2
Hemiptera	<i>Aphis gossypii</i> (Glover)	6	Egg to adult	Xia (1997)	6,1	31,4
Hemiptera	<i>Aphis spiraeicola</i> (Patch)	7	Egg to adult	Wang & Tsai (2000)	1,7	30,3
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ³	14	Egg to adult	Wagner (1995)	12,5	28,7
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ⁴	8	Egg to adult	Wagner (1995)	10,5	29,9
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ⁵	14	Egg to adult	Muniz & Nombela (2001)	9,7	32,5
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁶	6	Egg to adult	Liu & Yue (2000)	4,5	29,7
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁷	12	Egg to adult	Liu & Meng (2000)	6,7	30,6
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁸	12	Egg to adult	Liu & Meng (2000)	6,8	29,9
Hemiptera	<i>Macrolophus pygmaeus</i> (Rambur)	10	Larva	Perdikis & Lykouressis (1999)	8,9	30,9
Hemiptera	<i>Macrosiphum avenae</i> (F.)	7	Egg to adult	Dean (1974)	1,7	25,9
Hemiptera	<i>Metopolophium dirhodum</i> (Walker)	7	Egg to adult	Dean (1974)	1,95	21,6
Hemiptera	<i>Myzus persicae</i> (Sulzer) ⁹	10	Egg to adult	Liu & Meng (1999)	4,8	27,1
Hemiptera	<i>Myzus persicae</i> (Sulzer) ¹⁰	10	Egg to adult	Liu & Meng (1999)	4,4	26,9
Hemiptera	<i>Pemphigus populitransversus</i> (Riley)	7	Egg to adult	Royer, Edelson & Harris (1999)	6	27,9
Hemiptera	<i>Planococcus citri</i> (Risso)	5	Egg to adult	Arai (1996)	8,4	27,5
Hymenoptera	<i>Anaphes flavipes</i> (Forester)	8	Egg	Anderson & Paschke (1969)	9,6	28,9
Hymenoptera	<i>Aphidius gifuensis</i> (Ashmead)	8	Egg to adult	Ohta, Miura & Kobayashi (2001)	5,5	27,6
Hymenoptera	<i>Chelonus</i> sp. near <i>curvimaculatus</i> (Cameron)	29	Egg to adult	Hentz <i>et al.</i> (1998)	14	33,4
Hymenoptera	<i>Cirrospilus</i> sp. near <i>lyncus</i> (Walker)	16	Egg to adult	Urbaneja <i>et al.</i> (1999)	6	26,2
Hymenoptera	<i>Coccobius fulvus</i> (Compere & Annecke)	5	Egg to adult	Ogata (1987)	13,4	28,1

Hymenoptera	<i>Muscidifurax raptor</i> (Girault & Sanders)	10	Egg to adult	Lysyk (2000)	11,4	31,0
Hymenoptera	<i>Muscidifurax raptorellus</i> (Kogan & Legner)	10	Egg to adult	Lysyk (2001a)	12,3	30,9
Hymenoptera	<i>Muscidifurax zaraptor</i> (Kogan & Legner)	10	Egg to adult	Lysyk (2001b)	13,3	31,4
Hymenoptera	<i>Oomyzus sokolowski</i> (Kurdjmov)	6	Egg to adult	Wang <i>et al.</i> (1999)	12	32,3
Hymenoptera	<i>Venturia canescens</i> (Gravenhorst)	27	Egg to adult	Eliopoulos & Stathas (2003)	12	30,3
Lepidoptera	<i>Cadra cautella</i> (Walker)	19	Egg to adult	Nawrot (1979)	13,8	34,6
Lepidoptera	<i>Carposina sasakii</i> (Matsamura)	8	Egg	Kim, Lee & Yiem (2001)	10,5	34,6
Lepidoptera	<i>Endopiza viteana</i> (Clemens)	8	Egg to adult	Tobin, Nagarkatti & Saunders (2001)	9	31,1
Lepidoptera	<i>Harrisina brillians</i> (Barnes & MacDunnough)	9	Larva + pupa	Roltsch, Mayse & Clausen (1990)	11,4	26,3
Lepidoptera	<i>Lacanobia subjuncta</i> (Grote & Robinson)	7	Egg to adult	Doerr, Brunner & Jones (2002)	6,7	27,6
Lepidoptera	<i>Maruca vitrata</i> (Fabricius)	5	Egg to adult	Adati <i>et al.</i> (2004)	10,9	29,8
Lepidoptera	<i>Merophyas divulsana</i> (Walker)	7	Larva + pupa	Allsop, Cowie & Franzmann (1983)	8,1	28,6
Lepidoptera	<i>Palpita unionalis</i> (Hübner)	7	Egg	Loi (1990)	10	33,3
Lepidoptera	<i>Plutella xylostella</i> (L.)	12	Egg to adult	Liu, Chen & Zalucki (2002)	9,9	31,8
Lepidoptera	<i>Sesamia nonagrioides</i> (Lefebvre)	10	Egg to adult	Lopez <i>et al.</i> (2001)	11,9	30,0
Neuroptera	<i>Anomalochrysa frater</i> (Perkins)	5	Pupa	Tauber, Johnson & Tauber (1992)	7,8	26,5
Psocoptera	<i>Liposecelis bostrychophila</i> (Badonnel) ¹¹	7	Egg to adult	Wang <i>et al.</i> (2001)	11	34,6
Psocoptera	<i>Liposecelis bostrychophila</i> (Badonnel) ¹²	7	Egg to adult	Wang <i>et al.</i> (2001)	10,7	34,6
Psocoptera	<i>Liposecelis bostrychophila</i> (Badonnel) ¹³	7	Egg to adult	Wang <i>et al.</i> (2000)	10,7	34,7
Thysanoptera	<i>Ceratohripoides claratris</i> (Shumsher)	6	Egg to adult	Premachandra <i>et al.</i> (2004)	16,3	32,4

¹pea cultivar "Sancho"

²pea cultivar "Scout"

³biotype "B" on "DES119" cotton strain

⁴biotype "B" on "Pima S-6" cotton strain

⁵mixture of "B" and "Q" biotypes on sweet pepper

⁶Apterae; different strain than^{7,8}

⁷Alatae

⁸Apterae

⁹ Alatae

¹⁰ Apteræ

¹¹ reared in "control atmosphere 1" (10% CO₂ and 5% O₂)

¹² reared in "control atmosphere 2" (12% CO₂ and 9% O₂)

¹³ reared in standard atmosphere

Appendix S2. Analytical solution for the maximum temperature $t_{d\max}$ and numerical solution for the minimum temperature $t_{d\min}$.

Aim: To find the (i) maximum temperature ($t_{d\max}$; the temperature with maximum r by definition) and (ii) minimum temperature ($t_{d\min}$; the minimum temperature with $r = 0$ by definition) of the Lactin et al.'s (1995) model, which obeys Eq. 2 with parameters ρ , T_{\max} , Δ and λ .

Solution (i): We are searching for an extreme of the Eq. 2, thus for the root of $dr/dT = 0$.

Replacing $1/\Delta$ with a , and $e^{(\rho-1/\Delta)T_{\max}}$ with b , we get $dr(t_{d\max})/dT = \rho e^{\rho t_{d\max}} - bae^{\rho t_{d\max}} = 0$.

After logarithmizing and simplifying, $t_{d\max} = (\ln ba - \ln \rho)/(\rho - a)$, which is Eq. 4, after replacing the a and b back with the original values.

Solution (ii): The minimum temperature, $t_{d\min}$, can be solved numerically by the bisection method (the root-finding algorithm; e.g. http://en.wikipedia.org/wiki/Bisection_method).

Since we know that $\tau_{\min} \leq t_{d\min} \leq \tau_{\max}$ where $\tau_{\min} = 0$ and $\tau_{\max} = t_{d\max}$, we can bisect the

interval $\{\tau_{\min}; \tau_{\max}\}$ and compute $r(\tau_{\min})$, $r\left(\frac{\tau_{\min} + \tau_{\max}}{2}\right)$, and $r(\tau_{\max})$ using Eq. 2. If

$r(\tau_{\min})r\left(\frac{\tau_{\min} + \tau_{\max}}{2}\right) \leq 0$, we replace τ_{\max} with the midpoint of the interval,

$T = (\tau_{\min} + \tau_{\max})/2$, otherwise we replace τ_{\min} with the midpoint of the interval. This is

repeated until $\tau_{\max} - \tau_{\min} \leq \eta$, where η is the required accuracy.

Appendix S3. Summaries of Lactin et al.'s (1995) model parameters (modification 2) for the species included in the analysis, classified by insect order. r^2 = total explained variance; λ = the intersection of the fitted curve with abscissa at suboptimal temperatures that was used to estimate the lower developmental temperature threshold (t_{dmin}); ρ = the developmental rate to the optimal temperature t_{dmax} ; T_{max} = lethal maximum temperature (high temperature threshold); Δ = the width of the high temperature boundary layer (the width of the high temperature decline in developmental rate, over which thermal breakdown becomes the overriding influence). Orders, and species within orders, are arranged alphabetically. Source references are given in Appendix S1.

Order	Species	r^2	λ	ρ	T_{max}	Δ
Coleoptera	<i>Agasicles hygrophila</i> (Selman & Vogt)	0,9634	-1,0461	0,0035	30,6765	0,1560
Coleoptera	<i>Baris coerulescens</i> (Scopoli)	0,9937	-1,0135	0,0011	36,2221	0,2429
Coleoptera	<i>Carpophilus hemipterus</i> (L.)	0,9847	-1,0561	0,0036	52,6180	3,5601
Coleoptera	<i>Carpophilus humeralis</i> (F.)	0,9574	-1,3040	0,0201	42,9763	2,3252
Coleoptera	<i>Carpophilus mutilatus</i> (Erickson)	0,9926	-1,0823	0,0050	47,2887	2,5038
Coleoptera	<i>Chilocorus bipustulatus</i> (L.)	0,9465	-1,1472	0,0098	28,2612	0,0765
Coleoptera	<i>Cylas puncticollis</i> (Boehman)	0,9947	-1,0756	0,0052	62,4990	8,8233
Coleoptera	<i>Euhrychiopsis lecontei</i> (Dietz)	0,9478	-1,0967	0,0086	29,2612	0,0684
Coleoptera	<i>Hippodamia sinuata</i> (Mulsant)	0,8432	-1,1944	0,0193	30,5599	0,2497
Coleoptera	<i>Hylobius pales</i> (Herbst)	0,9898	-1,0144	0,0019	28,6310	0,1235
Coleoptera	<i>Leptinotarsa decimlineata</i> (Say)	0,9400	-1,1363	0,0143	28,3220	0,1383
Coleoptera	<i>Nephus bisignatus</i> (Boehman)	0,9994	-1,0194	0,0020	39,1573	1,4656
Coleoptera	<i>Nephus includens</i> (Kirsch)	0,9698	-1,0258	0,0024	35,4306	0,0977
Coleoptera	<i>Prostephanus truncatus</i> (Horn)	0,9741	-1,0690	0,0039	35,2929	1,3811
Coleoptera	<i>Pterostichus nigrata</i> (F.)	0,9554	-1,0163	0,0024	31,5196	0,3553
Diptera	<i>Anopheles gambia</i> (Giles)	0,9777	-1,0626	0,0054	38,6922	1,7546
Diptera	<i>Bactocera zonata</i> (Sanders)	0,9942	-1,0592	0,0044	46,8865	3,3324
Diptera	<i>Chironomus crassicaudatus</i> (Malloch)	0,9961	-0,8203	0,0105	82,4714	34,6972
Diptera	<i>Culiseta melanura</i> (Coquillett)	0,8771	-1,0266	0,0026	32,3318	0,0801
Diptera	<i>Dacus cucubritae</i> (Coquillett)	0,9881	-1,2687	0,0294	28,1609	0,0481
Diptera	<i>Dacus oleae</i> (Gmelin)	0,9654	-1,0441	0,0036	29,8343	0,2186
Diptera	<i>Drosophila funebris</i> (Fabricius)	0,9800	-1,0015	0,0001	36,7235	1,1948
Diptera	<i>Drosophila melanogaster</i> (Meigen)	0,8800	-1,37440	0,07970	33,50250	3,07660
Diptera	<i>Drosophila willistoni</i> (Sturtevant)	0,9900	-1,0025	0,0002	31,3797	0,3067
Diptera	<i>Stomoxys calcitrans</i> (L.)	0,9939	-1,0585	0,0048	45,2653	3,2066
Hemiptera	<i>Abgrallaspis cyanophylli</i> (Signoret)	0,9634	-1,0461	0,0035	30,6765	0,1560
Hemiptera	<i>Acrosternum hilare</i> (Say)	0,9980	-1,03743	0,00258	37,30482	1,82335
Hemiptera	<i>Acyrtosiphon pisum</i> (Harris) ¹	0,9996	-1,02955	0,01019	45,74162	8,13171
Hemiptera	<i>Acyrtosiphon pisum</i> (Harris) ²	0,9980	-1,00016	0,00557	27,20366	0,14000
Hemiptera	<i>Aphis gossypii</i> (Glover)	0,9741	-1,0551	0,0086	42,1178	2,7984
Hemiptera	<i>Aphis spiraeicola</i> (Patch)	0,9696	-1,0068	0,0045	35,5153	0,9505
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ³	0,9484	-1,0487	0,0038	39,4767	2,2491
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ⁴	0,9759	-1,0267	0,0028	42,1734	1,8248
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁵	0,9616	-1,0347	0,0077	30,4103	0,1056
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁶	0,9951	-1,0559	0,0082	42,7799	3,2811
Hemiptera	<i>Lipaphis erysimi</i> (Kaltenbach) ⁷	0,9925	-1,0637	0,0093	44,8637	4,5196
Hemiptera	<i>Macrolophus pygmaeus</i> (Rambur)	0,8339	-1,0312	0,0035	49,8484	4,4911
Hemiptera	<i>Macrosiphum avenae</i> (F.)	0,9894	-1,0002	0,0004	80,8079	9,8901
Hemiptera	<i>Metopolophium dirhodum</i> (Walker)	0,9639	-1,0006	0,0004	55,2017	5,4823
Hemiptera	<i>Myzus persicae</i> (Sulzer) ⁸	0,9859	-1,0336	0,0071	30,4553	0,6216
Hemiptera	<i>Myzus persicae</i> (Sulzer) ⁹	0,9940	-1,0344	0,0080	34,0973	1,6483
Hemiptera	<i>Pemphigus populitransversus</i> (Riley)	0,9710	-1,0325	0,0055	40,8923	3,1582

Hemiptera	<i>Planococcus citri</i> (Risso)	0,9805	-1,0212	0,0025	30,8060	0,4889
Hymenoptera	<i>Anaphes flavipes</i> (Forester)	0,9605	-1,6882	0,0587	38,2650	5,6736
Hymenoptera	<i>Aphidius gifuensis</i> (Ashmead)	0,9972	-1,0275	0,0050	35,1779	1,5393
Hymenoptera	<i>Chelonus</i> sp. near <i>curvimaculatus</i> (Cameron)	0,9857	-1,0435	0,0031	46,9998	2,8417
Hymenoptera	<i>Cirrospilus</i> sp. near <i>lyncus</i> (Walker)	0,8402	-0,7818	0,0084	93,6741	41,8048
Hymenoptera	<i>Coccobius fulvus</i> (Compere & Annecke)	0,9983	-1,0447	0,0033	40,6929	2,6326
Hymenoptera	<i>Muscidifurax raptor</i> (Girauld & Sanders)	0,9875	-1,0492	0,0042	41,4694	2,2060
Hymenoptera	<i>Muscidifurax raptorellus</i> (Kogan & Legner)	0,9927	-1,0576	0,0046	41,7639	2,3921
Hymenoptera	<i>Muscidifurax zaraptor</i> (Kogan & Legner)	0,9864	-1,0646	0,0047	44,2212	2,9496
Hymenoptera	<i>Oomyzus sokolowski</i> (Kurdjmov)	0,9955	-1,0549	0,0044	45,3806	2,9866
Hymenoptera	<i>Venturia canescens</i> (Gravenhorst)	0,9329	-1,0302	0,0025	44,9544	2,9634
Lepidoptera	<i>Cadra cautella</i> (Walker)	0,9607	-1,0159	0,0012	42,1214	1,1378
Lepidoptera	<i>Carposina sasakii</i> (Matsamura)	0,9900	-1,0861	0,0079	35,2619	0,0936
Lepidoptera	<i>Endopiza viteana</i> (Clemens)	0,9965	-1,0188	0,0021	35,9895	0,7495
Lepidoptera	<i>Harrisina brillians</i> (Barnes & MacDunnough)	0,9697	-1,0208	0,0018	28,3989	0,2699
Lepidoptera	<i>Lacanobia subjuncta</i> (Grote & Robinson)	0,9094	-1,0056	0,0009	48,3946	3,6156
Lepidoptera	<i>Maruca vitrata</i> (Fabricius)	0,9998	-1,0301	0,0028	39,0005	1,7094
Lepidoptera	<i>Merophyas divulsana</i> (Walker)	0,9987	-1,0208	0,0026	40,0606	2,2007
Lepidoptera	<i>Plutella xylostella</i> (L.)	0,9777	-1,0390	0,0039	32,4977	0,0855
Lepidoptera	<i>Sesamia nonagrioides</i> (Lefebvre)	0,9705	-1,0198	0,0017	50,7099	4,1578
Neuropera	<i>Anomalochrysa frater</i> (Perkins)	0,9958	-1,0356	0,0045	33,4064	1,3327
Psocoptera	<i>Liposcelis bostrychophila</i> (Badonnel) ¹⁰	0,9602	-1,0213	0,0019	35,6116	0,1193
Psocoptera	<i>Liposcelis bostrychophila</i> (Badonnel) ¹¹	0,9578	-1,0197	0,0019	35,4927	0,0985
Psocoptera	<i>Liposcelis bostrychophila</i> (Badonnel) ¹²	0,9557	-1,0317	0,0025	35,3391	0,0788
Thysanoptera	<i>Ceratothripoides claratris</i> (Shumsher)	0,9764	-1,1300	0,0075	43,9679	2,9804

¹pea cultivar "Sancho"

²pea cultivar "Scout"

³biotype "B" on "DES119" cotton strain

⁴mixture of "B" and "Q" biotypes on sweet pepper

⁵Apterae; different strain than^{6,7}

⁶Alatae

⁷Apterae

⁸Alatae

⁹Apterae

¹⁰reared in "control atmosphere 1" (10% CO₂ and 5% O₂)

¹¹reared in "control atmosphere 2" (12% CO₂ and 9% O₂)

¹²reared in standard atmosphere

Appendix S4. Summaries of Brière et al.'s (1999) model parameters of the species included in the analysis, classified by insect order. r^2 = total explained variance; a = empirical constant; T_0 = lower developmental threshold (t_{dmin}); T_L = lethal temperature (high temperature threshold; T_L is equal to T_{max} in S1). Orders, and species within orders, are arranged alphabetically. Source references are given in Appendix S1.

Order	Species	r^2	a	T_0	T_L
Coleoptera	<i>Chilocorus kuwanae</i> (Silvestri)	0,8229	0,0001	12,6210	31,7767
Coleoptera	<i>Silophilus oryzae</i> (L.)	0,9256	0,0001	13,7398	32,7569
Diptera	<i>Chrysomya rufifacies</i> (Macquart)	0,8699	0,0013	7,2577	33,8742
Diptera	<i>Feltiella acarisuga</i> (Vallot)	0,9797	0,0001	11,8795	30,8645
Diptera	<i>Lydella jalisco</i> (Woodley)	0,9962	0,0001	14,0500	38,7860
Hemiptera	<i>Bemisia tabaci</i> (Gennadius) ¹	0,9468	0,00004	10,42558	35,82238
Lepidoptera	<i>Palpita unionalis</i> (Hübner)	0,9325	0,0002	9,9845	40,2166

¹biotype "B" on "Pima S-6" cotton strain

Appendix S5. Partitioning of the variance in thermal windows.

We partitioned the variance in thermal windows into a part strictly due to (1) ecological traits, represented by insect body mass, latitude from which the experimental population originated, and species trophic specialization; (2) phylogeny; (3) joint influence of these two factors (i.e., phylogenetically structured variation of ecological traits); and (4) unexplained variation.

To ascertain the fractions of variation in thermal windows related to ecological traits that include embedded phylogenetically structured variation, the thermal windows of individual species were regressed on the ecological traits (trophic specialization, latitude and body mass, with the latter \ln transformed to normalize the data), beginning with the maximal model containing all predictors and their possible interactions, after which all non-significant terms were eliminated using deletion tests. This was done using an automatic step-wise process of model simplification of deviance tables (Crawley 2002), based on Akaike Information Criterion (AIC) (program S-Plus v. 6.2, Insightful Corp. 2003).

To ascertain the fractions of variation related to phylogeny that includes phylogenetically structured variation in ecological traits, forward selection procedures (S-Plus v. 6.2) were used to select the principal coordinates (PCs) that significantly contributed to the explanation of variation in thermal windows. (There was no need to use a more complicated selection procedure because by definition PCs are all orthogonal, i.e. zero correlated, with one another). The fractions of variation simultaneously related to both ecological traits and phylogeny were then ascertained by regressing the thermal windows simultaneously on all variables selected in the two previous steps of the variance partitioning, which indicated the fractions related to ecological traits with embedded phylogenetically structured variation, and fractions related to phylogeny with embedded phylogenetically structured variation in ecological traits (Desdevides *et al.* 2003).

The individual fractions of the total variation in thermal windows, i.e. (1) net variation due to ecological traits, (2) phylogenetically structured variation in ecological traits, (3) net variation due to phylogeny, and (4) unexplained variation, were then obtained by subtractions from the results of the previous models, following Desdevides *et al.* (2003). The subtractions were made based on adjusted coefficients of explained variance, r^2_{adj} , taking into account sample sizes and number of predictors (Legendre & Legendre 1998). Statistical significances of individual parts of the variance, except the phylogenetically structured variation of ecological traits, which cannot be tested, were calculated using parametric tests following Legendre & Legendre (1998).

All data in linear models used for variance partitioning were analyzed assuming normal distribution of errors and an identity link function. All predictors were checked for appropriate transformations by raw and residual plots, and for collinearity by calculating tolerance values (Quinn & Keough 2002 p. 128). Fitted models were checked by plotting standardized residuals against fitted values, and by normal probability plots (Crawley 1993).

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