Local adaptations and phenotypic plasticity may render gypsy moth and nun moth future pests in northern European boreal forests.

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Abstract

Phenotypic plasticity and local adaptations are important factors in predicting range expansions and shifts of pest insects in a changing climate. We reared two lepidopteran forest pests, *Lymantria monacha* and *L. dispar*, at three climatically different field sites from central Germany to northern Finland to investigate differences among populations in plasticity in the timing of pupation and adult emergence (measured as cumulative temperature sums, degree days > 5 °C), pupal mass, and duration of the pupal period. We also compared the phenologies of continental and boreal *L. monacha* populations feeding on Scots pine (*Pinus sylvestris*) to reveal possible local adaptations. *Lymantria dispar* was reared on different host plants – *Quercus robur*, *Betula pendula* and *B. pubescens* ssp. *czerepanovii* – to evaluate the possibilities of a range expansion northwards. There was stronger indication of adaptive phenotypic plasticity, which enables species to cope with changing environmental conditions, in continental *L. dispar* and boreal *L. monacha* populations than in the continental *L. monacha* population. Differences between boreal and continental *L. monacha* populations may denote adaptation to local conditions. All three host plants used for *L. dispar* proved suitable for the species, revealing that host plant availability would not limit its range expansion in Northern Europe.

Keywords: Climate change, Local adaptation, *Lymantria monacha*, *Lymantria dispar*, Phenotypic plasticity

Introduction

The influence of climate change on butterflies and moths – especially charismatic, conspicuous species and those considered as forest or agricultural pests – has been investigated intensively in recent years (e.g., Björkman & Niemelä 2015). The effect of rising temperatures on the distribution ranges of Lepidoptera has been considered (e.g.,Parmesan et al. 1999, Vanhanen et al. 2007, Jepsen et al. 2008, Ammunét et al. 2012, Yasukevich et al. 2015), as well as the possibility for phenological mismatches in synchrony between trophic levels, such as defoliator larvae or pollinators and their host plants (e.g., Buse & Good 1996, van Asch & Visser 2007, Memmott et al. 2007, Jepsen et al. 2011, Visser & Holleman 2001, Foster et al. 2013, Hindle et al. 2015). Several authors have voiced the need to take phenotypic plasticity as well as local adaptations (and even local adaptations of phenotypic plasticity) into account in such studies, as geographically distant populations of the same species may have developed the ability to thrive in different conditions and even to cope with a continuously changing climate (Ammunét et al. 2011, Valtonen et al. 2011, Kaitaniemi et al. 2012, Valladares et al. 2014).

Presumably insects optimize their life cycle in relation to prevailing conditions to obtain maximum fitness. This is facilitated by adaptive phenotypic plasticity of the life stage duration and timing, such as egg hatching, diapausing, pupation, adult emergence and oviposition – in other words by the ability to flexibly adapt the phenology to prevailing environmental conditions (Nylin & Gotthard 1998, Valtonen et al. 2011, Saikkonen et al. 2012, Valladares et al. 2014). In the life cycle of a univoltine insect, phenological events are commonly dependent on the accumulated temperature sum. Global climate change may influence the rate of temperature accumulation and the average dates when a required temperature sum is reached. However, day length – a variable not influenced by climate change – also commonly controls the timing of insect life cycles either independently or as a modifier of temperature effects (Danks 1987, Tauber et al. 1990, van Asch & Visser 2007, Valtonen et al. 2011). With sufficient adaptive phenotypic plasticity allowing insects to follow these environmental cues, many species may rapidly become established in new environments, or continue

thriving in the changing climate of their current distribution range, without a risk of asynchrony with their host plants before any genetic adaptation takes place.

In this paper we report the results of a field study where we investigated plasticity in the timing of pupation and adult emergence (measured in relation to accumulating temperature sums), pupal mass and the duration of the pupal period in different populations of two forest pests, the nun moth (*Lymantria monacha* (Linnaeus)) and the gypsy moth (*L. dispar* (Linnaeus) (Lepidoptera: Erebidae, Lymantriinae)). We examined the phenological differences between the *L. monacha* populations from continental mid-Germany and boreal Southern Finland when individuals from these both populations were reared in the same conditions, as these differences may indicate recent local adaptations in the Finnish population. We also investigated, whether *L. monacha* or *L. dispar* individuals, originating from the same population, differ in development timing when mesh bag-reared in climatically different field locations – both in areas where the species occur naturally, and more northern ones where they are not present. A further aim was to examine the timing of life cycle events of *L. dispar* to assess whether it could expand its range northwards in Northern Europe to areas where it is not yet present but where *L. monacha* is currently spreading (Leinonen et al. 2016). Finally, we wanted to compare *L. dispar* development on different host plants, namely oak (*Quercus robur* L.), silver birch (*Betula pendula* Roth.) and mountain birch (*B. pubescens* ssp. *czerepanovii* (Orl.) Hämet-Ahti) under field conditions.

Materials & Methods

2.1 Study species

Lymantria monacha and *L. dispar* are both univoltine medium-sized nocturnal moths that overwinter as small, fully developed larvae diapausing in eggs (Leonard 1974, Bejer 1988, Majunke et al. 2004). Both are considered serious forest defoliators and exhibit frequent though irregular outbreaks in at least some parts of their respective distribution ranges. *Lymantria monacha* occurs in most parts of temperate Europe and Asia (Vanhanen et al. 2007) and prefers conifers, namely Norway spruce

(*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) as its host plants, although it can also successfully feed and develop on a wide range of other conifer and broadleaf species (Keena 2003). The distribution range of *L. dispar* is slightly more southern than that of *L. monacha*. It comprises most of Europe (except for central and northern Fennoscandia and the British Isles) and Asia as well as parts of North America where it was introduced in the mid-19th century and where it quickly became a major pest species (Forbush & Fernald 1896, Liebhold et al. 1992, Liebhold et al. 2000). *Lymantria dispar* is a highly polyphagous generalist feeding on a large range of different tree genera, with *Quercus, Betula, Fagus, Larix* and *Populus* species being among the preferred hosts (Lechowicz & Mauffette 1986).

Previous studies on environmental variables controlling the life cycle of *L. monacha* are scarce. In *L. dispar* egg diapause and hatching are controlled chiefly by temperature, the effect of which may slightly be inhibited by a short day length (Tauber et al. 1990, Gray et al. 1991, Keena 1996, Gray 2010, Wei et al. 2014). An increase in temperature has also been shown to decrease the time needed for larval development for both species. At least in the range between 15 °C and 25 °C higher temperatures also increase survival rates for *L. dispar* but the effect is the opposite for *L. monacha* (Karolewski et al. 2007). Bogach et al. (1966) and Kireeva (1969) showed that the duration of the pupal phase of *L. dispar* is influenced by both light and temperature, with longer days and higher temperatures advancing the pupal development.

2.2 Locations

The study was conducted at three different sites in central and northern Europe with approximately ten latitudinal degrees between the two subsequent sites (Table 1, Fig. 1). The southernmost (henceforth referred to as "Tharandt") site was located in Tharandter Wald in Saxony, Germany, where both *L. monacha* and *L. dispar* occur naturally. Here, as in all other locations, *L. monacha* larvae were reared only on *P. sylvestris*, while *L. dispar* was reared on both *Q. robur* and *B. pendula*. The second site ("Turku") was located in Southern Finland, Turku, where *L. monacha* has become

more common during the recent decades (Leinonen et al. 2016), but where *L. dispar* is not present. Here all the *L. dispar* and some of the *L. monacha* larvae were reared at the Ruissalo botanical garden, while the remaining *L. monacha* larvae were reared on naturally regenerated Scots pines near the campus of the University of Turku, 6.5 km apart, due to the shortage of *P. sylvestris* in the botanical garden. In Turku *L. dispar* was reared on *Q. robur* only. The northernmost site ("Kevo") located at the Kevo Subarctic Research Station in Utsjoki, close to the northern border of Finland, is well beyond the natural range of both *Lymantria* species. Here *L. dispar* larvae were reared on *B. pubescens* ssp. c*zerepanovii*, the most abundant broadleaved tree found there, as *B. pendula* does not grow this far north.

2.3 Field experiment

Lymantria monacha eggs were obtained from females reared in mesh bags under field conditions in Tharandter Wald, Germany during the summer 2013, and they represent a second generation bred in captivity. The original females were collected in Brandenburg, Germany (later referred to as the "continental" population, following the definition of biogeographic regions in Europe by the European Environment Agency (2012)) and in the archipelago of South-Western Finland (later referred to as the "boreal" population) in summer 2012. *Lymantria dispar* eggs were collected from tree trunks in Brandenburg in August 2013. All the eggs were stored in closed glass vials in a climate chamber (Binder KBF 720) in Tharandt. The temperature was gradually lowered being 19.6 °C on 28th of July when the first *L. monacha* eggs were laid, 15.9 °C as the newly collected *L. dispar* eggs were added on 21st of August and reaching 0 °C on 25th of November. On 17th of December, all the eggs were moved into a freezer at the temperature of -5 °C.

On 3rd of April 2014, the eggs were randomly assigned to experimental groups, although clearly unfertilized red or flat eggs were omitted. Seven broods of continental *L. dispar* and *L. monacha* eggs as well as five broods of boreal *L. monacha* eggs were divided into batches of 16 eggs, with all the eggs in a batch coming from the same brood. Table 1 shows the batches assigned to the three

different field sites. All the egg batches were further divided into two glass vials with eight eggs in each to prevent crowding in later phases of the experiment.

All the eggs for the field site in Tharandt were transferred to an open shed on 3rd of April and to the forest on 7th of April, at all times together with a temperature logger. The eggs for Turku were stored at -5 °C until transported from Tharandt to Turku together with a temperature logger by express mail on 6-7th of May. For the following days, the eggs were kept at room temperature during the nights and outdoors during the days until transferred to the field sites at the Botanical Garden and at the campus on 10-17th of May. The eggs for Kevo were stored at -5 °C in Tharandt until they were sent by express mail to Turku on 13-14th of May. They were subsequently transported in a cool box by car to Kevo and there stored in a fridge at +2.6 °C until 28th of May when the experiment was started.

On the study trees the eggs – and later the larvae – were kept in 40 × 100 cm mesh bags of fine voile, each of which enclosed a branch on which the larvae could move and feed freely. The 16 eggs of each batch were kept in two bags on the same tree, except for a few cases where no trees large enough to support two bags were available. In these cases, two trees close to each other were used to host one of the two bags of a batch each.

At all three sites the experiment was started close to the time of oak or birch budburst to ensure that the neonate *L. dispar* larvae could start feeding directly after hatching. In Tharandt and Turku some of the pines had male cones during the experiment, producing pollen which is a preferred – though not obligatory (personal observation) – food source for *L. monacha* larvae. Temperature data for the field sites was obtained from nearby weather stations (Tharandt: "Wildacker Tharandter Wald", Turku: "Artukainen", Kevo: "Kevo") and complemented with data logger measurements. Data on day length was obtained using an online calculator (Gerding 2016).

The mesh bags were first checked weekly for damages and defoliation. If the branch in the bag was almost completely defoliated (which occasionally happened in the late instars), the larvae were moved to a new bag on another branch.

When the first larvae reached the last instar, the bags were checked at two- or three-day intervals for pupae. When the exact date of pupation was not evident, an approximation was used – if the control interval had been three days, the date in the middle was recorded as the pupating date; if the interval had been two days, every second pupa found that day was recorded for the first day in the interval and every second for the second day in the interval. The pupae were placed individually in plastic cups on a wad of moist *Sphagnum* moss and the cups were covered with a loose lid (except for Tharandt where they were covered with voile net) and stored in an open shed, out of direct sunlight.

The pupae were sexed and weighed with a precision scale 6-10 days after pupation. Each pupa was weighed three times consecutively on the same day and the average of the three measurements was recorded as the pupal mass. In capital breeders, i.e. moth species that do not feed as adults, the pupal mass of females correlates with the number of eggs they are able to produce (Hough & Pimentel 1978, Gilbert 1984, Honěk 1993, Tammaru & Haukioja 1996).

A set of five *L. monacha* and five *L. dispar* pupae from a parallel laboratory breeding were weighed once per day from the 5th to the 14th day of their pupal period to assess whether the pupal mass changes as the pupae mature. No considerable changes in pupal mass occurred between the 6th and the 10th day of the pupal period, thus we consider all the pupal masses measured in the experiment to be reliably comparable with each other.

The plastic cups were checked with one- to three-day intervals for emerged adults. The date of emergence was calculated in the same way as the date of pupation. The duration of the pupal period was measured in days.

We used degree days above 5 °C (dd5), i.e. the cumulative sum of daily average temperatures exceeding the base level of 5 °C, as a measurement for timing of the pupation and adult emergence.

The temperature sum was used instead of days, as temperature is much more likely to affect insect lifecycle than the simple passing of arbitrary time units. The 5 degrees Celsius threshold was chosen not because of its likely biological relevance for the phenological processes of the study species, but because it is well suited for comparing the progress of spring and summer on the three study sites (Figs. 1, A1). The true developmental threshold temperatures for the different life stages of these *L. monacha* and *L. dispar* populations are not known, and using a temperature threshold that differs from the one recognized by the moth may lead to false interpretations of differences between moths originating from the same population but reared in different locations. To avoid this problem, we compared the results obtained using the 5 °C threshold with the results from the same statistical analyses performed using 2-10 °C with one degree Celsius intervals as threshold values. The 5 °C threshold for the analyses of pupation and emergence timing gave, most of the time, similar results as higher (up to 10 °C) thresholds and was rather conservative in comparison to lower (down to 2 °C) thresholds, which tended to reveal more significant differences between the test groups reared at the different sites. Thus, if the true developmental thresholds for *L. monacha* and *L. dispar* are higher than 5°C, the results remain valid, and if they are lower than that, the evidence for the differences we found would be even stronger. The cases where the results obtained using temperature thresholds other than 5 °C strongly conflict with the ones obtained using 5 °C are pointed out in the results.

2.4 Statistical analysis

Because the experimental design (e.g., numbers of host plants and populations of different origin) differed between *Lymantria monacha* and *L. dispar*, they were analysed separately. Nevertheless, the final data available for the analyses did not satisfy full factorial design for either species (see below and Table 1), obscuring tests of interactions among explanatory factors like the host plant, field site, sex, and population of origin. To obtain the highest possible number of treatment combinations per species, we were forced to merge field site, sex and, in the case of *L. monacha* also the population of origin, into one fixed factor, henceforth referred to as the test group. This yielded,

for example, “continental females reared at Kevo” and “boreal males reared in Tharandt” as two separate groups for the analysis.

Henceforth we refer to differences between test groups of individuals originating from the same population but reared in different locations (such as boreal males reared in Tharandt and boreal males reared in Turku) as *intrapopulation* differences. Correspondingly, differences between test groups of individuals of different origins but reared in the same location (such as continental females reared at Kevo and boreal females reared at Kevo) are here called *interpopulation* differences.

We used linear mixed models with the test group as the fixed factor to explain the following response variables: temperature sum at date of pupation, temperature sum at date of adult emergence, pupal mass and duration of pupal period. *A priori* contrasts were used to determine significant pairwise differences between the test groups of interest. To control for possible effects of genetic differences between the eggs of different females, batch was set as a random explanatory factor in all the models. Similarly, mesh bag (nested within batch) was set as a random factor to account for possible differences (e.g. in shade) between the two bags that each batch was divided into. The significances of the variation that the random explanatory factors accounted for were tested using likelihood-ratio tests (LRTs). A significant difference here means that part of the observed variation in the results can be explained by differences between broods or between the two mesh bags the eggs of a brood were divided into. Investigation of these random effects were not among the aims of this study, but they were accounted for in order to achieve more powerful tests for the fixed factors that were the main target of the study.

We refrained from comparing *L. dispar* groups in Turku, where *L. dispar* was reared on oak, and Kevo, where *L. dispar* was reared on birch, as the possible differences may have been contributed by the different host plants. However, we compared *L. dispar* groups in Tharandt and Kevo reared on the local birch species, *B. pendula* and *B. pubescens ssp. czerepanovii* respectively, despite possible differences between these two host species. *Betula pubescens* ssp. *czerepanovii* is a potential and the

most abundant food source for *L. dispar* in northern Fennoscandia beyond the distribution range of *B. pendula* and was, for the purpose of this study, considered similar enough to *B. pendula* for a comparison to be meaningful.

To test the effects of host plants on the timing of phenological events and pupal mass of *L. dispar* in Tharandt, a second set of models was used with the same random explanatory variables and host plant, sex and the interaction between the two as fixed factors.

Model assumptions on the normality and homoscedasticity were checked from residuals. Denominator degrees of freedom and standard errors of the fixed factors were approximated by the Kenward-Roger adjustment, facilitating accurate F-tests of the fixed factors (Kenward & Roger 1997, Littell et al. 2006). The GLIMMIX procedure in SAS v. 9.4 (SAS Institute Inc., Cary) was used for all analyses (Littell et al. 2006, Stroup 2013).

In certain cases, single measurements or moth individuals were omitted from the dataset. This was done in a) 32 cases where the sex of the pupa could not be determined, b) 15 cases where the adult moth at Kevo did not emerge from the pupae during the experimental period outdoors, but over a month later at room temperature (pupal mass and pupation date was still included in the data), c) 10 cases where the pupa was parasitized, d) 4 cases where either the emergence or pupation dates were uncertain (pupal mass was still included in the data) and e) 3 cases where the pupa was clearly dead on the day of weighing (date of pupation was still included in the data, but not pupal mass). In addition, continental *L. monacha* pupae from Kevo were omitted from the analyses, as there were only four of them, one male and three of undetermined sex.

Results

The number of pupae and emerged adult moths and their share of the original number of eggs in the experiment is presented in Table 1. Figure A1 in the appendix shows the development of summer temperatures and day length as well as the pupation and emergence periods of *L. monacha* and *L. dispar* at each field site.

3.1 Pupation

Boreal *L. monacha* larvae pupated at lower temperature sums than continental ones in both Turku and Tharandt (Fig. 2a, b, Table A1). There were intrapopulation differences in the timing of pupation for boreal *L. monacha*. Both males and females pupated at a lower temperature sum at Kevo than in Tharandt. In addition the males pupated at a lower temperature sum in Turku than in Tharandt, and the females at a lower temperature sum at Kevo than in Turku. No such indications of phenotypic plasticity were found in pupation timing between continental *L. monacha* in Tharandt and Turku (Fig. 2a, b, Table A1). The test group (field site, sex and, in the case of *L. monacha* also the population of origin were merged into one variable) was a significant fixed factor in the temperature sum model for both species (*L. monacha*: $F_{9,\ 111.8}$=8.2; p<0.0001, *L. dispar*: $F_{7,\ 202.9}$=42.0; p<0.0001). The batch, as a random factor, was not statistically significant for either species (LRTs: *L. monacha*: p=0.13, *L. dispar*: p=0.074), while the mesh bag (nested within the batch) was a significant random factor for both species (LRTs: *L. monacha*: p=0.0037, *L. dispar*: p=0.0036).

Both male and female *L. dispar* pupated at lower temperature sums at Kevo than in Tharandt. In addition, *L. dispar* females pupated at a lower temperature sum in Turku than in Tharandt, and the tendency was the same for males (Fig. 2c, Table A1), although for males the significance of the difference varied greatly depending on the temperature threshold used, and could therefore not be reliably determined.

In Tharandt *L. dispar* reared on oak pupated at a lower temperature sum than those reared on birch, the difference in estimates of pupation timing being 55.0 dd5 (*SE*=11.0). Sex and host plant were both significant fixed factors in the host plant model for *L. dispar* (sex: $F_{1,\ 101.3}$=4.08, p=0.046; host plant: $F_{1,\ 104.7}$=24.9, p<0.0001), while the interaction between host plant and sex was not significant ($F_{1,\ 99.92}$=2.69, p=0.104).

3.2 Pupal mass

Continental *Lymantria monacha* females were larger than boreal females both in Tharandt and in Turku. There were no significant intrapopulation differences in pupal mass between *L. monacha* individuals reared at different field sites (Fig. 3a, b, Table A1). The test group (see 3.1 for definition) was a significant fixed factor in the pupal mass model for both species (*L. monacha*: $F_{9, 96.9}$=24.3; p<0.0001, *L. dispar:* $F_{7, 199.2}$=59.0; p<0.0001). Neither batch nor mesh bag (nested within batch) as a random factor was statistically significant for either species (LRTs: *L. monacha*: batch: p=0.45, mesh bag: p=0.49; *L. dispar*: batch: p=0.19, mesh bag: p=0.38).

At Kevo the female *L. dispar* pupae were significantly heavier than in Tharandt (Fig. 3c, Table A1). In Tharandt pupae were about 0.11 g (*SE*=0.046), that is, about 10 %, heavier on oak than on birch. Sex and host plant were both significant fixed factors in the host plant model for *L. dispar* (sex: $F_{1, 110.9}$=199.2, p<0.0001; host plant: $F_{1, 111.2}$=5.9, p=0.017), while the interaction between host plant and sex was not significant ($F_{1, 108.3}$=0.11, p=0.75).

3.3 Duration of the pupal period

The only interpopulation difference was the shorter pupal period of continental *L. monacha* males than that of boreal ones in Turku. Intrapopulation differences among the field sites were found for continental *L. monacha* males and boreal *L. monacha* females, both of which had a significantly longer pupal period in Tharandt than in Turku (Fig. 4a,b, Table A1). The test group (see 3.1 for definition) was a significant fixed factor in the model for the duration of the pupal period for both species (*L. monacha*: $F_{7, 53.4}$=8.7; p<0.0001, *L. dispar*: $F_{5, 107.8}$=7.6; p<0.0001). Neither batch, nor mesh bag (nested within the batch) as a random factor was statistically significant for *L. dispar* (LRTs: batch: p=0.42, mesh bag: p=0.42), but mesh bag was significant for *L. monacha* (LRTs: batch: p=0.36, mesh bag: p=0.014).

Lymantria dispar had a longer pupal period in Tharandt than in Turku (Fig. 4c, d, Table A1). Neither host plant, nor sex or the interaction between the two were significant fixed factors in the

host plant model for *L. dispar* (sex: $F_{1, 73.6}$=2.54, p=0.12; host plant: $F_{1, 73.3}$=1.28, p=0.26; interaction: $F_{1, 73.0}$=0.28, p=0.60).

3.4 Adult emergence

Continental *L. monacha* emerged at higher temperature sums than boreal ones (Fig. 5a, b, Table A1). Intrapopulation differences were significant only for boreal male *L. monacha*, which emerged at a higher temperature sum in Tharandt than in Turku (Fig. 5b, Table A1). The test group (see 3.1 for definition) was a significant fixed factor in the temperature sum model of the timing of adult emergence for both species (*L. monacha*: $F_{7, 73.0}$=5.4; p<0.0001, *L. dispar*: $F_{5, 107.7}$=7.2; p<0.0001). Neither batch, nor mesh bag (nested within batch) as a random factor was statistically significant for *L. dispar* (LRTs: batch: p=0.14, mesh bag: p=0.38), but both were significant for *L. monacha* (batch LRT: p=0.021, mesh bag LRT: p=0.033).

Lymantria dispar adults had the tendency to emerge at a lower temperature sum in Turku than in Tharandt, but the significance of the differences in varied greatly depending on what temperature threshold was used, and thus nothing certain can be concluded about them (Fig. 5c, d, Table A1). In Tharandt, *L. dispar* reared on oak emerged at a lower temperature sum than those reared on birch, the difference in timing being 75.4 dd5 (*SE* 16.9) which corresponds to 5-6 days (Fig. A1a, Table A1). The host plant was a significant fixed factor in the host plant model for *L. dispar* ($F_{1, 69.5}$=19.9; p<0.0001), while the sex had no effect on the timing of adult emergence (sex: $F_{1, 69.8}$=0.07, p=0.79; host plant × sex interaction: $F_{1, 68.8}$=0.09, p=0.77).

4. Discussion

Individuals from all lymantriin populations in the experiment succeeded in pupating and emerging as adults both in Tharandt, Germany and in Turku, Southern Finland. The number of pupae and adults was slightly higher in Tharandt for *L. monacha* and in Turku for *L. dispar* (Table 1). All *L. monacha* and *L. dispar* failed to complete their entire life cycle at Kevo in the short, cool summer of northern Finland (Fig. A1c). However, a few of the pupae of both species hatched considerably later

in mid-October when transferred to room temperature. This suggests that adult emergence in these species is regulated by temperature – either the pupal development slowed down considerably in the low outdoor temperatures and the process was not yet finished by the time the experiment was cancelled, or some threshold temperature or temperature sum crucial for the development was not reached. Although we cannot draw any conclusions about the adaptive nature of this delay based on our data, it is conceivable that such a temperature dependent delay in pupal development would allow the pupae to "wait out" temporary unfavourable cold periods in late summer, postponing adult emergence to a time more favourable for flight.

Our temperature sum model revealed interpopulation differences – that is, differences between test moths originating from different populations but reared in the same location – for *L. monacha* with the boreal ones both pupating and emerging at a lower temperature sum, that is, earlier in the season, than the continental ones (Figs. A1a, b; 2a, b; 5a, b). This may reflect a local adaptation to shorter summers in the boreal *L. monacha* population. If so, the adaptation may have developed rapidly, as the species was probably established in the country first after the 1950's (Grönblom & Suomalainen 1950). However, it would be interesting to compare the Finnish boreal population with its closest neighbours in Sweden and Estonia. Jankovic et al. (1960) discovered similar local differences in timing of life cycle events between northern and southern *L. dispar* populations in former Yugoslavia, and different strains of the species have also been studied at least by Leonard (1966), but to our knowledge no such comparisons have previously been made with *L. monacha*.

Intrapopulation differences – here referring to differences between moths originating from the same population but reared in different locations – in life cycle timing potentially indicate adaptive phenotypic plasticity that allows fast, within-generation reactions to varying environments. Such differences between locations were most evidently absent for continental *L. monacha.* They pupated and emerged at approximately the same temperature sum both in Turku and in Tharandt (Figs. 2a, b; 5a, b; Table A1), which translated to a later date in Turku (Fig. A1a, b). A significant difference in pupation and emergence timing could only be found using the lowest temperature threshold, 2 °C,

and even then only for males. It appears that the continental *L. monacha* was not able to adjust its life cycle timing within one generation to follow optimally the northern summer season. Instead, it attempted to pupate at a similar temperature sum as in its region of origin. The effect was driven to its limit in the northernmost location, where only four continental *L. monacha* succeeded in pupating at all.

For boreal *L. monacha* and continental *L. dispar* the picture was more complicated. However, both had a tendency to pupate and emerge at a lower temperature sum in the north than in the south, even more so when using temperature thresholds below 5 °C (Figs. 2, 5, Table A1). It is possible, that the boreal *L. monacha* population, which struggles at the northern limit of the distribution range of the species, has greater adaptive phenological plasticity than the continental population, facilitating acclimation to varying environments. According to this hypothesis, *L. monacha* would display *high margin plasticity* or *high leading edge plasticity*, as defined by Valladares et al. (2014). However, this would not explain the similar results obtained with continental *L. dispar*.

Both *L. monacha* and *L. dispar* had a tendency towards a shorter pupal period in Turku than in Tharandt. This is likely due to faster pupal development at higher temperatures (Fig. A1). Duration of the pupal period might also simply be linked to the previous results concerning timings of pupation and emergence timing. The progress of both temperature sum and day length is steeper in Turku than in Tharandt (Fig. A1a, b), which could mean that limiting cue values for pupation and emergence follow each other with a shorter interval in Turku, accelerating the pupal development.

The experiment revealed that *L. dispar* was fully able to complete its life cycle in southern Finland. In fact, more *L. dispar* larvae pupated in Turku than in Tharandt. However, the difference in numbers of emerged adults was negligible (Table 1), which means that pupal mortality was higher in Turku. Interestingly, *Lymantria dispar* has been observed more frequently in Finland during the past decade than earlier (Insect Observation Data Base). Based on our results, it seems possible that the species has established a local population on the south coast of the country.

Even though no *L. dispar* adults emerged at Kevo, the larvae were able to complete their development and pupate on *B. pubescens* ssp. *czerepanovii*, the same being true for larvae on *B. pendula* in Tharandt, which indicates that host plant availability would not limit the range expansion of this generalist pest in Fennoscandia, where various *Betula* species are readily available. However, *L. dispar* developed slightly faster on *Q. robur* than on *B. pendula*, and the pupae of larvae reared on *Q. robur* were heavier. All three tree species are listed as preferred host plants for *L. dispar* by Lechowicz & Mauffette (1986), though the specific subspecies of *B. pubescens* is not mentioned on the list. Although we considered the two birch species similar enough for relevant comparisons, there does remain a possibility that our results concerning the differences between *L. dispar* at Kevo and in Tharandt are, at least partly, influenced by the host plant. However, we strongly doubt that host plant species has influenced the major conclusion that *L. dispar* is able to finish its life cycle in Tharandt and Turku but not in Kevo.

The data contained certain unexpectedly short pupal periods of both *L. monacha* and *L. dispar*. The shortest pupal period observed was only 5.5 days (boreal *L. monacha* in Turku), and a total of 38 pupae had pupal periods below 10 days, most of them observed in Turku. Generally pupal periods of *L. monacha* and *L. dispar* are reported to be about two weeks (Campbell 1967), which is clearly longer than that reported for most test groups here (Fig. 4). The effect may, at least partly, be explained by the longer day in Turku accelerating the pupal development (Bogach et al. 1966, Kireeva 1969). The method of determining the date of pupation (see Chapter 2.3) may have led to an error of 3-3.5 days in four cases and 2.5 days in eight additional cases, with the error being maximally 2 days in all other cases, but this was as more likely to falsely lengthen rather than to shorten the pupal period.

Our study setup was not designed to reveal any possible developmental temperature sum thresholds for the studied species. Instead, the temperature sum as a response variable enabled comparison of the summer seasons at our three field sites, giving biologically more meaningful measurements for ”earlier” or ”later” than mere calendar dates would have allowed. Day length, instead of

temperature, is estimated to be the most important environmental cue for the timing of phenology in temperate insects (de Wilde 1962, Bale et al. 2002). Previous literature confirms that day length also plays a role also for at least *L. dispar* (Bogach et al. 1966, Leonard 1968, Kireeva 1969, Denlinger et al. 1992). However, almost all previous research on life cycle timing of our study species concerns diapause induction and termination, which occurs in winter during the pharate-larval stage in eggs (Tauber et al. 1990, Gray et al. 1991, Keena 1996, Patterson et al. 1999, the latter, however, listing the photoperiod as irrelevant for *L. dispar* diapause control). The triggers relevant for other life cycle events are not well understood. There were differences between the summer seasons at our field sites not only in the temperatures, but also in day length (Fig. A1). It is conceivable that these differences of several hours could hamper the range expansion of *L. monacha* and *L. dispar* across latitudes and require special adaptations or adaptive phenotypic plasticity in the same way as temperature differences do.

We conclude that, while neither *L. monacha* nor *L. dispar* were able to fully complete their life cycle in northernmost Finland, both local and continental *L. monacha* strains as well as continental *L. dispar*, a species not yet established in Finland, performed well when reared outdoors on the south coast of the country. Intrapopulation differences in life cycle timing, possibly indicative of adaptive phenotypic plasticity facilitating a fast reaction to new environmental conditions, were clearer for continental *L. dispar* and boreal *L. monacha* than for continental *L. monacha*. Interpopulation differences in life cycle timing and pupal mass were revealed between boreal and continental *L. monacha*, possibly pointing to an adaptation to local environmental conditions. The three host plants used for *L. dispar*, *Q. robur*, *B. pendula* and *B. pubescens* ssp. c*zerepanovii* all proved suitable for the species, revealing that host plant availability would not limit range expansion of *L. dispar* in northern Fennoscandia.

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References

Ammunét, T., Klemola, T., and Saikkonen, K. 2011. Impact of host plant quality on geometrid moth expansion on environmental and local population scales. Ecography **34**(5): 848–855. doi: 10.1111/j.1600-0587.2011.06685.x

Ammunét, T., Kaukoranta, T., Saikkonen, K., Repo, T., and Klemola, T. 2012. Invading and resident defoliators in a changing climate: cold tolerance and predictions concerning extreme winter cold as a range-limiting factor. Ecol. Entomol. **37**(3): 212–220. doi: 10.1111/j.1365-2311.2012.01358.x

van Asch, M., and Visser, M.E. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. Annu. Rev. Entomol. **52**: 37–55. doi: 10.1146/annurev.ento.52.110405.091418

Bale, J.S., Masters, G.J., Hodkinson, I. D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., and Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. **8** (1): 1–16. doi: 10.1046/j.1365-2486.2002.00451.x

Bejer, B., 1988. The nun moth in European spruce forests. *In* Dynamics of forest insect populations. Patterns, causes, implications. *Edited by* A.A. Berryman. Plenum Press, New York and London. pp. 211–231.

Björkman, C., and Niemelä, P. (editors). 2015. Climate Change and Insect Pests. CABI Publishing. 291 p.

Bogach, A.V., Zolotoverkha, I.M., and Kirichenko, O.I. 1966. The importance of light and temperature in the reproduction of some species of Lepidoptera (*Porthetria dispar* L. and *Bombyx mori* L.). Dopov. Akad. Nauk Ukr. **6**:825–827. [In Ukrainian, English summary.]

Buse, A., and Good, J. 1996. Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. Ecol. Entomol. **21**(4): 335–343. doi: 10.1046/j.1365-2311.1996.t01-1-00001.x

Campbell, R.W. 1967. The analysis of numerical change in gypsy moth populations. Forest Sci., Monograph 13 (Supplement to Number 3): a0001–z0001 (1).

Danks H.V. 1987. Insect dormancy: An Ecological Perspective. Biological Survey of Canada Monograph Series, No 1. Entomological Society of Canada, Ottawa, Canada. 439 p.

Denlinger, D.L., Lee, R.E., Yocum, G.D., and Kukal, O. 1992. Role of chilling in the acquisition of cold tolerance and the capacitation to express stress proteins in diapausing pharate larvae of the gypsy moth, *Lymantria dispar*. Arch. Insect Biochem. Physiol. **21**(4): 271–280. doi: 10.1002/arch.940210404

European Environment Agency 2012. Biogeographic regions in Europe. [online] Available from e001d623865845e3ba8f6bd2f28a5ed3. European Environment Agency, Copenhagen, Denmark. [accessed 3 November 2016]

Forbush, E. H., and Fernald, C. H. 1896. The gypsy moth. Wright and Potter, Boston. 495 p.

Foster, J.R., Townsend, P.A., and Mladenoff, D.J. 2013. Mapping asynchrony between gypsy moth egg-hatch and forest leaf-out: Putting the phenological window hypothesis in a spatial context. For. Ecol. Manage. **287**: 67–76. doi: 10.1016/j.foreco.2012.09.006

Gerding, G. 2016. Finden Sie hier die Zeiten des Sonnenaufgangs und des Sonnenuntergangs für jeden beliebigen Ort [online]. Available from http://www.sonnenaufgang-sonnenuntergang.de [accessed 26 August 2016].[in German.]

Gilbert, N. 1984. Control of fecundity in Pieris rapae: I. The problem. J. Anim. Ecol. 53(2): 581–588. doi: 10.2307/4536

Gray, D.R., Logan, J.A., Ravlin, F.W., and Carlson, J.A. 1991. Toward a model of gypsy moth egg phenology: using respiration rates of individual eggs to determine temperature–time requirements of prediapause development. Environ. Entomol. **20**(6):1645–1652. doi: 10.1093/ee/20.6.1645

Gray, D.R.. Hitchhikers on trade routes: A phenology model estimates the probabilities of gypsy moth introduction and establishment. Ecol. Appl. **20**(08): 2300–2309. doi: 10.1890/09-1540.1

Grönblom, T., and Suomalainen, E. 1950. Über das Vorkommen der Nonne, *Lymantria monacha L.* in Finnland. Ann. Ent. Fennici **16**: 178–181. [in German.]

Hindle, B. J., Kerr, C. L., Richards, S. A., and Willis, S. G. 2015. Topographical variation reduces phenological mismatch between a butterfly and its nectar source. J. Insect Conserv. **19**(2): 227–236. doi:10.1007/s10841-014-9713-x

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos **66**(3): 483–492.

Hough, J.A., and Pimentel, D. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. Environ. Entomol.**7**(1): 97–102.

Insect Observation Data Base (Hyönteistietokanta) [online] Available from http://hyonteiset.luomus.fi/insects/main/EntDatabase.html. Finnish Museum of Natural History, Helsinki, Finland. [accessed 26 August 2016] [In Finnish.]

Jankovic, M., Zecevic, D., and Vojnovic, V. 1960. Races of the gipsy moth in Yugoslavia (Report for 1959). Zaštita Bilja **56**: 99–107. [In Serbo-Croatian, English summary.]

Jepsen, J.U., Hagen, S.B., Ims, R.A., and Yoccoz, N.G. 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. J. Anim. Ecol. **77**(2): 257–264. doi: 10.1111/j.1365-2656.2007.01339.x

Jepsen, J.U., Kapari, L., Hagen, S.B., Schott, T., Vindstad, O.P.L., Nilssen, A.C., and Ims, R.A. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Glob. Change Biol. **17**(6): 2071–2083. doi: 10.1111/j.1365-2486.2010.02370.x

Kaitaniemi, P., Scheiner, A., Klemola, T., and Ruohomäki, K. 2012. Multi-objective optimization shapes ecological variation. Proc. R. Soc. B **279** (1729): 820–825. doi: 10.1098/rspb.2011.1371

Karolewski, P., Grzebyta, J., Oleksyn, J., and Giertych, M. J. 2007. Effects of temperature on larval survival rate and duration of development of *Lymantria monacha* (L.) on needles of *Pinus sylvestris* (L.) and of *L. dispar* (L.) on leaves of *Quercus robur* (L.). Pol. J. Ecol. **55**(3): 595–600.

Keena, M.A. 1996. Comparison of the hatch of *Lymantria dispar* (Lepidoptera: Lymantriidae) eggs from Russia and the United States after exposure to different temperatures and durations of low temperature. Ann. Entomol. Soc. Am. **89**(4):564–572. doi: 10.1093/aesa/89.4.564

Keena, M.A. 2003. Survival and Development of *Lymantria monacha* (Lepidoptera: Lymantriidae) on North American and Introduced Eurasian Tree Species. J. Econ. Entomol. **96**(1): 43–52. doi: 10.1093/jee/96.1.43

Kenward, M.G., and Roger, J.H. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics **53:**983-997. Available from

http://people.umass.edu/bioep740/topics/biometrics-1997-kenward.pdf [accessed 3 November 2016].

Kireeva, I. M. 1969 Peculiarities of the *Porthetria dispar* L. pupal development under different photothermal conditions. Vestnik Zoologii **1**:86–88. [In Ukrainian, English summary.]

Lechowicz, M.J., and Mauffette, Y. 1986. Host preferences of the gypsy moth in eastern North American versus European forests. Revue d'entomologie du Quebec. **31**(1), 43–51.

Leinonen, R., Pöyry, J., Söderman, G., and Tuominen-Roto, L. 2016. Suomen yöperhosseuranta (Nocturna) 1993–2012. Suomen ympäristökeskuksen raportteja 15/2016. Suomen ympäristökeskus, Helsinki, Finland. [In Finnish.]

Leonard, D.E. 1966. Differences in development of strains of the gypsy moth, *Porthetria dispar* (L.). 1966. Bulletin of the Connecticut Agricultural Experiment Station, New Haven. No. 680.

Leonard, D.E. 1968. Diapause in the gypsy moth. J. Econ. Entomol. **61**(3): 596–598. doi: 10.1093/jee/61.3.596

Leonard, D.E. 1974. Recent developments in ecology and control of the gypsy moth. Annu. Rev. Entomol. **19**(1):197–229. doi: 10.1146/annurev.en.19.010174.001213

Liebhold, A.M., Halverson, J.A., and Elmes, G.A. 1992. Gypsy moth invasion in North America: a quantitative analysis. J. Biogeogr. (5):513–520.

Liebhold, A.M., Elkinton, J., Williams, D., and Muzika, R.M. 2000. What causes outbreaks of the gypsy moth in North America? Popul. Ecol. **42**(3):257–266. doi: 10.1007/PL00012004

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., and Schabenberger, O. 2006. SAS® for mixed models, 2nd edition, SAS Institute Inc., Cary, NC, USA

Majunke, C., Möller, K., and Funke, M. 2004.Waldschutz-Merkblatt 52 – Die Nonne. 3 edn. Eberswalde und Finkenkrug: Landesforstanstalt Eberswalde. Eberswalde, Germany. 24 p.

Memmott, J., Craze, P.G., Waser, N.M., and Price, M.V. 2007. Global warming and the disruption of plant–pollinator interactions. Ecol. Lett. **10**(8): 710–717. doi: 10.1111/j.1461-0248.2007.01061.x

Nylin, S.,and Gotthard, K. 1998. Plasticity in life-history traits. Annu. Rev. Entomol.**43**:63–83. doi: 10.1146/annurev.ento.43.1.63

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., and Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature **399**(6736): 579–583. doi:10.1038/21181

Patterson, D.T., Westbrook, J.K., Joyce, R.J.V., Lingren, P.D., and Rogasik, J. 1999. Weeds, insects, and diseases. Clim. Change **43**(4): 711–727. doi: 10.1023/A:1005549400875

Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I., Nissinen, A., and Helander, M. 2012. Climate change–driven species' range shifts filtered by photoperiodism. Nat. Clim. Change **2**(4), 239–242. doi:10.1038/nclimate1430

Stroup, W.W. 2013. Generalized linear mixed models: modern concepts, methods and application, CRC Press, Boca Raton, FL, USA

Tammaru, T., and Haukioja, E. 1996. Capital breeders and income breeders among Lepidoptera: consequences to population dynamics. Oikos 77(3):561–564. doi: 10.2307/3545946

Tauber, M.J., Tauber, C.A., Ruberson, J.R., Tauber, A.J., and Abrahamson, P. 1990. Dormancy in Lymantria dispar (Lepidoptera: Lymantriidae): analysis of photoperiodic and thermal responses. Ann. Entomol. Soc. Am. **83**(3): 494–503. doi: 10.1093/aesa/83.3.494

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell W., van Kleunen, M., Naya D.E., Nicotra, A.B., Poorter, H., and Zavala, M.A. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. **17**(11): 1351–1364. doi: 10.1111/ele.12348

Valtonen, A., Ayres, M.P., Roininen, H., Pöyry, J., and Leinonen, R. 2011. Environmental controls on the phenology of moths: predicting plasticity and constraint under climate change. Oecologia **165**(1): 237–248. doi:10.1007/s00442-010-1789-8

Vanhanen, H., Veteli, T.O., Päivinen, S., Kellomäki, S., and Niemelä, P. 2007. Climate change and range shifts in two insect defoliators: gypsy moth and nun moth – a model study. Silva Fenn. **41**(4): 621–638. Available from http://www.metla.fi/silvafennica/full/sf41/sf414621.pdf [accessed 26 August 2016].

Visser, M.E., and Holleman, L.J., 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. Proc. R. Soc. B **268**(1464): 289–294.

Wie, J., Luo, Y.Q., Shi, J., Wang, D.P. and Shen, S.W., 2014. Impact of temperature on postdiapause and diapause of the Asian gypsy moth, *Lymantria dispar asiatica*. J. Insect Sci. **14** (5). doi: 10.1673/031.014.05

de Wilde, J. 1962. Photoperiodism in insects and mites. Annu. Rev. Entomol. 7(1): 1–26. doi: 10.1146/annurev.en.07.010162.000245

Yasyukevich, V.V., Titkina, C.N., Davidovich, E.A., and Yasyukevich, N.V. 2015. Changes in range boundaries of the gypsy moth and the nun moth (*Lymantria dispar*, *L. monacha*, Lymantriidae, Lepidoptera) due to the global warming: a model approach. Entomol. Rev. **95**(8): 1144–1148. doi:10.1134/S0013873815080229

Tables

Table 1. The number of egg batches, eggs, pupae and adult moths per species and host plant assigned for the three field sites. Each batch consisted of 16 eggs, divided into two vials (later two mesh bags). Individuals and single measurement values excluded from analyses (see Chapter 2.4) are not shown in the table – the discrepancy between the number of pupae used for the pupation time and pupal mass analyses is explained by cases where the pupation date was available but the pupal mass was not.

Field site	**Species and population of origin**	**Host plant**	**number of batches/eggs**	**Pupae for analysis (pupation/mass)**	**Adults for analysis**
Tharandt	*L. dispar* DE	Birch	7/112	57/57	41
50°58’N	*L. dispar* DE	Oak	7/112	61/61	37
13°50’E	*L. monacha* DE	Pine	7/112	41/40	28
	L. monacha S. FI	Pine	5/80	56/55	50
Turku	*L. dispar* DE	Oak	7/112	81/77	42
60°26’N,	*L. monacha* DE	Pine	7/112	21/20	13
22°10’E	*L. monacha* S. FI	Pine	5/80	41/32	20
Kevo	*L. dispar* DE	Birch	7/112	24/20	0
69°44'N,	*L. monacha* DE	Pine	7/112	0/0	0
27°00' E	*L. monacha* S. FI	Pine	5/80	21/21	0

Figures and figure captions

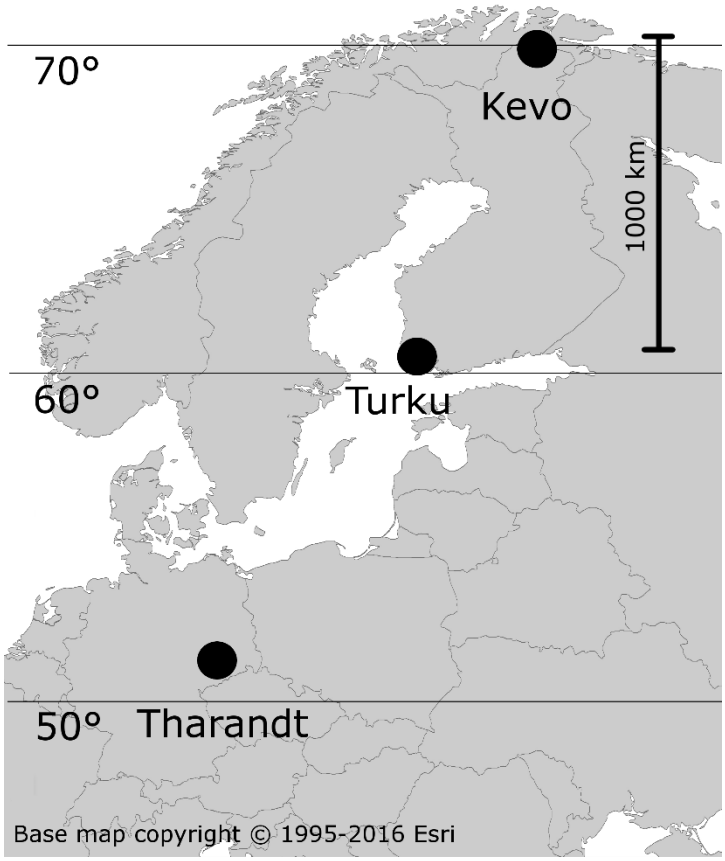

Fig. 1. Locations of the three field sites.

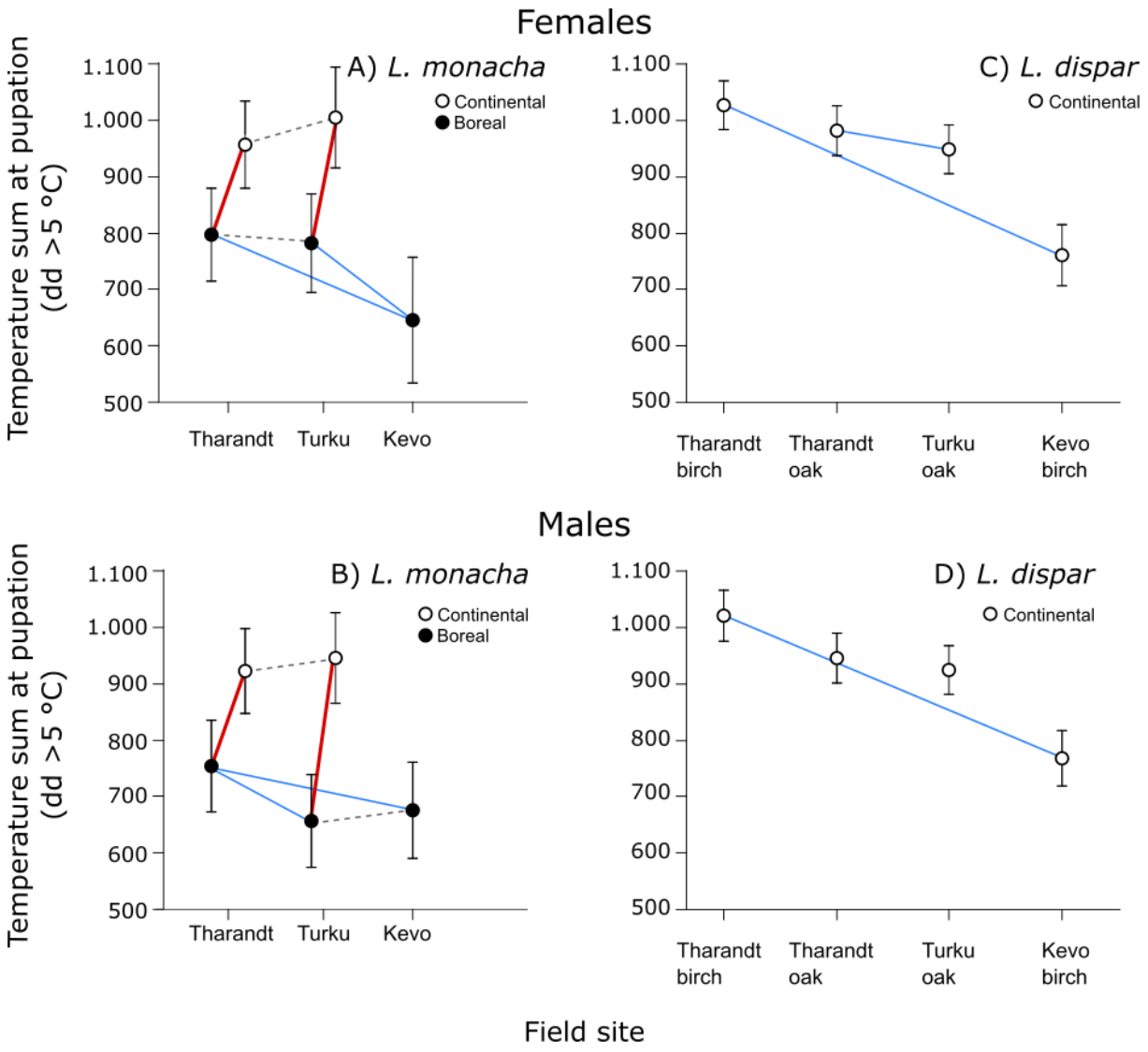

Fig. 2 Model-derived marginal mean estimates with 95% confidence limits for accumulated temperature sums (dd>5 °C) at pupation of *L. monacha* (A, B) and *L. dispar* (C, D). A priori contrasts marking pairwise differences between the test groups are displayed with lines: grey dashed lines (not statistically significant), thick red lines (significant interpopulation differences) and thin blue lines (significant intrapopulation differences). Exact statistical values are presented in Table A1.

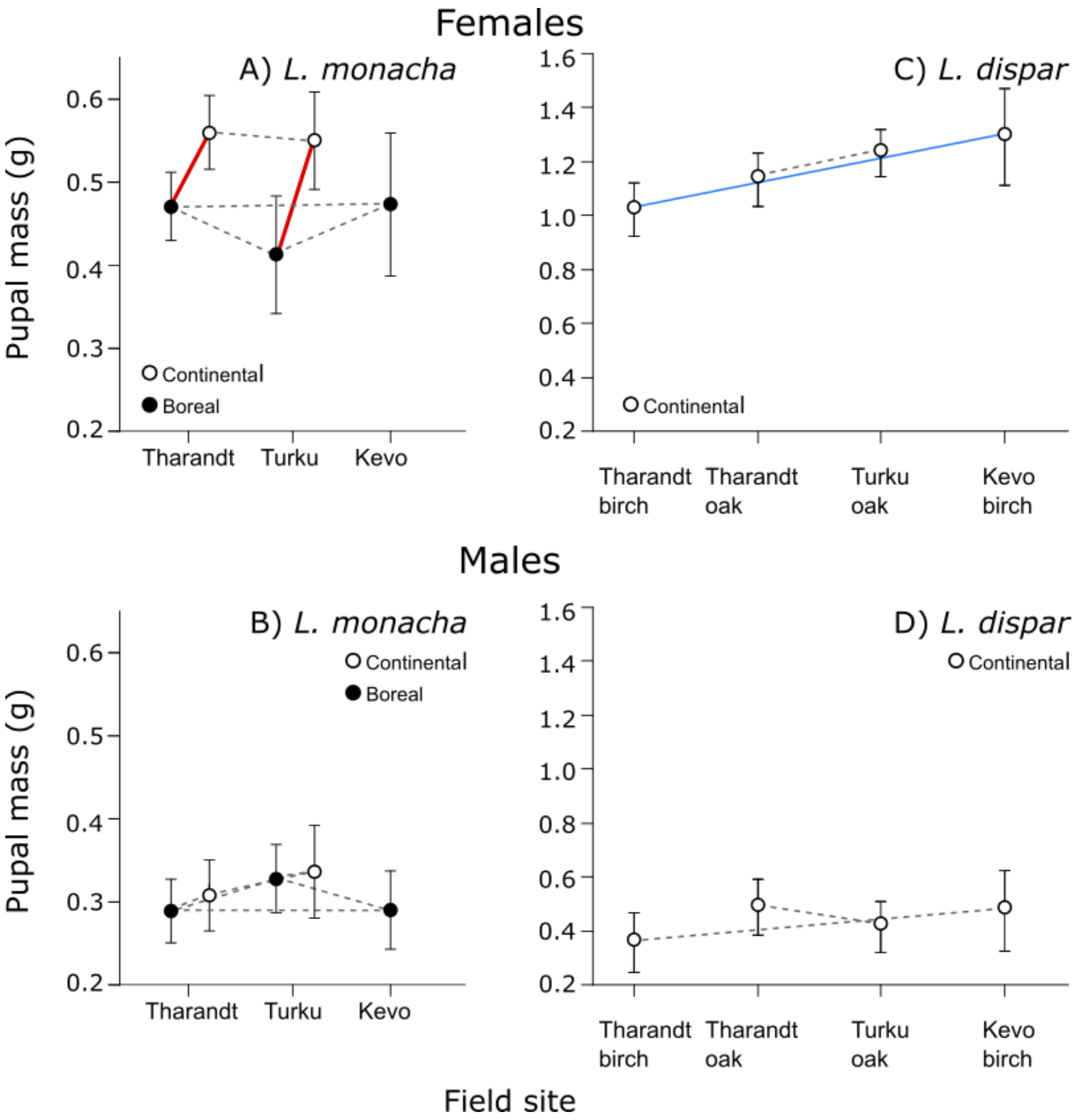

Fig. 3 Model-derived marginal mean estimates with 95% confidence limits for pupal mass (grams) of *L. monacha* (A, B) and *L. dispar* (C, D). A priori contrasts marking pairwise differences between test groups are displayed with lines: grey dashed lines (not statistically significant), thick red lines (significant interpopulation differences) and thin blue lines (significant intrapopulation differences). Exact statistical values are presented in Table A1. Note the different scales on the y-axis.

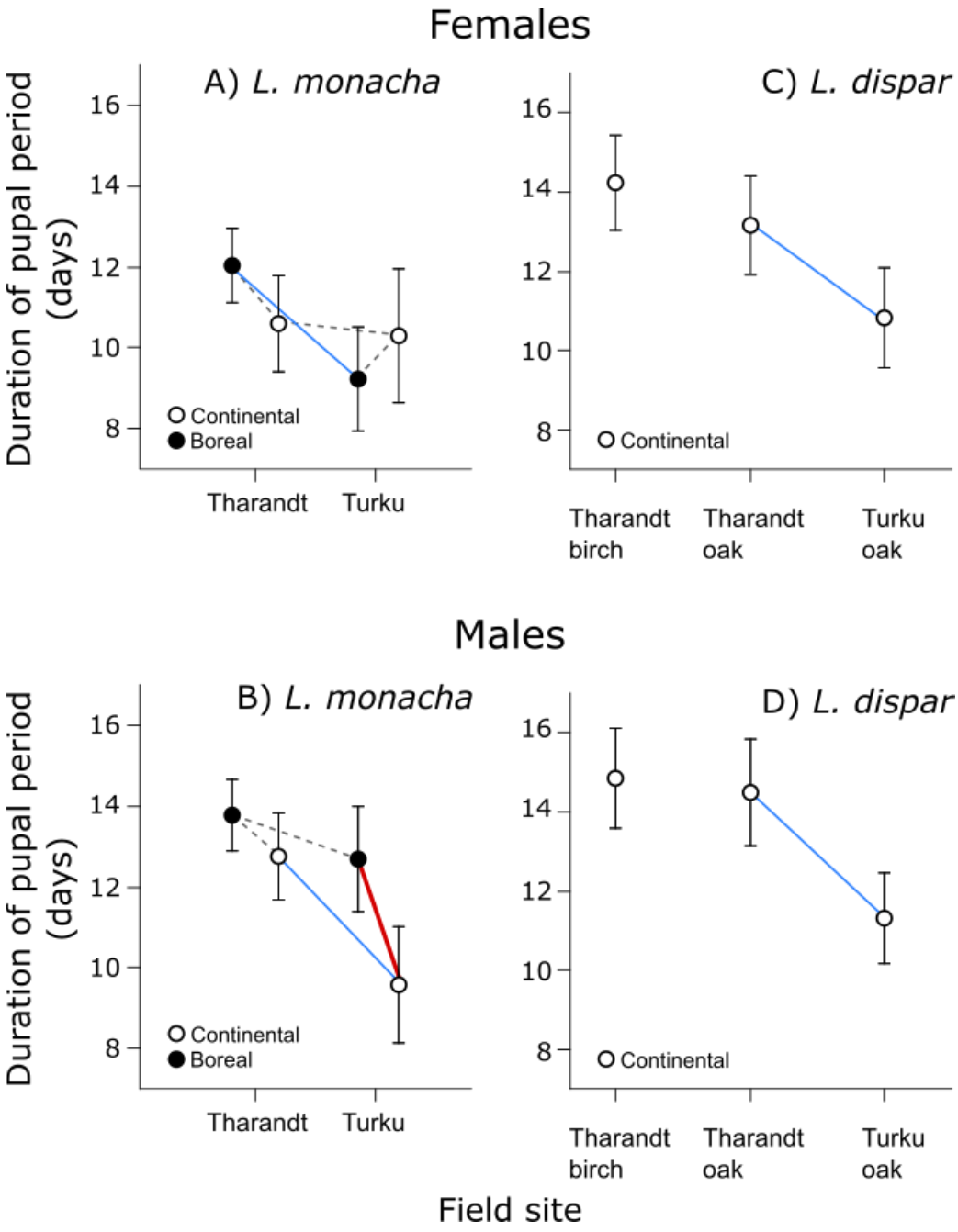

Fig. 4 Model-derived marginal mean estimates with 95% confidence limits for the duration of the pupal period (days) of *L. monacha* (A, B) and *L. dispar* (C, D). A priori contrasts marking pairwise differences between the test groups are displayed with lines: grey dashed lines (not statistically significant), thick red lines (significant interpopulation differences) and thin blue lines (significant intrapopulation differences). Exact statistical values are presented in Table A1.

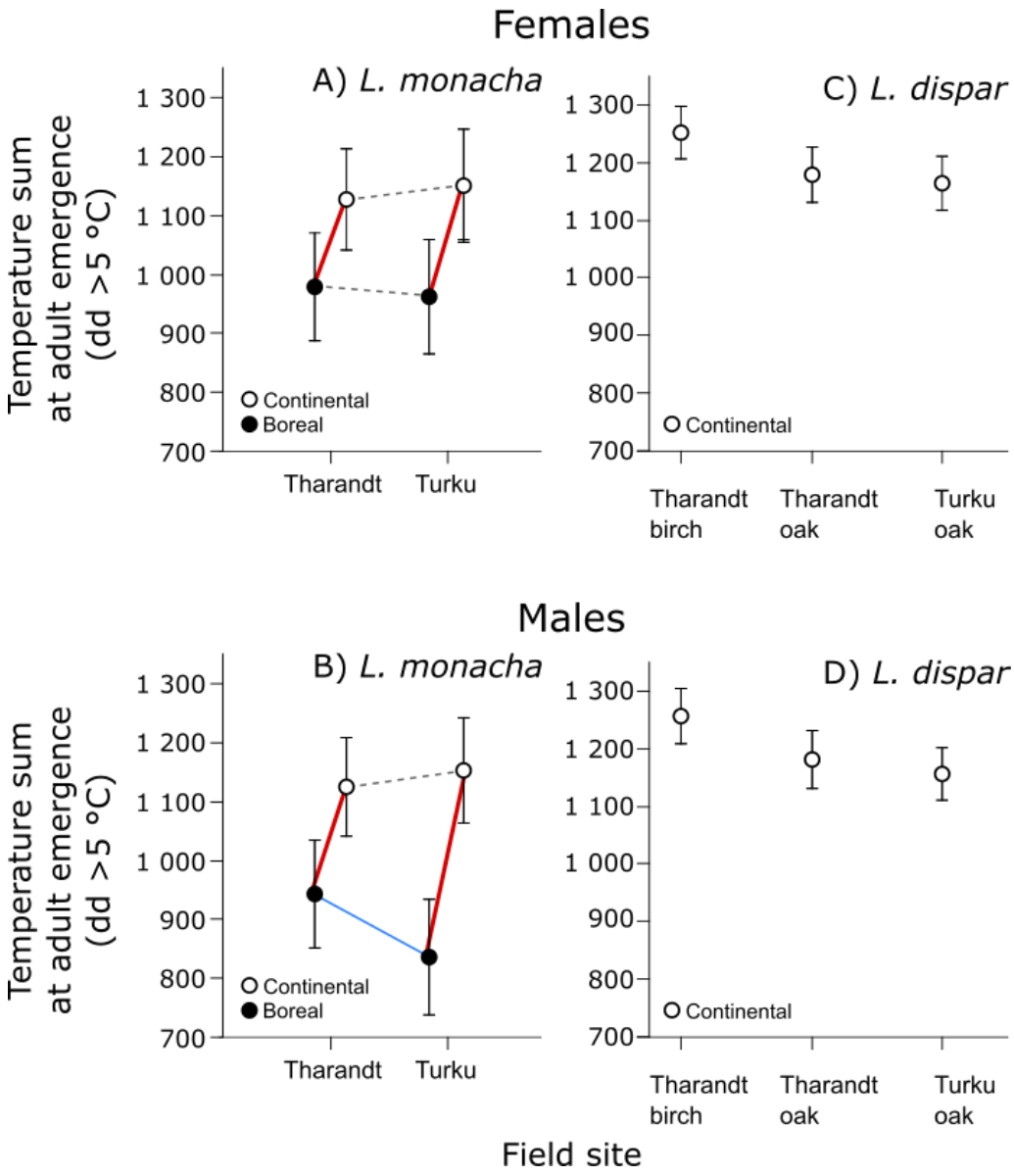

Fig. 5 Model-derived marginal mean estimates with 95% confidence limits for accumulated temperature sums (dd>5 °C) at adult emergence of *L. monacha* (A, B) and *L. dispar* (C, D). A priori contrasts marking pairwise differences between the test groups are displayed with lines: grey dashed lines (not statistically significant), thick red lines (significant interpopulation differences) and thin blue lines (significant intrapopulation differences). Exact statistical values are presented in Table A1.

Appendix

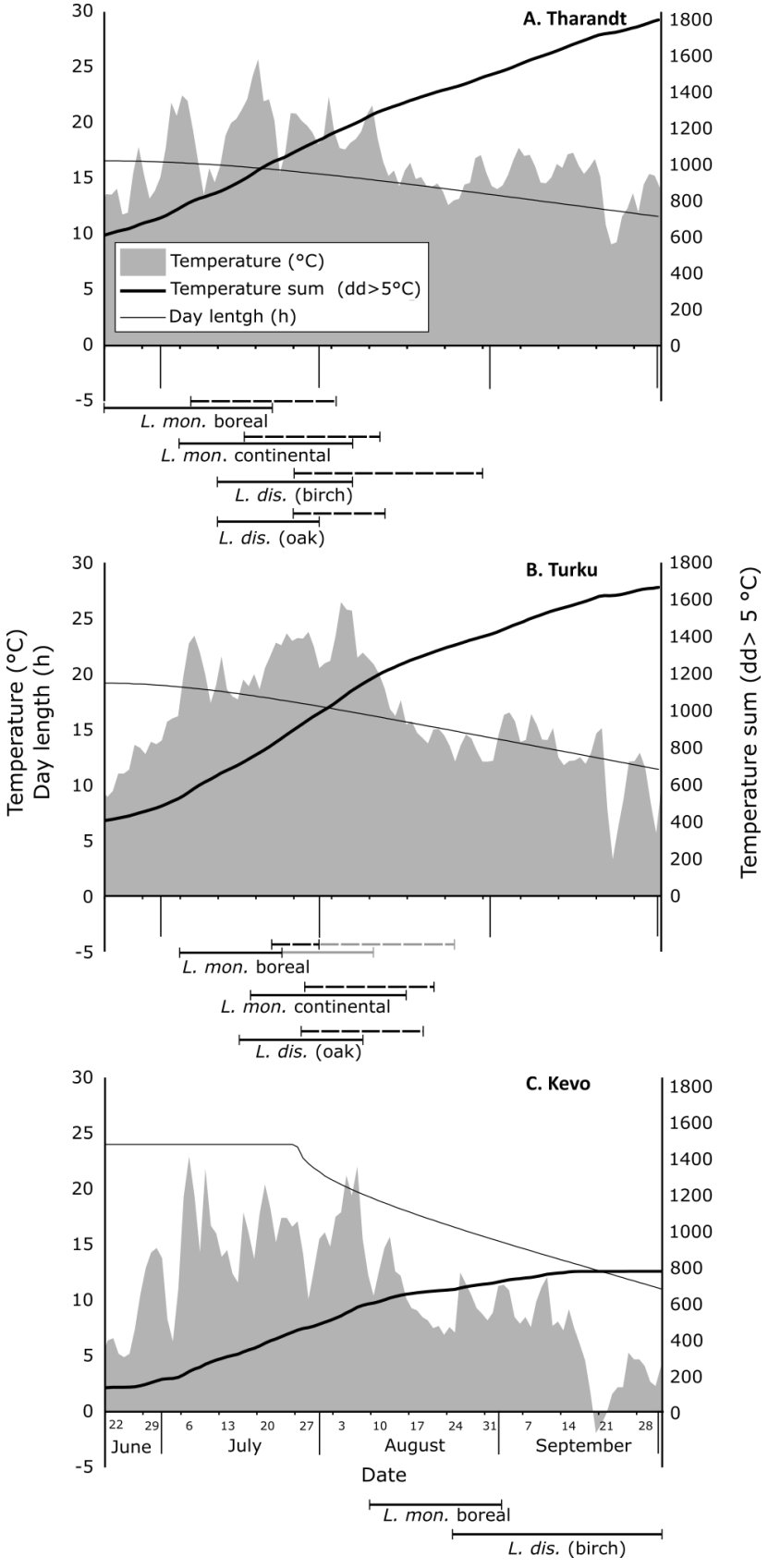
A. Tharandt
B. Turku
C. Kevo
Temperature (°C)
Day length (h)
Temperature sum (dd> 5 °C)
Temperature (°C)
Temperature sum (dd>5°C)
Day lentgh (h)
L. mon. boreal
L. mon. continental
L. dis. (birch)
L. dis. (oak)
22 29 6 13 20 27 3 10 17 24 31 7 14 21 28
June
July
August
September
Date

Fig. A1The phenology of *L. monacha* and *L. dispar* at the three field sites compared to local temperatures, temperature sums accumulated above 5 °C and day length. The lines below each graph correspond with the pupation period (solid line) and adult emergence (dashed line) of the test groups reared at each site. In Turku, there were two boreal *L. monacha* larvae that pupated considerably later than the rest and consequently one adult moth that emerged very late. The lines displaying *L. monacha* phenology in Turku have therefore been extended in grey to include these outliers. Removing these from the data would not have crucially changed the statistical significance of any of the results.

Table A1. A priori contrast statistics for pairwise comparisons of test groups. Statistically significant p-values in bold. Notice, that *intrapopulation* differences here simply refer to differences between test groups of individuals originating from the same population but reared in different location and *interpopulation* differences correspondingly to differences between test groups of individuals of different origins but reared in the same location.

			Pupation	**Pupal mass**	**Duration of pupal period**	**Adult emergence**
Interpopulation differences (indicative of local adaptations)			Temperature sum	Grams	Days	Temperature sum
L. monacha						
Tharandt	Bor. vs. Cont.	males	$F_{1,13.57}$=10.7, ***p*=0.006**	$F_{1,27.03}$=0.44, p=0.511	$F_{1,19.41}$=2.31, p=0.145	$F_{1,12.95}$=10.25, **p=0.007**
Tharandt	Bor. vs. Cont.	females	$F_{1,14.34}$=9.15, ***p*=0.009**	$F_{1,32.98}$=8.94, ***p*=0.005**	$F_{1,40.8}$=3.70, p=0.061	$F_{1,14.41}$=6.29, ***p*=0.025**
Turku	Bor. vs. Cont.	males	$F_{1,16.71}$=28.19, ***p*<0.0001**	$F_{1,47.48}$=0.07, p=0.799	$F_{1,60.67}$=10.44, ***p*=0.002**	$F_{1,19.07}$=25.09, ***p*<.0001**
Turku	Bor. vs. Cont	females	$F_{1,25.01}$=13.50, ***p*=0.001**	$F_{1,110.9}$=8.72, ***p*=0.004**	$F_{1,78.81}$=1.03, p=0.313	$F_{1,21.76}$=8.30, ***p*=0.009**
Intrapopulation differences (indicative of adaptive phenotypic plasticity)						
L. monacha						

Contin	Thar. vs.	mal	$F_{1,161.1}$=0.53,	$F_{1,156.2}$=0.82,	$F_{1,104.2}$=13.73,	$F_{1,99.07}$=0.60,
ental	Turku	es	p=0.467	p=0.368	***p*=0.0003**	p=0.440
Contin	Thar. vs.	fem	$F_{1,168.8}$=1.22,	$F_{1,144.5}$=0.07,	$F_{1,98.78}$=0.08, p=0.774	$F_{1,86.18}$=0.30,
ental	Turku	ales	p=0.270	p=0.791		p=0.588
Boreal	Thar. vs.	mal	$F_{1,155}$=16.6,	$F_{1,155.4}$=2.75,	$F_{1,97.69}$=2.10, p=0.151	$F_{1,87.9}$=13.79,
	Turku	es	***p*<0.0001**	p=0.099		***p*=0.0004**
Boreal	Thar. vs.	fem	$F_{1,155.3}$=0.28,	$F_{1,144.5}$=0.07,	$F_{1,94.41}$=14.38,	$F_{1,90.55}$=0.35,
	Turku	ales	p=0.60	p=0.791	***p*=0.0003**	p=0.553
Boreal	Thar. vs.	mal	$F_{1,156.8}$=7.99,	$F_{1,141}$=0.00,	-	-
	Kevo	es	***p*=0.005**	p=0.976		
Boreal	Thar. vs.	fem	$F_{1,149.7}$=10.7,	$F_{1,150.8}$=0.00,	-	-
	Kevo	ales	***p*=0.001**	p=0.949		
Boreal	Turku vs.	mal	$F_{1,150.5}$=0.47,	$F_{1,153.1}$=2.00,	-	-
	Kevo	es	p=0.495	p=0.159		
Boreal	Turku vs.	fem	$F_{1,154.4}$=7.14,	$F_{1,152.8}$=1.20,	-	-
	Kevo	ales	***p*=0.008**	p=0.274		
	L. dispar					

Contin	Thar. vs.	mal	$F_{1,204.2}$=2.1,	$F_{1,204}$=1.20,	$F_{1,107.6}$=12.20,	$F_{1,107.4}$=1.00,
ental	Turku	es	*p=0.149*	*p*=0.274	***p*=0.0007**	*p*=0.320
Contin	Thar. vs.	fem	$F_{1,203.6}$=5.27,	$F_{1,207.1}$=2.36,	$F_{1,113}$=6.58, ***p*=0.012**	$F_{1,110.3}$=0.39,
ental	Turku	ales	***p*=0.023**	*p*=0.126		*p*=0.534
Contin	Thar. vs.	mal	$F_{1,204}$=145.3,	$F_{1,198}$=1.64,	-	-
ental	Kevo	es	***p*<0.0001**	*p*=0.202		
Contin	Thar. vs.	fem	$F_{1,201.7}$=129.69,	$F_{1,208.6}$=7.20,	-	-
ental	Kevo	ales	***p*<0.0001**	***p*=0.008**		
Contin	Turku vs.	mal	not compared	not compared	-	-
ental	Kevo	es				
Contin	Turku vs.	fem	not compared	not compared	-	-
ental	Kevo	ales				
Influence of host plant on *L. dispar*						
L.	birch vs.		Oak 55 dd5 lower	Oak 0.11 g	(Oak 0.8 days	Oak 75 dd5 lower
dispar	oak		*SE*=11.0	heavier	shorter)	*SE*=16.9
			$F_{1,104.7}$=24.9,	*SE*=0.046	*SE*=0.67	$F_{1,69.5}$=19.93,
			***p*<0.0001**	$F_{1,111.2}$=5.87,	$F_{1,73.33}$=1.28, *p*=0.262	***p*<.0001**
				***p*=0.017**		