GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Climate change-driven elevational changes among boreal nocturnal moths

Netta M. Keret[1] · Marko J. Mutanen[1] · Markku I. Orell[1] · Juhani H. Itämies[1,2] · Panu M. Välimäki[1]

Abstract

Climate change has shifted geographical ranges of species northwards or to higher altitudes on elevational gradients. These changes have been associated with increases in ambient temperatures. For ectotherms in seasonal environments, however, life history theory relies largely on the length of summer, which varies somewhat independently of ambient temperature per se. Extension of summer reduces seasonal time constraints and enables species to establish in new areas as a result of over-wintering stage reaching in due time. The reduction of time constraints is also predicted to prolong organisms' breeding season when reproductive potential is under selection. We studied temporal change in the summer length and its effect on species' performance by combining long-term data on the occurrence and abundance of nocturnal moths with weather conditions in a boreal location at Värriötunturi fell in NE Finland. We found that summers have lengthened on average 5 days per decade from the late 1970s, profoundly due to increasing delays in the onset of winters. Moth abundance increased with increasing season length a year before. Most of the species occurrences expanded upwards in elevation. Moth communities in low elevation pine heath forest and middle elevation mountain birch forest have become inseparable. Yet, the flight periods have remained unchanged, probably due to unpredictable variation in proximate conditions (weather) that hinders life histories from selection. We conclude that climate change-driven changes in the season length have potential to affect species' ranges and affect the structure of insect assemblages, which may contribute to alteration of ecosystem-level processes.

Keywords Season length · Phenology · Altitude · Lepidoptera · Temporal trends · Flight period

Introduction

As a response to global climate warming, a taxonomically wide range of organisms have reacted to derived environmental changes by shifting or expanding their distributions to higher latitudes and/or altitudes (Parmesan 2006; Parmesan et al. 1999; Walther et al. 2002; Root et al. 2003; Hickling et al. 2005; Fox et al. 2014; Nieto-Sánchez et al. 2015; Fält-Nordmann et al. 2018). The phenomenon is particularly strong among ectotherms and in mountainous regions because insect physiology and performance depend on temperature (Angilletta 2009) and elevational gradients allow species to track changing conditions over reasonably short distances (Pounds et al. 1999; Hill et al. 2002; Peñuelas and Boada 2003; Wilson et al. 2005; Franco et al. 2006; Merrill et al. 2008; Chen et al. 2009). Species' distribution is not only determined by abiotic but also by biotic environments. Herbivorous insects, for example, cannot expand beyond geographic ranges of certain host plants that permit high juvenile performance although the prevailing climate would sustain population persistence (Merrill et al. 2008). This explains why generalist species appear to be the main beneficiaries of warming climates (Warren et al. 2001; Menéndez et al. 2006, 2007; González-Megías et al. 2006, 2008; Pöyry et al. 2009; Clavel et al. 2010). Indeed, recent changes in species' ranges have modified structures of certain insect assemblages as a whole (González-Megías et al. 2006, 2008; Chen et al. 2009; Zografou et al. 2014; Nieto-Sánchez et al. 2015).

✉ Netta M. Keret
  netta.keret@oulu.fi

[1] Ecology and Genetics Research Unit, University of Oulu, PO Box 3000, FI-90014 Oulu, Finland

[2] Present Address: Kaitoväylä 25 A 6, FI-90570 Oulu, Finland

Temperate insects at high latitudes and altitudes face a range of external conditions that constrain individual fitness, such as low ambient temperatures and short favorable seasons for growth and reproduction (Angilletta 2009). Given that ambient temperature affects insect body size, the warming climate may affect fitness in a predictable manner; increasing temperature increases body size, and thus fecundity (see Honěk 1993), until a certain point beyond which an opposite pattern emerges (Davidowitz and Nijhout 2004). A perspective that an increase in ambient temperature as such would underlie climate change responses across species is, however, overly simple and presumably applicable to species that show pronounced thermal determination of life histories, i.e., species with short generation times and multiple generations within a season (Chown and Gaston 1999; Blanckenhorn and Demont 2004). Rather, a theory of insect life history evolution that explains variation in fitness in seasonal environments is grounded upon variation in the length of favorable season than ambient temperature per se (Roff 1980; Iwasa et al. 1994; Kivelä et al. 2013). Season length represents an ultimate constraint; an individual has to reach a specific developmental stage that is capable of diapause to survive the forthcoming winter (Tauber et al. 1986; Angilletta 2009). A mismatch between generation time and season length constrains fitness and may thus affect geographic distribution of insects (Van Dyck et al. 2015). Still, the central role of season length in theoretical considerations is either obscured or only implicitly acknowledged in empirical attempts to understand implications of the ongoing climate warming for insect population dynamics and range modifications.

Latitudinal and altitudinal changes in the environment are expected to result in genetically determined clinal variation in life histories. When the season length becomes sufficiently long, an increase in the number of generations within a year is predicted (Roff 1980; Iwasa et al. 1994; Kivelä et al. 2013). Within a certain degree of voltinism, increasing season length relaxes selection for early maturation and high initial reproductive effort, which enables a long adult life span and high life time fecundity (Kivelä et al. 2013). Assuming a constant adult mortality, a long adult lifespan would be attributable to a prolonged flight period of a particular species. These predictions are applicable to temporal trends as long as season length changes over time. Empirical evidence of prolonged adult periods is reported, although possibly confounded by simultaneous increase in the expression of multivoltinism (Roy and Sparks 2000; Pöyry et al. 2011). Exploration of these variables within a strictly univoltine region would unambiguously avoid collinearity between the pattern of voltinism and duration of adult period.

It is implicitly assumed that increasing temperature as such underlies changes in species' distribution. We argue

that the causality between the habitable climatic envelope and temperature is not straightforward but dependent on a correlated change in the season length, a key factor of theoretical considerations of insect life history evolution in seasonal environments (Roff 1980; Iwasa et al. 1994; Kivelä et al. 2013). The effect of season length on insect population dynamics is not explicitly accounted for thus far, which undermines the theoretical background of many earlier contributions on the implications of recent climate warming. By combining long-term data on nocturnal moth (Lepidoptera) catches with climatic variables from a boreal location, we explored if the season length has increased over time and if the season length has a capacity to constrain insect fitness. The latter would be indicated by a positive correlation between moth abundance and season length a year before. Second, we tested temporal trends in mean elevation values (i.e., elevational center-of-gravity) among strictly univoltine moth species with adequate data and explored ecological dimensions of variation in species-specific responses. The approach is warranted because the historical prewarming distributions of different taxonomic groups may vary and species with different habitat associations, dispersal capacities or thermal physiologies (Thomas et al. 2001; Warren et al. 2001; Hill et al. 2002; Menéndez et al. 2006; González-Megías et al. 2006, 2008; Pöyry et al. 2009; Clavel et al. 2010) as well as their host plants (Kullman 2002; Maliniemi et al. 2018; Franke et al. 2019) might show different responses to changing climate. Third, we analyzed if flight periods of the most abundant species have prolonged in time, which would be consistent with the theoretical prediction based on relaxing seasonal time constraints (Kivelä et al. 2013) and ambiguous empirical evidence (Roy and Sparks 2000; Pöyry et al. 2011). Finally, we explored temporal changes at the community level to evaluate the potential of species level responses in modifying direct and indirect species interactions.

Materials and methods

Study site

Värriö Strict Nature Reserve is located in NE Finland (67° 44′ N, 29° 37′ E), ca. 100 km north of the Arctic Circle. The area has remained pristine without anthropogenic disturbance such as settlement, roads or forestry, except a long tradition of reindeer husbandry. The area is in the boreal zone; the snow-free period lasts approximately from the end of May to mid-October. The average temperatures in January (the coldest month) and July (the warmest month) are − 11.4 °C and + 13 °C, respectively. Annual precipitation averages 595 mm. A period of continuous daylight when

the sun does not set below the horizon lasts from 30 May to 14 July.

Moth sampling

For long-term monitoring of nocturnal moths, a transect of 11 light traps (Jalas 1975) ranging from 340 to 470 m a.s.l. on the north-facing slope of Värriötunturi fell was established in 1978 (Pulliainen and Itämies 1988). Three traps were located in a ravine of Norwegian spruce (*Picea abies*)-dominated forest (340–344 m a.s.l.), three traps in an old-growth Scots pine (*Pinus sylvestris*) forest (360–366 m a.s.l.), three traps in a mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest (385–418 m a.s.l.), and two traps on the treeless summit of the fell (462–470 m a.s.l.). Each trap was provided with a 500 W mixed light bulb that was switched on between 20:00 and 08:00 h each night from mid-May to mid-October 1978–2012. Catches were collected each morning. Captured moths were identified by species and counted.

The total moth catch (1978–2012) consisted of 417, 631 individuals representing 463 species. Data were reduced to the most abundant species for analysis to avoid multiple consecutive years of zero catches. We first excluded species that were not resident at the time the survey was started (years 1978–1979) and each regular seasonal migrant, as we were particularly interested in temporal changes in spatial distribution of the resident fauna. From the resident species, we selected the ones that were observed at least in 30 different years with a mean annual catch of more than seven individuals. The selected 57 species were divided among 18 families (Online Resource 1) and comprised 376, 329 individuals (ca. 90% of the total catch). We acknowledge that data reflect measures of abundance and activity of the species collected rather than their population densities in a strict sense. This does not pose severe interpretational ambiguities as our analyses concern temporal changes in moth abundance and phenology among years, and there is no reason to assume that trapping efficiency would significantly change within a species over time (see "Discussion").

Data analysis

Data analyses were conducted in R 3.2.3 environment (R Development 2015).

Temporal trends in timing of the favorable season

The Finnish Meteorological Institute has operated synoptic climate measurements at Värriö Subarctic Research Station since 1971. Manual measurements conducted twice a day by the station staff were replaced by an automatic weather station in the 1990s. The station is located at 360 m a.s.l.; the closest light trap is only a few tens of meters away from the weather station. To characterize temporal trends in climate, we generated three climate variables: "season start", "season length" and "season end" for years 1977–2013. The "season length" specific to a particular year was estimated as the number of days when average daily temperature had been either above or equal to 10 °C. The threshold effectively characterizes the period available for insect growth and development as temperatures this high coincide with larval or pupal periods of most of the studied species and insect growth practically ceases below the threshold due to temperature dependence of insect development rate (Angilletta 2009). A generalized additive model (GAM) [function *gam* (Wood 2006)] was fitted to the data on average daily temperatures in a particular year to determine robust year-specific estimates for the first and the last date the temperature threshold exceeded. Generalized additive models with the threshold values of 8 °C and 3 °C were then fitted to the year-specific weather data to determine dates for the "season start" and "season end" in Julian days, respectively. These thresholds represented mean daily temperatures across the 35-year study period when the first moth was captured in spring or the last one in autumn. In addition to the biological relevance, underlying rationale of using different threshold values was to avoid strong correlation between any two climate variables.

To explore temporal trends in the climate variables, we regressed the "season start", "season length" and "season end" against the year [function *lm* (R Development Team 2015)]. Temporal autocorrelations were all weak or moderate ($|\rho| < 0.35$) [function *durbinWatsonTest* (Fox and Weisberg 2011)], thus the model assumption of independent residuals was not violated. The "season length" and the "season end" expressed significant temporal trends (see "Results") and were thus used to explain variance in annual moth catch. The estimates of "season length" and "season end" were not correlated ($r = 0.098$, $t = 0.583$, $df = 35$, $p = 0.564$).

Bayesian approach

To explore effects of the climate variables on moth population dynamics, species-specific elevation changes and shifts in flight periods across the years, we applied generalized linear mixed-effect models (GLMM) fitted with a Bayesian Markov chain Monte Carlo sampler [function *MCMCglmm* (Hadfield 2010)]. We used inverse-Gamma as required prior distributions of the analysis-specific variance components, the priors being set uninformative by a low degree of belief parameters ($V = 1$, $v = 0.002$). In the case of random regression models, we used uninformative inverse-Wishart distributions as priors ($v = 1.002$). The priors were parameterized to approximate to inverse-Gamma (0.001, 0.001) on variances and to some extent Beta (0.001, 0.001)

on correlations. Prior sensitivity was analyzed by fitting the same models, but parameterizing the priors so that the observed variance would divide evenly among the variance components with a slight increase in the degree of belief ($v = k + 1$, where k is the number of random factors) (Gelman 2006). The results were insensitive to prior assumptions and thus only those based on our primary parameterization are reported. In each analysis, a total of 2,500,000 MCMC iterations were run with a burn-in period of 50,000 iterations. The remaining iterations were sampled with a thinning interval of 100. Upper and lower limits of 95% highest posterior density (HPD) credibility intervals for parameter estimates were derived with the function HPDinterval (Plummer et al. 2006).

Effects of the climate variables on moth abundance

To explore if the climate variables that show temporal trends across the study period potentially affect population dynamics of moths, we fitted a GLMM to data on annual moth catch (i.e., abundance). In the model, log-transformed annual catch of a particular species in a particular trap [$\log_{10}(n+1)$] was set as the response variable, whereas fixed effects were estimated for the season length and season end in the preceding year and for elevation and the two-way interactions between the climate variables and elevation. The interaction terms were generated because we were not only interested in the main effects of the climate variables but also if the response among moths varies across the elevational gradient. To increase statistical power of the analysis, elevation was considered as a categorical factor with four levels [spruce forest (340–344 m a.s.l.), Scots pine forest (360–366 m a.s.l.), mountain birch forest (385–418 m a.s.l.), and treeless tundra (462–470 m a.s.l.)], whereas individual traps were considered as repeated measurements within a particular elevation and included as a random factor in the model ($v_{trap} = 0.002$). The random effect structure included also random intercepts for year and species that was correlated with elevation ($v_{year} = 0.002$, $v_{elevation:species} = 1.002$, $v_{residual} = 0.002$). For species-specific random slope estimation, elevation was considered a continuous variable ranging from 0 to 130 m (340–470 m a.s.l.). Thus, random effect structure took into account year-specific random variation in moth abundance not attributable to the climate variables a year before and species-specific abundances at various elevations.

Species' elevation changes across years

To explore species' elevation changes (i.e., changes in elevational "center-of-gravity") during the study period, we fitted a GLMM to data where each individual was considered as an independent observation with a unique elevation value derived from altitude of a trap that had captured it. Variation in individual elevation values was explained by a model with only a fixed intercept that translates altitude of a trap into elevation value of an individual. Species-specific responses were estimated by a random effect structure that included random intercepts for the species that were correlated with year ($v_{year:species} = 1.002$, $v_{residual} = 0.002$). This approach approximates to estimation of the elevational "center-of-gravity" for the 57 species for each year that is then regressed against the year (i.e., slope value). The approach is particularly well suited in this case as the studied elevational range is rather limited and thus any trap may occasionally capture some individuals of any species.

To explain variation in species-specific responses (see "Results"), we fitted a GLMM with species-specific slope values as the response variable and a combination of species characteristics (diapause stage, life cycle, host specificity) and ecological factors (host plant characteristics) as well as historical range as the fixed factors (Online Resource 1). Diapause stage was considered a factor with four levels (adult, egg, adolescent larva, fully grown larva or pupa). Species whose fully grown larvae hibernate but do not continue feeding in spring after over-wintering were grouped together with species that over-winter in the pupal stage. This is justified as over-wintering fully grown larvae that complete their growth in autumn, face the same seasonal time constraints as larvae heading for autumnal pupation. The species were classified by their life cycle into two groups that follow either annual or biennial life cycle. The rationale of this division is that species that need to complete their development within a year or season (annual) are more likely affected by seasonal time constraints than the ones that follow a 2-year life cycle (biennial). Host plant growth form was considered a factor with six levels and defined as follows: dwarf shrubs (including deciduous and evergreen species), herbaceous plants, mixed diet (woody dwarf shrubs and herbaceous plants), trees or bushes (plants that form forest canopy layer), non-vascular plants (mosses or lichens), and non-plants (fungi, rotten wood or animal feathers and hairs). Host specificity was considered a factor with four levels and defined as follows: monophagy (only one host species or a maximum of two hosts that belong to the same genus), oligophagy (a minimum of three hosts that belong to the same genus, or a maximum of two closely related host genera), and polyphagy (several host species or a minimum of three host genera). The fourth group consisted of species whose host specialization is unknown. Historical range was defined as species-specific mean elevation value (i.e., center-of-gravity) at the beginning of the surveillance period (1978–1982). Absolute elevation values were standardized prior to analysis by subtracting the sample mean and dividing by the standard deviation in the whole sample. The model included both the first- and the second-order terms of

the historical range. The linear term controlled for possible variation among species that would simply emerge due to the fact that species with a high early elevation value would have less space to expand their range upwards compared to species that occur at a lower elevation. The quadratic term was included to control for habitat-specific expansion propensity that the linear term may not necessarily capture. For example, species associated with the Scots pine zone (the second lowest vegetation zone) showing either strong or weak expansion rates relative to species associated with any other vegetation zone would result in negative or positive quadratic terms, respectively. To control for any bias due to variable evolutionary history (i.e., phylogenetic relatedness) among the species, we included Superfamily, Family and Genus a certain species belong to as random factors. Moran's I for different nested levels of taxonomic hierarchy suggests only negligible phylogenetic signal in the species-specific responses [0.29 (Genus)–− 0.04 (Superfamily)] (Online Resource 2), which justifies only inclusion of the robust grouping variables instead of specific metrics of phylogenetic interdependencies. Moran's I was calculated with the function *correlogram.formula* in the R package *Ape 5.2* (Paradis et al. 2018) based on the robust taxonomical hierarchy given by Finnish Biodiversity Info Facility (https ://laji.fi).

Flight periodic shifts across years

To explore changes in adult flight periods across the years, we first estimated the length of the annual flight periods of a set of species with the most comprehensive data. The group of 57 selected species was reduced to ones with an average yearly abundance of more than 30 individuals. Then, only species with more than 20 such years were selected. Altogether 27 species fulfilled these criteria. To estimate species-specific annual flight periods, we fitted separate GAMs [function *gam* (Wood 2006)] to year-specific phenological data of each species. The annual flight period was estimated as the number of days when [$\log^{10}(n+1)$]-transformed average daily catch exceeded 0.2, which corresponds to a daily catch of 1.6 individuals. This threshold was selected to estimate the length of the main flight period neither affected by single exceptionally early nor late individuals.

Temporal variation in flight periods was explored with a GLMM where the estimated annual flight period was set as the response variable. Fixed effects were estimated for year, moth abundance as well as for average temperature and thermal variation during a species-specific flight period and their two-way interaction. Moth abundance was included to control for uncertainty in the estimation of year-specific flight periods arising from occasional small sample sizes and a possible positive relationship between abundance and flight period. The latter could emerge because in peak

years exceptionally early or late individuals are more likely detected compared to years when population size is low. Variation in thermal conditions during the flight periods within a year was characterized by coefficient of variation in mean daily temperatures. Random effect structure included only species-specific random intercepts ($v_{species} = 0.002$, $v_{residual} = 0.002$).

Moth assemblages in space and in time

Moth assemblage structure was explored with non-metric multidimensional scaling (NMDS) [function *metaMDS* (Oksanen et al. 2017)]. In describing assemblage structures, each species resident in 1978–1979 (249 species, 234,404 individuals) was included irrespective of their abundance. Each trap was considered an independent replicate sampling site within the vegetation (i.e., elevation) zone it was placed. To explore temporal trends in moth assemblage structures, we arbitrarily divided the sampling period 1978–2012 into nine 4-year periods (the last one 2010–2012: 3 years) that would represent the moth assemblage at that particular sampling site and time. With this procedure, we ended up with a total of 99 [$(3 \times 3 \times 9) + (2 \times 9)$] assemblages. The 4-year species-specific moth catches at each sampling site were [$\log^{10}(n+1)$]-transformed prior to analysis. The NMDS was first run with the whole data and then for the three lowest habitat types only. To explore correspondence between assemblage configurations with the environment, we fitted environmental variables [elevation of a particular trap (i.e., assemblage), time period (an ordered factor with nine levels) and minimum season length within a particular time period] onto the NMDS configurations with the function envfit (Oksanen et al. 2017).

Results

Temporal trends in climate

The beginning of the favorable season (i.e., "season start") varied considerably among the years (range: May 14–June 25), but did not become earlier during the period of 1977–2013 ($b = -0.2183$, S.E. $= 0.1518$, $t = -1.438$, $p = 0.1593$) (Fig. 1). The "season length" varied in an order of magnitude among years (range: 40–108 days) and became longer during the monitoring period at the average rate of 5 days per decade ($b = 0.549$, S.E. $= 0.216$, $t = 2.538$, $p = 0.016$) (Fig. 1). At the same time, the "season end" (range: September 10–October 20) became later at the average rate of 3 days per decade ($b = 0.3250$, S.E. $= 0.1353$, $t = 2.402$, $p = 0.0218$) (Fig. 1).
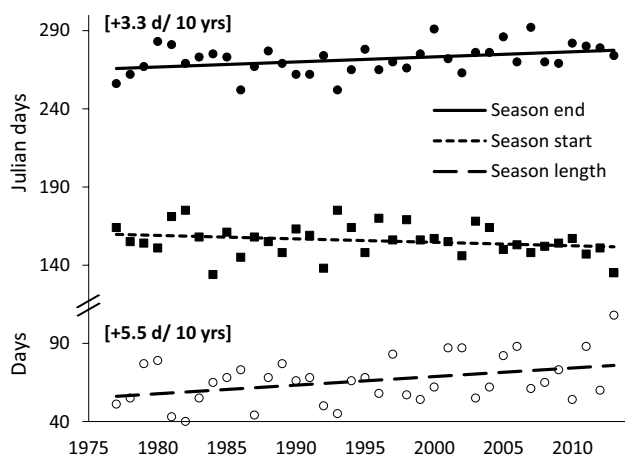
Fig. 1 Temporal trends in the three climate variables (season length, season start, season end) in Värriö 1977–2013 [effect sizes given in brackets for statistically significant trends]

Effects of season length and onset of winter on moth abundance

The total moth catch varied considerably among the years (range: 2238–32,261 individuals), population dynamics of the Autumnal moth (*Epirrita autumnata*) alone being largely responsible of that absolute interannual variation. The length of the preceding season explained variation in moth abundance in general so that moth abundance increased with increasing season length after controlling for species-specific random variation (Table 1, Fig. 2). This suggests that natural variation in the season length has a capacity

to constrain realized fitness of moths and thus affect their occurrence in the area. The response was similar at different elevations except for the treeless tundra where moth abundance was invariably low (Table 1). A positive association between late onset winter and moth abundance emerged at the second highest elevation (385–418 m a.s.l.) (Table 1).

Temporal trends in species' elevation changes

The elevational center-of-gravity changed uphill over the course of study in 39 out of the 57 selected species (Table 2). Fifteen species did not show statistically significant trends in time, whereas for three species the elevational center-of-gravity changed downhill (Table 2). Responding and non-responding species as well as species with either increasing or decreasing slope values were found in each larger taxonomic group (Online Resource 1) and phylogeny did not explain variance in slope values (see Table 3). A significant negative quadratic term of the historical elevation value suggests that species originally associated with mid-elevation habitats showed an exaggerated response compared to species that occurred either at low or high elevations in 1978–1981 (Table 3). A significant positive term for the diapause stage "larva (fully grown)/pupa" implies that species completing their growth period in autumn, thus facing the most severe risks of autumn frosts, moved uphill more than an average species that over-winters at any other developmental stage (Table 3, Fig. 3a). Similarly, species that follow a 2-year life cycle expressed lower slope values compared to species that complete their development within a year

Table 1 Fixed effects of a GLMM explaining annual variation in moth abundance among the 57 moth species in relation to elevation as well as the length and ending of the previous season

Parameter	Estimate (posterior mean)	95% HPD credibility interval		N_{eff}
		Lower limit	Upper limit	
Intercept (elevation a)	0.41	-0.76	1.55	4500
Elevation (b)	-0.10	-0.56	0.37	4288
Elevation (c)	-1.29	-1.73	-0.76	4400
Elevation (d)	-0.16	-0.76	0.37	4500
Season length	2.62×10^{-3}	8.7×10^{-5}	4.75×10^{-3}	4500
Season end	8.35×10^{-4}	-3.03×10^{-3}	4.4×10^{-3}	4716
Elevation (b) × season length	1.87×10^{-5}	-9.99×10^{-4}	1.0×10^{-3}	4500
Elevation (c) × season length	-2.61×10^{-4}	-1.20×10^{-3}	7.76×10^{-4}	4500
Elevation (d) × season length	-2.58×10^{-3}	-3.63×10^{-3}	-1.40×10^{-3}	4500
Elevation (b) × season end	-3.39×10^{-5}	-1.53×10^{-3}	1.51×10^{-3}	3731
Elevation (c) × season end	4.33×10^{-3}	2.83×10^{-3}	5.89×10^{-3}	4500
Elevation (d) × season end	-6.67×10^{-4}	-2.30×10^{-3}	1.12×10^{-3}	4500

The model was parameterized so that the lowest elevation [$a = 340$–344 m a.s.l. (spruce-dominated coniferous forest)] forms the reference category to which the higher elevations [$b = 360$–366 m a.s.l (Scots pine-dominated coniferous forest), $c = 385$–418 m a.s.l. (mountain birch-dominated deciduous forest), $d = 462$–470 m a.s.l. (treeless tundra)] are compared. Random effects included individual traps (i.e., repeated measurements within a particular elevation zone) as well as random intercepts for year and species that was correlated with elevation (a continuous variable ranging 0–130 m)

Fig. 2 Correspondence between the season length a year before and moth abundance in the following summer at different elevations (i.e., vegetation zones: 340–344 m a.s.l. = spruce-dominated coniferous forest), 360–366 m a.s.l = Scots pine-dominated coniferous forest), 385–418 m a.s.l. = mountain birch-dominated deciduous forest, 462–470 m a.s.l. = treeless tundra)
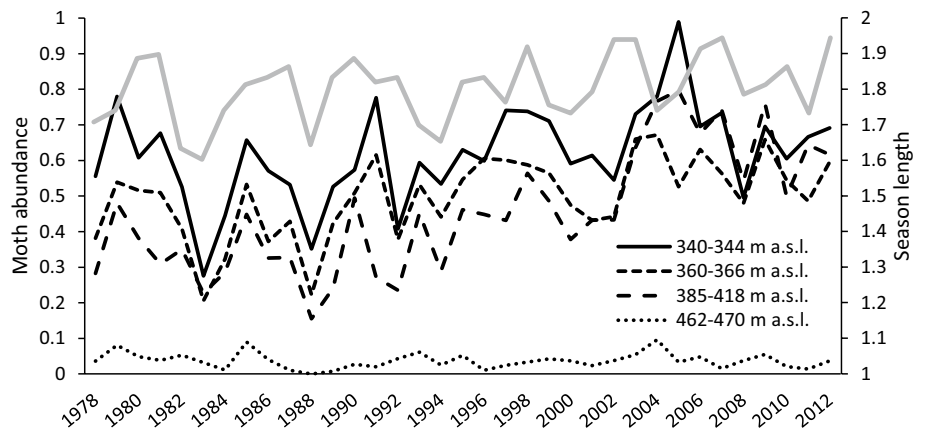
Table 2 Species-specific temporal changes in the elevational center-of-gravity (i.e., posterior mean of correlation between annual elevation values and time, a slope value) based on a GLMM with a fixed intercept and a random effect structure including random intercepts for the species that were correlated with year

Species	Slope	95% HPD interval		Species	Slope	95% HPD interval	
		Lower	Upper			Lower	Upper
Acleris maccana	0.21	0.17	0.25	*Mompha idaei*	0.23	− 0.01	0.44
Ancylis myrtillana	0.60	0.55	0.65	*Mompha locupletella*	0.02	− 0.15	0.19
Ancylis unguicella	1.52	1.27	1.77	*Monopis laevigella*	0.27	− 0.12	0.62
Argyresthia svenssoni	0.28	2.0×10^{-3}	0.53	*Monopis spilotella*	0.56	0.27	0.85
Bryotropha galbanella	0.33	0.20	0.47	*Nemapogon cloacellus*	− 0.15	− 0.39	0.11
Chionodes continuellus	0.19	0.13	0.26	*Neofaculta infernella*	− 0.07	− 0.20	0.05
Chionodes nubilellus	0.09	− 0.08	0.31	*Operophtera brumata*	0.34	0.26	0.42
Clepsis senecionana	1.63	1.37	1.88	*Paraswammerdamia conspersella*	0.55	0.52	0.58
Coleophora glitzella	0.55	0.40	0.69	*Phiaris bipunctana*	1.45	1.21	1.67
Coleophora idaeella	0.54	0.25	0.82	*Phiaris heinrichana*	0.43	0.30	0.57
Coleophora vacciniella	0.73	0.52	1.01	*Phiaris obsoletana*	0.64	0.58	0.70
Denisia similella	0.30	0.21	0.38	*Phiaris palustrana*	1.03	0.85	1.19
Denisia stipella	0.08	0.03	0.15	*Phiaris schulziana*	− 0.50	− 0.55	− 0.45
Dystroma citratum	0.08	$− 8.0 \times 10^{-3}$	0.18	*Pleurota bicostella*	0.55	0.47	0.62
Eana osseana	1.61	1.51	1.70	*Poecilocampa populi*	− 0.19	− 0.29	− 0.01
Ectoedemia weaveri	0.46	0.36	0.59	*Pseudatemelia josephinae*	− 0.17	− 0.38	0.06
Elachista parasella	0.01	− 0.16	0.18	*Scopula ternata*	0.42	0.32	0.53
Elophos vittarius	0.44	0.32	0.56	*Selenia dentaria*	0.30	0.14	0.46
Entephria caesiata	0.27	0.24	0.29	*Sparganothis rubicundana*	0.80	0.67	0.92
Epinotia maculana	0.35	0.24	0.46	*Stigmella lapponica*	0.71	0.45	0.94
Epinotia solandriana	0.12	$− 6.0 \times 10^{-3}$	0.32	*Syngrapha interrogationis*	− 0.23	− 0.36	− 0.11
Epirrita autumnata	0.37	0.36	0.39	*Taleboria borealis*	0.44	0.24	0.64
Eudonia murana	0.51	0.30	0.69	*Thera obeliscata*	0.42	0.24	0.62
Eulia ministrana	0.07	− 0.12	0.27	*Trichiura crataegi*	− 0.07	− 0.27	0.14
Eulithis populate	0.53	0.49	0.56	*Xanthorhoe decoloraria*	− 0.07	− 0.24	0.01
Eulithis testata	0.61	0.38	0.87	*Ypsolopha parenthesella*	0.22	0.09	0.37
Eupithecia pusillata	0.35	0.20	0.48	*Zeiraphera griseana*	0.42	0.26	0.59
Hellinsia tephradactyla	− 0.04	− 0.34	0.29	Increased	39 species		
Incurvaria vetulella	0.10	− 0.02	0.23	Stable	15 species		
Lithomoia solidaginis	0.58	0.51	0.65	Decreased	3 species		

Table 3 Fixed effects of a GLMM explaining variation in species-specific uphill change in center-of-gravity in relation to historical range (COG1978 = standardized mean center-of-gravity in 1978–1982), over-wintering developmental stage (adult; egg; adolescent larva; larva in a unspecified developmental stage; fully grown larva or pupa), life cycle (annual; biennial), host type (dwarf shrubs; her- baceous plants; trees and bushes = canopy; mixed diet = woody dwarf shrubs and herbaceous plants; non-vascular plants = mosses or lichens; non-plants = rotten wood, fungi or animal feathers and hairs), and the degree of host specificity (polyphagy; oligophagy; monophagy; unspecified)

Source of variation	Parameter	Estimate (posterior mean)	95% HPD credibility interval		N_{eff}
			Lower limit	Upper limit	
	(Intercept)	10.18	− 11.3	31.81	> 20,000
Historical range	COG1978	0.50	− 0.02	1.22	> 20,000
	$(COG1978)^2$	− 0.02	− 0.03	− 1.65×10^{-4}	> 20,000
Over-wintering stage (adult)	Egg	18.08	− 3.70	39.70	> 20,000
	Larva (unspecified)	19.45	− 3.02	42.13	> 20,000
	Larva (adolescent)	18.15	− 2.91	39.12	> 20,000
	Larva (fully grown)/pupa	26.95	5.47	48.04	> 20,000
Host type (dwarf shrubs)	Herbaceous plants	− 28.90	− 40.76	− 17.32	> 20,000
	Mixed diet	1.14	− 14.13	12.20	> 20,000
	Trees or bushes	− 14.34	− 22.04	− 6.51	> 20,000
	Non-vascular plants	− 0.63	− 14.59	13.52	> 20,000
	Non-plants	− 14.44	− 29.92	1.03	> 20,000
Life cycle (annual)	Biennial	− 12.37	− 23.78	− 1.17	13,732
Host specificity (polyphagy)	Monophagy	6.73	− 0.015	13.49	> 20,000
	Oligophagy	− 1.83	− 10.15	6.40	> 20,000
	Unspecified	− 2.95	− 15.45	9.22	> 20,000

Random effect variances: superfamily: 3.53 (1.40×10^{-4}..0.18.25), family: 5.33 (1.20×10^{-4}…28.5), genus: 36.99 (1.04×10^{-4}..0.109.80), model residuals: 57.36 (8.05…112.00)

Random effect structure included grouping factors genus, family and superfamily to control for varying evolutionary history of species

(Table 3). Species whose larvae dwell on the forest canopy or feed on herbaceous plants were less likely to expand their range compared to species that feed on dwarf shrubs (Table 3, Fig. 3b). A seemingly positive effect of the "mixed diet" [low sample size ($N = 3$), Fig. 3b] was over-ruled by a marginally non-significant positive term for "monophagy" over the more diverse diets (Table 3). Yet, host specificity per se did not explain variation in slope values among the species.

Temporal trends in flight periods

There was no temporal trend in the length of adult flight periods among the studied 27 moth species after control-ling for variation in moth abundance (Table 4). Variation in flight periods was explained by interaction between mean ambient temperature and variability of thermal conditions during the adult phase (Table 4). A high mean temperature shortened the flight period of a species, but the effect was mitigated by high daily fluctuations in ther-mal conditions that have a tendency to prolong the flight period.

Moth communities in space and in time

Moth assemblages at the two highest sampling sites located in the treeless tundra differed from those at the lower altitude sampling sites located in forested habitats (Fig. 4a). Eleva-tional gradient was strong in the direction of the first NMDS axis (NMDS 1: 0.99; NMDS 2: 0.05; $r^2 = 0.76$; $p < 0.001$), whereas time from the beginning of the moth monitor-ing and the minimum season length correlated to a lesser extent with the second NMDS axis (time: NMDS 1: − 0.08; NMDS 2: 0.99; $r^2 = 0.11$; $p < 0.003$; season length: NMDS 1: − 0.14; NMDS 2: 0.99; $r^2 = 0.08$; $p < 0.072$). There was more variation in assemblage structure in time among tundra assemblages than among assemblages at forested sites. A fitted ordination surface reveals that variation among tundra assemblages is highly stochastic in relation to season length compared to assemblages of the forested sites.

Exclusion of the tundra sites indicated that any varia-tion among moth assemblages of the different forested veg-etation zones can be explained by the elevational gradient (NMDS 1: − 0.60; NMDS 2: 0.80; $r^2 = 0.77$; $p < 0.001$). The main direction of variation within a certain vegetation zone (spruce and pine forests, in particular) was almost parallel

Fig. 3 Variation in elevational changes among the groups of species with **a** different over-wintering developmental stage [unspecified larva refers to species that over-winter in the larval stage, but it is not known whether larvae continue feeding after diapause] and **b** host type [×=mean; black line=median; box=the first and the third quartiles; whiskers=minimum and maximum values excluding outliers (open circles)]
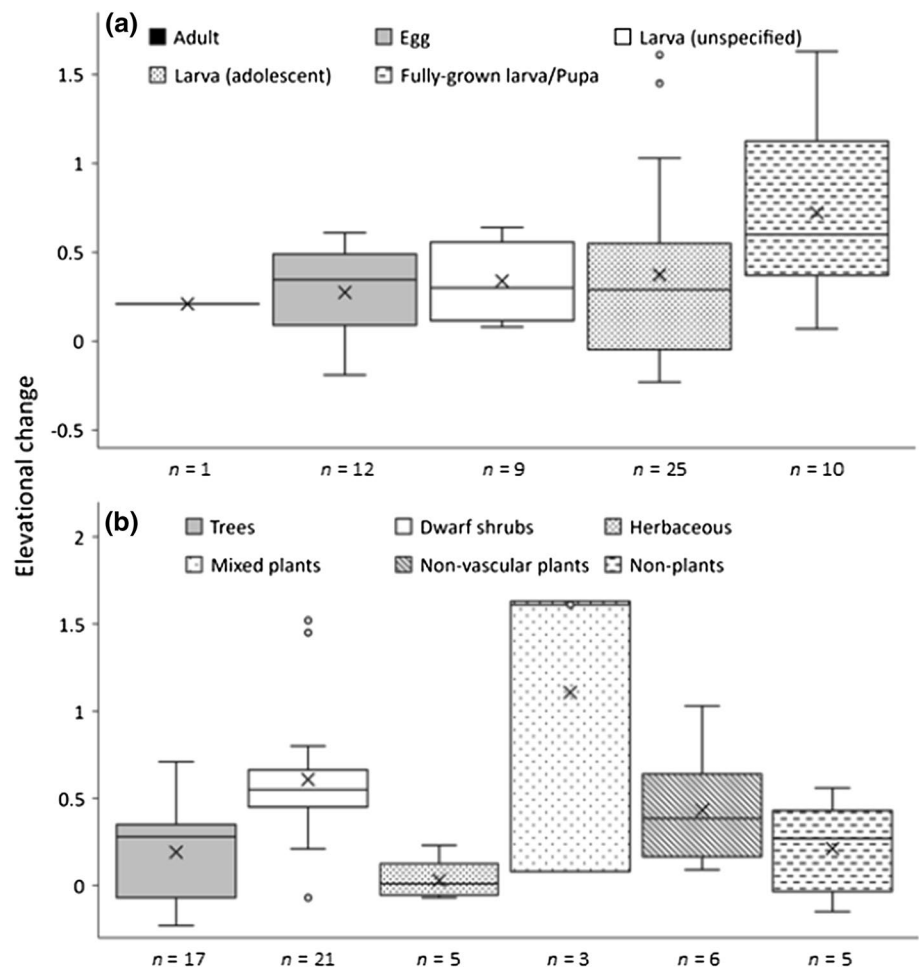

Table 4 Fixed effects of a GLMM explaining variation in the annual flight periods among the 27 moth species in relation to time [year] and weather conditions during the adult stage [mean/coefficient of variation]

Parameter	Estimate (posterior mean)	95% HPD credibility interval		N_{eff}
		Lower limit	Upper limit	
(Intercept)	− 37.29	− 139.77	67.62	> 200,000
Year	0.04	− 0.01	0.10	> 200,000
Abundance	5.38	4.35	6.43	> 200,000
Temperature-$_{mean}$	− 2.00	− 2.39	− 1.60	> 200,000
Temperature$_{cv}$	− 5.17	− 10.67	0.49	> 200,000
Temperature-$_{mean}$ × temperature$_{cv}$	2.52	1.58	3.45	> 200,000

Random effects included species-specific random intercepts. Random effect variances: species: 35.10 (16.68…57.38), model residuals: 58.70 (53.15…64.27)

to the time and season length axes indicating season length-dependent temporal trends in assemblage structures (time: NMDS 1: 0.28; NMDS 2: 0.96; $r^2 = 0.63$; $p < 0.001$; season length: NMDS 1: 0.32; NMDS 2: 0.95; $r^2 = 0.56$; $p < 0.001$) (Fig. 4b). Moreover, direction of the season length axis together with the fitted surface reveals that moth assemblages at the mountain birch zone have changed and become practically inseparable from those at the Scots pine zone as the season length has increased. This is because the species whose elevational center-of-gravity had changed uphill were mostly species originally associated with the Scots pine-dominated vegetation zone but expanded their range into the Mountain birch-dominated zone during the period 1978–2012 (Fig. 5). In contrast, only three species associated with spruce forest had changed uphill.

Discussion

The length of the favorable season for insect growth and development has increased and the onset of winter has delayed in Värriö over the years 1977–2013. Moth
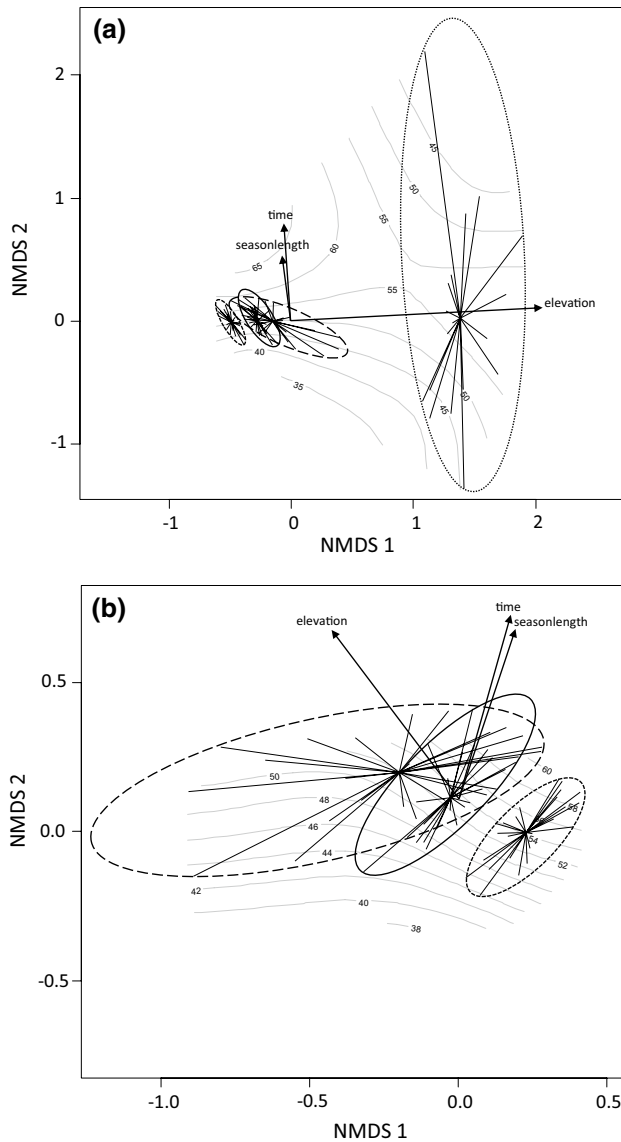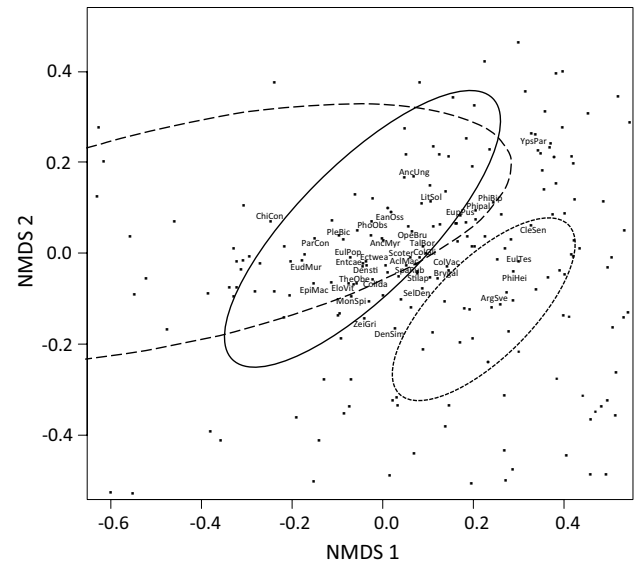
Fig. 5 Associations of individual moth species with certain habitat-specific moth assemblages [short dash line = spruce-dominated coniferous forest (340–344 m a.s.l.), solid line = Scots pine-dominated coniferous forest (360–366 m a.s.l), long dash line = mountain birch-dominated deciduous forest (385–418 m a.s.l.)] according to a two-dimensional NMDS configuration. Species that showed temporal changes in the elevational center-of-gravity are abbreviated (the three first letters of genus and species names, see Table 2 for the whole binomial names), whereas the others are only given as dummy numbers

Fig. 4 Two-dimensional NMDS configurations of moth assemblages (ellipsoid hull and spider web diagrams) plotted on fitted thin plate spline surfaces in relation to the minimum season length: **a** each elevation zone included, **b** only the three lowest elevation zones included [short dash line = spruce-dominated coniferous forest (340–344 m a.s.l.), solid line = Scots pine-dominated coniferous forest (360–366 m a.s.l), long dash line = mountain birch-dominated deciduous forest (385–418 m a.s.l.), dotted line = treeless tundra (462–470 m a.s.l.)]. Tips of the lines represent a certain assemblage and the respective line its distance to an average assemblage within a particular elevation zone. Black arrows represent the main directions of variation in assemblage structures in relation to the minimum season length, time and elevation, while arrow lengths illustrate the strength of the respective correlations

abundance and the season length a year before were positively correlated in forest habitats, but not necessarily in the treeless summit of the Värriötunturi fell. A remarkable proportion of moth species shows an upward trend on the

elevational gradient over time. Flight periods of the moths did not prolong in time, but were determined by the proximate weather conditions within a certain year. The most prominent upward changes were observed among species that complete their resource acquisition before over-wintering within a season and were associated with pine heat forest. At the community level, moth assemblages in the pine and mountain birch forests have become inseparable, whereas assemblages in the spruce forest and treeless tundra have remained characteristic despite a remarkable year-to-year variation in the latter.

Climatic effects of the global climate warming vary geographically, climatic change becoming somewhat exaggerated towards the poles. The freeze-free periods in high latitudes are lengthening with a concomitant decrease in snow cover (Walther et al. 2002). Changes in the precipitation are neither spatially nor temporally uniform. Increases in autumn and/or winter precipitation have been reported in high latitudes, whereas precipitation tends to decrease in the sub-tropics (Walther et al. 2002). In our boreal study site, significant increases in spring, autumn, and winter temperatures, and in winter precipitation have been reported (Hunter et al. 2014). Our analysis adds a prolonged favorable season among the climate variables that show significant temporal change. The pattern emerged mostly as a response to

onsets of winters occurring later (an increase in autumn temperatures) and to a lesser extent to advancing springs. The favorable season has become longer at a rate of 5 days per decade, which means a 34% increase in the season length (57 vs. 76 days) over the course of the monitoring period. Such a change is unlikely trivial for organisms whose development depends on external sources of heat, such as insects. Accordingly, the season length a year before appeared positively correlated with moth abundance in the following season. The increasing season length and its seemingly deterministic effects on moth abundance explains well the reported overall temporal increase in moth abundance in Värriö (Hunter et al. 2014, cf. Fig. 2), which contradicts a recent finding of dramatic decrease of insects in the temperate zone (Hallmann et al. 2017). More importantly, the correlation withstands theoretical investigations (Roff 1980; Iwasa et al. 1994; Kivelä et al. 2013) that emphasize the importance of season length in determining insect fitness. In addition, the positive association of the late onset of winter and moth abundance close to the timber line further stresses the need to reach a species-specific over-wintering stage before the autumn frosts (Tauber et al. 1986).

A taxonomically wide range of organisms have reacted to climate warming or derived environmental changes by shifting or expanding their distributions to higher latitudes and/or altitudes (Parmesan 2006; Walther et al. 2002; Fält-Nordmann et al. 2018). Unlike for plants or vegetation (e.g., Kullman 2002; Walther et al. 2002; Peñuelas and Boada 2003; Franke et al. 2019), unambiguous empirical evidence of insects shifting to higher altitudes with demonstration of causality is few (but see Wilson et al. 2005; Franco et al. 2006; Merrill et al. 2008). The missing evidence is probably due to a lack of adequate long-term data as changes in species' distributions are expected particularly when elevational gradients allow organisms to track changing conditions over reasonably short distances (Pounds et al. 1999; Hill et al. 2002). Accordingly, we observed that 39 (68%) of the selected 57 boreal moths had increased or expanded upwards on the elevational gradient in Värriötunturi fell from the late 1970s. The species with different responses distributed evenly among groups of species that face different light conditions (see Online Resource 1). Accordingly, the general pattern is unlikely driven by sampling bias due to increasingly suitable flight conditions in late summer (higher trapping efficiency due to longer dark period). This corresponds closely to observations of 68% geometrid moths ($N = 102$) showing increases in their center-of-gravity in Mt. Kinabalu in Borneo (Chen et al. 2009) and 73% butterfly species ($N = 19$) in Sierra de Guadarrama in Spain (Wilson et al. 2005) within a comparable time. In Sierra de Guadarrama, local extinctions at low elevation margins rather than changes in upper elevational limits explained the increase in center-of-gravity, which contradict the mechanism in Värriö

based only on relative changes in abundance at different elevations. Nevertheless, the observed correlation between season length and moth abundance offers a causal link not only for the expanding cool range margins, but may equally apply also to contractions of warm margins where a changing thermal environment has a capacity to result in mismatches between season length and phenology of essential life history events (see Van Dyck et al. 2015).

Herbivorous insects cannot readily expand beyond ranges of certain host plants although the prevailing climate would sustain population persistence (Merrill et al. 2008; but see Pateman et al. 2012). Thus, generalists have been considered as the main beneficiaries of climate warming (Warren et al. 2001; Menéndez et al. 2006, 2007; González-Megías et al. 2006, 2008; Pöyry et al. 2009; Clavel et al. 2010). In our case, the degree of host specificity per se did not explain variation in slope values among the species. There was, however, a tendency of the monophagous species to show the strongest response, which simply reflects the fact that host plants of such moth species in our sample, like *Vaccinium vitis-idaea*, *Calluna vulgaris* and *Betula pubescens* are abundant and occur everywhere in the landscape. The former two plant species also reflect a more general tendency of species associated with dwarf shrubs readily expanding their range uphill. Dwarf shrubs are known to respond to climate change and expand their range (Kullman 2002; Walther et al. 2002). We have no data on possible changes in vegetation in Värriö. Yet, shrubs utilized by the moth species are invariably abundant and thus a more likely explanation for the uphill range expansions is the changing climatic envelope. In accordance with the climatic explanation grounded on the assumption that season length constrains insect fitness, species that complete acquisition of resources used for reproduction before over-wintering within a season and thus face the most severe seasonal time constraints were the ones taking advantage of the changing climate the most. This is applicable to a majority of nocturnal moths that over-winter in the pupal stage or as a full-grown larva, but not necessarily to species with 2-year life cycle or species whose reproductive potential depends on adult feeding such as many butterflies (see Pöyry et al. 2009). To explicitly test for the latter hypothesis, data that include species covering the whole capital vs. income breeding continuum would be needed.

The theoretical predictions of prolonged adult lifespan and high fecundity as a response to relaxing seasonal time constraints (Kivelä et al. 2013) would be attributable to a prolonged flight period of a particular species. Although the underlying premise of relaxing time constraints held true, flight periods of the 27 most abundant species did not change over time in Värriö. Thus, this mechanism cannot explain increasing overall moth abundance in the area (Hunter et al. 2014). The lack of temporal change may reflect a fact that natural selection acts via ultimate factors, but the proximate

environment determines the expressed phenotype for selection to act on (Ghalambor et al. 2007). Proximate weather conditions during the adult phase determined the length of flight periods among the moth species. High ambient temperatures resulted in relatively short flight periods, whereas highly fluctuating daily temperatures tended to prolong them. This being the case, any temporal trends would reflect changes in the proximate environment, while phenotypic plasticity due to temperature dependence of insect physiology (see Angilletta 2009) would mask possible variation among genotypes and hinder evolutionary responses. This is not to say that selection would not underlie the reported prolongations of flight periods among Lepidoptera that at least partly arise from increases in voltinism (Roy and Sparks 2000; Pöyry et al. 2011). Selection readily favors multivoltinism as long as the favorable season becomes sufficiently long (Roff 1980; Iwasa et al. 1994; Kivelä et al. 2013) and in addition to environmental determination, variation in the degree of voltinism has a genetic component among Lepidoptera (Välimäki et al. 2008; Kivelä et al. 2012; Välimäki et al. 2013a, b).

Habitat and/or host plant associations partly explain the curvilinear trend of species at middle elevations expressing the strongest expansion upwards. For obvious reasons, species that prefer open tundra did not show any increase in their center-of-gravity, while species tightly associated with Norwegian spruce forest are necessarily constrained to low elevations. The pronounced responses among species originally associated with the pine heat forest at middle elevation resulted in a merged moth assemblage of pine and mountain birch zones on the elevational gradient. The change is of similar magnitude like mean uphill shifts of Geometrid assemblages (41.9 m) in Mt. Kinabalu (Chen et al. 2009). Such a modification of insect assemblages due to upward range expansion is not exceptional elsewhere either (González-Megías et al. 2008; Zografou et al. 2014; Nieto-Sánchez et al. 2015). We, however, stress that the turnover of species assemblages in Värriö was completely due to changes in species abundance, as we considered only species that were resident already in the late 1970s and none of the species became extinct over the course of the study. Our results imply that if host plants do not constrain occurrence, assemblages that consist of habitat specialist are less likely to show temporal trends compared to assemblages dominated by species with loose habitat preferences. Accordingly, Nieto-Sánchez et al. (2015) have suggested that habitat-specific biotic interactions constrain species assemblages from responding to environmental change. The moth assemblage in the spruce forest zone changed somewhat over time but remained characteristic overall. The same applies to the moth community in the treeless tundra, except that short-term random turnover of the assemblage structure was evident. This probably mirrors a variable degree of environmental stochasticity (Martin 2001). In the forested areas, tree canopy mitigates environmental uncertainty and results, for example, in relatively stable snowpack and snowmelt in winter–spring as well as in stable temperatures, humidity and wind conditions in summertime. In the treeless tundra, a lack of tree cover translates to stochastic variation in the abovementioned variables that are known to affect the habitable climatic envelope of phytophagous insects (e.g., Menéndez et al. 2007; Merrill et al. 2008). We, however, acknowledge that the rapid turnover of moth assemblages in tundra may partly arise due to low numbers of species and individuals involved, which likely increases sampling error.

To conclude, the length of the favorable season apparently constrains fitness of certain insects. Easing seasonal time constraints due to climate change enables such species to expand their distributions on elevational gradients. This applies to species that are generalists or associated with common host plants and thus relatively free of restrictive biotic interactions with their host plants. At the assemblage level, different proximate factors determine temporal resilience at different timescales. Strong biotic interactions buffer assemblages against long-term directional environmental change, whereas short-term environmental variation results in stochastic assemblage dynamics that obscure long-term patterns. Nevertheless, long-term changes in species assemblages modify biotic interactions. Direct interactions (i.e., competition) among herbivorous insects is unlikely important because plant productivity usually exceeds herbivory except occasionally within the boreal populations of the Autumnal moth (*Epirrita autumnata*) or the Winter moth (*Operophtera brumata*) (Tenow et al. 2007). Indirect interactions mediated by shared parasitoids or predators at a higher trophic level, in turn, may profoundly affect moth population dynamics (Klemola et al. 2009). At the landscape scale, simultaneously expanding cool margins of several moth species results in diverse and stable larval assemblages widely distributed in time within a season, which is likely beneficial for insectivorous birds whose reproductive output depends on food availability during nestling (Visser et al. 2006) and/or postnestling (Pakanen et al. 2015) phases of the reproductive cycle.

Compliance with ethical standards

References

Angilletta MJ Jr (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York

Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integr Comp Biol 44:413–424. https://doi.org/10.1093/icb/44.6.413

Chen I-C, Shiu H-J, Benedick S, Holloway JD, Chey VK, Barlow HS, Hill JK, Thomas CD (2009) Elevation increases in moth assemblages over 42 years on a tropical mountain. Proc Natl Acad Sci 106:1479–1483. https://doi.org/10.1073/pnas.0809320106

Chown SL, Gaston KJ (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biol Rev 74:87–120. https://doi.org/10.1111/j.1469-185X.1999.tb00182.x

Clavel J, Juilliard R, Devictor V (2010) Worldwide decline of specialist species: towards a global functional homogenization? Front Ecol Environ 9:222–228. https://doi.org/10.1890/080216

Davidowitz G, Nijhout HF (2004) The physiological basis of reaction norms: the interaction among growth rate, the duration of growth and body size. Integr Comp Biol 44:443–449. https://doi.org/10.1093/icb/44.6.443

Fält-Nordmann JJJ, Tikkanen OP, Ruohomäki K, Otto LF, Leinonen R, Pöyry J, Saikkonen K, Neuvonen S (2018) The recent northward expansion of *Lymantria monacha* in relation to realised changes in temperatures of different seasons. For Ecol Manag 427:96–105. https://doi.org/10.1016/j.foreco.2018.05.053

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Los Angeles

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD, Roy DB (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. J Appl Ecol 51:949–957. https://doi.org/10.1111/1365-2664.12256

Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B, Thomas CD (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Glob Change Biol 12:1545–1553. https://doi.org/10.1111/j.1365-2486.2006.01180.x

Franke AK, Feilhauer H, Bräuning A, Rautio P, Braun M (2019) Remotely sensed estimation of vegetation shifts in the polar and alpine tree-line ecotone in Finnish Lapland during the last three decades. For Ecol Manag. https://doi.org/10.1016/j.foreco.2019.117668

Gelman A (2006) Prior distributions for variance parameters in hierarchical models. Bayesian Anal 1:515–533. https://doi.org/10.1214/06-BA117A

Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

González-Megías A, Menéndez R, Roy D, Breretons T, Thomas CD (2008) Changes in the composition of British butterfly assemblages over two decades. Glob Change Biol 14:1464–1474. https://doi.org/10.1111/j.1365-2486.2008.01592.x

Hadfield J (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. J Stat Softw 33:1–22. https://doi.org/10.18637/jss.v033.i02

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12:e0185809. https://doi.org/10.1371/journal.pone.0185809

Hickling R, Roy DB, Hill JK, Thomas CD (2005) A northward shift of range margins in British Odonata. Glob Change Biol 11:502–506. https://doi.org/10.1111/j.1365-2486.2005.00904.x

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. Proc R Soc B 269:2163–2171. https://doi.org/10.1098/rspb.2002.2134

Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66:483–492. https://doi.org/10.2307/3544943

Hunter MD, Kozlov MV, Itämies J, Pulliainen E, Bäck J, Kyrö E-M, Niemelä P (2014) Current temporal trends in moth abundance are counter to predicted effects of climate change in an assemblage of subarctic forest moths. Glob Change Biol 20:1723–1737. https://doi.org/10.1111/gcb.12529

Iwasa Y, Ezoe H, Yamauchi A (1994) Evolutionary stable seasonal timing of univoltine and bivoltine insects. In: Danks HV (ed) Insect life-cycle polymorphism. Kluwer Academic Publishers, Netherlands, pp 69–89

Jalas I (1975) Perhoskeräilijän opas, 2nd edn. Otava, Helsinki

Kivelä SM, Välimäki P, Mäenpää MI (2012) Genetic and phenotypic variation in juvenile development in relation to temperature and developmental pathway in a geometrid moth. J Evol Biol 25:881–889. https://doi.org/10.1111/j.1420-9101.2012.02478.x

Kivelä SM, Välimäki P, Gotthard K (2013) Seasonality maintains alternative life-history phenotypes. Evolution 67:3145–3160. https://doi.org/10.1111/evo.12181

Klemola N, Heisswolf A, Ammunét T, Ruohomäki K, Klemola T (2009) Reversed impacts by specialist parasitoids and generalist predators may explain a phase lag in moth cycles: a novel hypothesis and preliminary field tests. Ann Zool Fennici 46:380–393. https://doi.org/10.5735/086.046.0504

Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. J Ecol 90:68–77. https://doi.org/10.1046/j.0022-0477.2001.00630.x

Maliniemi T, Kapfer J, Saccone P, Skog A, Virtanen R (2018) Long-term vegetation changes of treeless heath communities in northern Fennoscandia: links to climate change trends and reindeer grazing. J Veg Sci 29:469–479. https://doi.org/10.1111/jvs.12630

Martin K (2001) Wildlife in Alpine and Sub-alpine Habitats. In: Johnson DH, O'Neil TA (eds) Wildlife habitat relationships in Oregon and Washington. Oregon State University Press, USA, pp 285–310

Menéndez R, Gonzáles-Megías A, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB, Thomas CD (2006) Species richness changes lag behind climate change. Proc R Soc B 273:1465–1470. https://doi.org/10.1098/rspb.2006.3484

Menéndez R, González-Megías A, Collingham Y, Fox R, Roy DB, Ohlemüller R, Thomas C (2007) Direct and indirect effects of climate and habitat factors on butterfly diversity. Ecology 88:605–611. https://doi.org/10.1890/06-0539

Merrill RM, Gutiérrez D, Lewis OT, Gutiérrez J, Díez SB, Wilson RJ (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. J Anim Ecol 77:145–155. https://doi.org/10.1111/j.1365-2656.2007.01303.x

Nieto-Sánchez S, Gutiérrez D, Wilson RJ (2015) Long-term change and spatial variation in butterfly communities over an elevational gradient: driven by climate, buffered by habitat. Divers Distrib 21:950–961. https://doi.org/10.1111/ddi.12316

Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin RR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) Vegan: community ecology package—ordination methods, diversity analysis and other functions for community and vegetation ecologists. R Package, Version 2.4–3. http://cran.r-project.org/

Pakanen V-M, Orell M, Vatka E, Rytkönen S, Broggi J (2015) Different ultimate factors define timing of breeding in two related species. PLoS One 11:e0162643. https://doi.org/10.1371/journal.pone.0162643

Paradis E, Bolker B, Claude J, Sien Cuong H, Desper R, Durand B, Dutheil J, Gascuel O, Heibl C, Lawson D, Lefort V, Legendre P, Lemon J, Noel Y, Nylander J, Opgen-Rhein R, Popescu A, Schliep K, Strimmer K, de Vienne D (2018) Ape: analyses of phylogenetics and evolution. R Package, Version 5.2. http://cran.r-project.org/

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583. https://doi.org/10.1038/21181

Pateman RM, Hill JK, Roy DB, Fox R, Thomas CD (2012) Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. Science 336:1028–1030. https://doi.org/10.1126/science.1216980

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Glob Change Biol 9:131–140. https://doi.org/10.1046/j.1365-2486.2003.00566.x

Plummer M, Best N, Cowles K, Vines K (2006) CODA: convergence diagnosis and output analysis for MCMC. R News 6:7–11

Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 398:611–615. https://doi.org/10.1038/19297

Pöyry J, Luoto M, Heikkinen RK, Kuussaari M, Saarinen K (2009) Species traits explain recent range shifts of Finnish butterflies. Glob Change Biol 15:732–743. https://doi.org/10.1111/j.1365-2486.2008.01789.x

Pöyry J, Leinonen R, Söderman G, Nieminen M, Heikkinen RK, Carter TR (2011) Climate-induced increase of moth multivoltinism in boreal regions. Glob Ecol Biogeogr 20:289–298. https://doi.org/10.1111/j.1466-8238.2010.00597.x

Pulliainen E, Itämies J (1988) *Xestia* communities (Lepidoptera, Noctuidae) in eastern Finnish Forest Lapland as indicated by light trap sampling. Ecography 11:235–240. https://doi.org/10.1111/j.1600-0587.1988.tb00805.x

R Development Team (2015) R: A language and environment for statistical computing. Version 3.2.3. R Foundation for Statistical Computing, Vienna, http://www.r-project.org/

Roff DA (1980) Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. Oecol 45:202–208. https://doi.org/10.1007/BF00346461

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60. https://doi.org/10.1038/nature01333

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. Glob Change Biol 6:407–416. https://doi.org/10.1046/j.1365-2486.2000.00322.x

Tauber MJ, Tauber CA, Masaki S (1986) Seasonal adaptations of insects. Oxford University Press, New York

Tenow O, Nilssen AC, Bylund H, Hogstad O (2007) Waves and synchrony in *Epirrita autumnata/Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. J Anim Ecol 76:258–268. https://doi.org/10.1111/j.1365-2656.2006.01204.x

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L (2001) Ecological and evolutionary processes at expanding range margins. Nature 411:577–581. https://doi.org/10.1038/35079066

Välimäki P, Kivelä SM, Jääskeläinen L, Kaitala A, Kaitala V, Oksanen J (2008) Divergent timing of egg-laying may maintain life-history polymorphism in potentially multivoltine insects in seasonal environments. J Evol Biol 21:1711–1723. https://doi.org/10.1111/j.1420-9101.2008.01597.x

Välimäki P, Kivelä SM, Mäenpää M (2013a) Temperature- and density-dependence of diapause induction and its life history correlates in the geometrid moth *Chiasmia clathrata* (Lepidoptera: Geometridae). Evol Ecol 27:1217–1233. https://doi.org/10.1007/s10682-013-9657-8

Välimäki P, Kivelä SM, Mäenpää M, Tammaru T (2013b) Latitudinal clines in alternative life histories in a geometrid moth. J Evol Biol 26:118–129. https://doi.org/10.1111/jeb.12033

Van Dyck H, Bonte D, Puls R, Gotthard K, Maes D (2015) The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? Oikos 124:54–61. https://doi.org/10.1111/oik.02066

Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecol 147:164–172. https://doi.org/10.1007/s00442-005-0299-6

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395. https://doi.org/10.1038/416389a

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69. https://doi.org/10.1038/35102054

Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. Ecol Lett 8:1138–1146. https://doi.org/10.1111/j.1461-0248.2005.00824.x

Wood SN (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton

Zografou K, Kati V, Wilson RJ, Tzirkalli E, Pamperis LN, Halley JM (2014) Signals of climate change in butterfly communities in a Mediterranean protected area. PLoS One 9:e87245. https://doi.org/10.1371/journal.pone.0087245