Current temporal trends in moth abundance are counter to predicted effects of climate change in an assemblage of subarctic forest moths

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Abstract

Changes in climate are influencing the distribution and abundance of the world's biota, with significant consequences for biological diversity and ecosystem processes. Recent work has raised concern that populations of moths and butterflies (Lepidoptera) may be particularly susceptible to population declines under environmental change. Moreover, effects of climate change may be especially pronounced in high latitude ecosystems. Here, we examine population dynamics in an assemblage of subarctic forest moths in Finnish Lapland to assess current trajectories of population change. Moth counts were made continuously over a period of 32 years using light traps. From 456 species recorded, 80 were sufficiently abundant for detailed analyses of their population dynamics. Climate records indicated rapid increases in temperature and winter precipitation at our study site during the sampling period. However, 90% of moth populations were stable (57%) or increasing (33%) over the same period of study. Nonetheless, current population trends do not appear to reflect positive responses to climate change. Rather, time-series models illustrated that the per capita rates of change of moth species were more frequently associated negatively than positively with climate change variables, even as their populations were increasing. For example, the per capita rates of change of 35% of microlepidoptera were associated negatively with climate change variables. Moth life-history traits were not generally strong predictors of current population change or associations with climate change variables. However, 60% of moth species that fed as larvae on resources other than living vascular plants (e.g. litter, lichen, mosses) were associated negatively with climate change variables in time-series models, suggesting that such species may be particularly vulnerable to climate change. Overall, populations of subarctic forest moths in Finland are performing better than expected, and their populations appear buffered at present from potential deleterious effects of climate change by other ecological forces.

Keywords: biodiversity, climate change, forest insects, lepidoptera, life-history traits, moth declines, time-series analysis

Introduction

Global climate change is altering the distribution, abundance, and population dynamics of species on earth (Parmesan, 2006; Maclean & Wilson, 2011; Cornulier *et al.*, 2013). In combination with land use change, climate change represents a significant threat to biological diversity worldwide (Parmesan & Yohe, 2003; Thomas *et al.*, 2004a; Forister *et al.*, 2010) with potential consequences for many ecosystem processes (Cardinale *et al.*, 2006; Ball *et al.*, 2008; Kurz *et al.*, 2008). Understanding which species are most at risk from climate change, and

which are not, has therefore become a matter of some urgency (Walther *et al.*, 2002; Parry *et al.*, 2007).

Among the many species affected by climate change, several authors have raised particular concerns about changes in the distribution and abundance of insects (Forister *et al.*, 2011; Wilson & Maclean, 2011; Fox, 2013). For example, densities of the green oak tortrix, *Tortrix viridana,* began declining markedly in Wytham Woods, England, during the 1950s and 1960s (Hunter *et al.*, 1997). Similarly, long-term monitoring at Rothamstead Research began registering declines in the diversity and abundance of moths during the 1950s (Woiwod & Gould, 2008), which have continued since (Conrad *et al.*, 2004, 2006). Changes in the flight phenology of moths (Woiwod, 1997) and in the latitudinal

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distributions of butterflies (Parmesan *et al.*, 1999) have both been associated with climate change, and insects may be declining at a faster rate than are some other taxa (Thomas *et al.*, 2004b; Thomas, 2005).

At the same time, other studies have described climate-related increases in the local abundance of insects, some of which are important pests of production systems (Gregory *et al.*, 2009). For example, a recent outbreak of mountain pine beetle in British Columbia, Canada, has been an order of magnitude greater in both extent and severity than any previous outbreak (Kurz *et al.*, 2008). In Europe, outbreaks of *Ips typographus* are expected to increase along with the increasing variability in temperature and precipitation that climate models predict (Kausrud *et al.*, 2012). Likewise, climate change is creating a significant challenge to insect pest management in Finland (Hakala *et al.*, 2011) and increasing defoliator outbreaks in the Patagonian Andes (Paritsis & Veblen, 2011). Given the direct positive effects of temperature on the performance of some insect herbivores (Bale *et al.*, 2002), we might expect climate change to increase the abundance of at least some insect species (Kozlov *et al.*, 2013).

It therefore seems probable that, in any single location, some insect species will respond positively to climate change while others will respond negatively (Groenendijk & Ellis, 2011; Pateman *et al.*, 2012). Studies that have compared responses to climate change in diverse insect assemblages remain relatively rare and restricted to a few geographic locations (Conrad *et al.*, 2004; Fox, 2013). Limitations in the availability of data remain a key issue for analyzing diverse insect communities over appropriate timescales to infer the effects of climate change (Woiwod, 1997; Kocsis & Hufnagel, 2011). Simple correlations between organism abundance and time can be misleading because systematic changes in abundance can be caused by a wide variety of processes in addition to climatic factors, including disturbance, habitat loss, and ecological succession (Odum, 1953; Bishop, 2002; Brower *et al.*, 2012). Untangling the effects of climatic factors from other drivers of systematic population change requires long datasets suitable for multivariate time-series modeling (Forchhammer *et al.*, 1998; Price & Hunter, 2005). Yet such studies are crucial because of the important role that insects play as agricultural pests (Hunter, 1994), pollinators (Tylianakis, 2013), food sources for vertebrates (Speight *et al.*, 2008), and drivers of ecosystem processes (Hunter *et al.*, 2012); they are the 'little things that run the world' (Wilson, 1987).

Studying population trends within large assemblages of species is particularly useful, in part because we may identify any shared ecological or life-history characteristics that are the ultimate causes of population declines or increases under climate change (Koh *et al.*, 2004; Brook *et al.*, 2008). Moths and butterflies are ecologically diverse and well-studied, which makes them an ideal group with which to investigate associations between life history and population responses to climate change (Mattila *et al.*, 2009, 2011). Previous work has associated habitat specificity (Kadlec *et al.*, 2009), narrow feeding niches, restricted resource distribution, poor dispersal abilities, and short flight periods with vulnerability to climate change (Kotiaho *et al.*, 2005; Franzen & Johannesson, 2007). In other work, increases in abundance have been observed in macrolepidoptera whose larvae feed on lichens and conifers, while species associated with shrubs and grasses have exhibited declining trends; hibernating stage and flight period also contributed to the observed variation (Conrad *et al.*, 2004). However, in most of these studies (except for Kadlec *et al.*, 2009) it is challenging to separate species' responses to climatic change from their responses to potentially confounding changes in the environment.

Here, we consider the effects of climate change on an assemblage of moth species in a subarctic forest at Värriö Strict Nature Reserve, in Finnish Lapland. Studies of the effects of climate change at high latitudes are particularly important because climatic change appears disproportionately rapid toward the poles (Walther *et al.*, 2002; Parry *et al.*, 2007). Our main goal was to provide a comprehensive view of changes in moth abundance, both negative and positive, that may result from climate change. We were particularly interested in comparing simple changes in moth abundance over time with time-series models that estimate the effects of climate variables on moth per capita rates of change. The former describe how moth abundances are changing while the latter attempts to untangle potential effects of climate on those changes.

We used 32 years of continuous light-trapping data to explore (i) which among the common species of Lepidoptera demonstrated directional trends in abundance between 1978 and 2009; (ii) associations between moth per capita population growth rates and climatic change; and (iii) which life-history and demographic characteristics of moth species are associated with the direction and strength of their responses to recent climatic change.

Materials and methods

Study area and climate data

Värriö Strict Nature Reserve (Värriön luonnonpuisto) is located in Eastern Lapland, Finland (67°44′N, 29°37′E). The reserve lies 250 km north of the Arctic Circle and 6 km from the Finnish-Russian border. There are no settlements close by,

and the nearest major road is located 100 km from the reserve; thus, the natural ecosystems remain practically undisturbed. The area is snow free approximately from the end of May to mid-October; the average temperature during January (the coldest month) is −11.4 °C and during July (the warmest month) +13 °C. Annual precipitation averages 595 mm. A period of continuous daylight lasts from 30 May to 14 July.

The Finnish Meteorological Institute has been operating synoptic climate measurements at Värriö Subarctic Research Station since 1971 as a part of a national network of weather observation. The first complete measurement year was 1975. In addition to manual measurements conducted twice each day by the permanent staff, an automatic weather station was installed in the 1990's. The station is located at 360 m a.s.l.; the closest light trap is only few tens of meters away from the weather station. The daily mean temperatures for 1975–2011 are available at: http://www.helsinki.fi/metsatieteet/varrio/tutkimus/weather1971.html.

To characterize trends in climate over the period of data collection, we collated climate data into four seasonal periods; spring (mid-March to mid-May), summer (mid-May to mid-July), fall (mid-July to mid-October) and winter (mid-October to mid-March). We then generated three climate variables for each of these seasons; average daily maximum temperature, average daily minimum temperature, and average daily precipitation. We also included average annual snow depth as an additional yearly measure. Uninterrupted climate data were available for all 32 years (1978–2009) during which moths were sampled. In order to assess patterns of climatic change, we used Pearson correlation coefficients to examine relationships between our climate measures and sample year.

Study sites and sampling protocol

The project, aimed at long-term monitoring of subarctic moth fauna, was designed and initiated by EP, and 11 light traps have been in operation at Värriö since 1978. They cover an area of about 1300 × 300 m, within which altitude ranges from 340 to 470 m a.s.l. (for a map, consult Pulliainen & Itämies (1988)).Three traps were established in an old-growth Scots pine (*Pinus sylvestris*) forest, three traps in a ravine of spruce (*Picea abies*) dominated mixed forest, three traps in a mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest on the northern slope of Värriötunturi fell, and two traps on the treeless summit of this fell. Pulliainen & Itämies (1988) provide a list of vascular plants recorded in the immediate vicinity of each trap at the beginning of the study.

Trap construction followed Jalas (1960). Traps were equipped with 500 W blended light lamps, and were switched on between 20:00 and 08:00 hours each night from approximately mid-May to mid-October. Catches were collected each morning, stored in a freezer, and moths were identified at the University of Oulu by JI. Identifications were generally based on external characters. However, for specimens in poor condition and for those groups like Coleophoridae and Nepticulidae that include externally similar species, moth genitalia were always examined. The voucher specimens are deposited in the Zoological museum of the University of Oulu.

Moth data

Over the 32 years of sampling, moth catches totaled 388 779 individuals from 456 species. Nomenclature of moths follows Fauna Europaea (Karsholt *et al.*, 2012). Species records from all traps were summed for a single annual value per species. Hence, data reported (Table S1) are the numbers of individuals per species per year per 11 traps. We fully appreciate that our data reflect measures of abundance and activity of the species that we collected, rather than their population densities in the strict sense. However, most of our analyses are concerned with temporal changes in moth abundance among years, and we assume that differences in trapping efficiency among species are constant over time. For the sake of brevity, we sometimes use the term 'density' in the following text (e.g., in the term 'density-dependent').

Many of the 456 moth species that we captured occurred in low abundance. We have therefore restricted our analyses to the 80 species that averaged at least eight individuals per year over the 32 years of sampling, which minimizes multiple consecutive years of zero catches. The total catch of these 80 species amounted 378 429 individuals, i.e. 97.3% of all specimens collected. Of the 80 species that we analyzed in detail, 25 were macrolepidoptera (belonging to families Lasiocampidae, Geometridae and Noctuidae; consult Tables S1 and S2; Table 1 for the list) and 55 were microlepidoptera (all remaining families). While these categories are largely historical in nature, rather than taxonomic or ecological, they continue to be used in publications in this field; we include them here for ease of comparison with other studies. Annual catches were transformed $\log_e(x + 1)$ prior to analysis of population trends and time-series models. Species in which there was a significant positive correlation between abundances two years apart were considered hemivoltine and analyzed separately from univoltine species. In the time-series analysis of hemivoltine species (below), counts in even years were analyzed separately from counts in odd years (Redfern & Hunter, 2005; Kozlov *et al.*, 2010). The final analyses were conducted on 65 univoltine species and 15 hemivoltine species.

Time-series analysis of moth populations

First, we calculated Pearson's correlation coefficients between annual abundance and study year for each moth species. Based on the significance of these relationships in a two-tailed test ($P < 0.05$ for significance), we assigned each species into one of three population trends: stationary (no significant trend), increasing or decreasing over time.

We then used time-series analysis (Royama, 1992) to estimate the effects of density dependence and climatic variables on moth population dynamics (Forchhammer *et al.*, 1998). Nonstationary time-series were detrended prior to the analysis (Hunter *et al.*, 1997). As in previous work (Redfern & Hunter, 2005; Kozlov *et al.*, 2010), we compared statistical models that associated moth per capita rates of change with prior moth abundance and climatic variables. Per capita rate of change is a useful metric for studies of population dynamics because it integrates both direct and indirect effects of

Table 1 Summary data describing population trends and demographic traits of 80 moth species sampled over 32 years in a subarctic forest in Finnish Lapland. Voltinism refers to univoltine (Uni) or hemivoltine (Hemi) species. Time-series models, chosen with AICc so as not to overparameterize models (see number of Final Variables), provided estimates of intrinsic rates of increase (R_{max}) and the strength of density dependence (Rapid DD). Current trends reflect current population trajectories in sampling data, expected responses reflect associations with climate change variables in time-series models, and a comparison of current and expected responses provides the Difference (assuming that higher abundance is always better than lower abundance). No difference is provided when time-series models gave rise to mixed associations with climate change variables

Family	Species	Voltinism	Years analyzed	Average annual count	Final variables	Model R-Sqd	R_{max}	Rapid DD (Slope)	Current trend	Expected response	Difference
Nepticulidae	Ectoedemia weaveri	Uni	all	46.90	1	51.80	3.43	−1.033	stationary	stationary	none
	Stigmella lapponica	Uni	all	8.84	1	29.09	1.04	−0.663	increasing	stationary	better
Incurvariidae	Incurvaria circulella	Uni	all	13.68	3	44.42	0.64	−0.543	stationary	decreasing	better
	Incurvaria vetulella	Uni	all	35.58	2	46.04	1.92	−0.706	stationary	stationary	none
Psychidae	Dahlica lazuri	Uni	all	8.16	3	52.93	1.40	−0.897	stationary	decreasing	better
	Taleporia tubulosa	Uni	all	15.84	3	46.00	1.57	−0.768	stationary	increasing	worse
Tineidae	Monopis spilotella	Uni	all	8.06	2	56.06	1.98	−1.009	stationary	decreasing	better
	Nemapogon cloacellus	Uni	all	10.68	2	41.02	1.49	−0.665	increasing	decreasing	better
Yponomeutidae	Parastvammerdamia conspersella	Hemi	even	118.75	4	91.08	3.58	−0.814	stationary	mixed	.
	Parastvammerdamia conspersella	Hemi	odd	998.19	2	62.41	4.58	−0.690	stationary	increasing	worse
Argyresthiidae	Argyresthia svenssoni	Uni	all	11.90	2	50.66	2.06	−0.978	increasing	decreasing	better
	Argyresthia pygmaeella	Uni	all	13.06	2	33.62	1.06	−0.587	decreasing	stationary	worse
Plutellidae	Plutella xylostella	Uni	all	26.32	2	68.42	3.12	−1.400	stationary	stationary	none
Ypsolophidae	Ypsolopha parenthesella	Uni	all	340.65	1	18.31	0.95	−0.300	increasing	stationary	better
Oecophoridae	Denisia similella	Uni	all	117.65	3	48.74	2.58	−0.655	decreasing	stationary	worse
	Denisia stipella	Uni	all	136.23	3	50.60	3.51	−0.777	stationary	decreasing	better
	Pleurota bicostella	Uni	all	73.77	1	31.59	2.44	−0.672	stationary	stationary	none
	Pseudatemelia josephinae	Uni	all	14.10	2	44.50	2.14	−0.676	increasing	stationary	better
Elachistidae	Elachista excelsicola	Uni	all	21.23	3	59.39	2.37	−0.874	stationary	decreasing	better
Coleophoridae	Coleophora glitzella	Uni	all	35.81	1	58.83	3.90	−1.199	increasing	stationary	better
	Coleophora idaeella	Uni	all	8.48	1	47.86	1.90	−1.005	stationary	stationary	none
	Coleophora vacciniella	Uni	all	8.58	5	66.79	1.62	−0.914	stationary	decreasing	better
Momphidae	Mompha idaei	Uni	all	11.97	3	69.21	3.00	−1.290	stationary	mixed	.
	Mompha locupletella	Uni	all	20.45	4	57.79	1.43	−0.544	increasing	mixed	.
Gelechiidae	Bryotropha galbanella	Uni	all	29.58	3	69.65	3.16	−1.168	stationary	decreasing	better
	Chionodes continuella	Uni	all	115.06	5	69.30	3.88	−0.919	stationary	decreasing	better
	Chionodes nubilella	Uni	all	15.32	2	60.19	1.76	−0.772	stationary	stationary	none
	Neofaculta infernella	Uni	all	55.26	3	63.86	2.71	−0.824	increasing	increasing	none
Pterophoridae	Hellinsia osteodactyla	Uni	all	9.23	3	55.42	1.07	−0.842	increasing	decreasing	better
Tortricidae	Acleris aspersana	Uni	all	171.81	2	49.81	0.90	0.013	stationary	stationary	none

Table 1 (continued)

Family	Species	Voltinism	Years analyzed	Average annual count	Final variables	Model R-Sqd	R_{max}	Rapid DD (Slope)	Current trend	Expected response	Difference
	Acleris maccana	Uni	all	178.42	3	44.71	2.07	−0.593	stationary	decreasing	better
	Ancylis myrtillana	Uni	all	306.74	4	45.16	2.27	−0.491	stationary	increasing	worse
	Ancylis unguicella	Uni	all	19.26	5	58.48	1.46	−0.642	increasing	decreasing	better
	Apotomis boreana	Hemi	odd	20.06	1	65.12	2.27	−1.038	stationary	stationary	none
	Clepsis senecionana	Uni	all	11.19	3	54.55	1.48	−0.886	increasing	stationary	better
	Eana osseana	Uni	all	126.26	3	55.93	2.15	0.007	increasing	decreasing	better
	Epinotia brunnichana	Uni	all	27.03	1	21.93	0.52	−0.495	increasing	stationary	better
	Epinotia maculana	Uni	all	97.35	2	53.59	2.36	−0.997	stationary	stationary	none
	Epinotia solandriana	Uni	all	28.65	2	35.79	1.50	−0.691	increasing	stationary	better
	Eriopsela quadrana	Uni	all	8.26	2	39.56	1.21	−0.734	decreasing	increasing	worse
	Eulia ministrana	Uni	all	38.65	3	74.26	3.14	−1.380	increasing	mixed	.
	Gypsonoma nitidulana	Hemi	odd	46.75	4	95.20	4.05	−1.206	increasing	mixed	.
	Loxoterma bipunctana	Hemi	even	5.50	1	42.08	1.05	−0.960	stationary	stationary	none
	Loxoterma bipunctana	Hemi	odd	39.56	1	46.17	2.68	−0.936	increasing	stationary	better
	Lozotaenia forsterana	Hemi	even	3.06	1	40.09	0.74	−0.922	stationary	stationary	none
	Lozotaenia forsterana	Hemi	odd	52.50	2	60.53	3.65	−1.038	stationary	stationary	none
	Orthotaenia undulana	Hemi	even	5.25	2	56.29	0.69	−0.546	increasing	stationary	better
	Orthotaenia undulana	Hemi	odd	25.75	2	42.62	1.14	−0.612	increasing	decreasing	better
	Phiaris heinrichiana	Uni	all	33.48	5	74.08	3.66	−1.238	stationary	decreasing	better
	Phiaris obsoletana	Uni	all	284.94	1	48.25	4.83	−0.986	increasing	stationary	better
	Phiaris palustrana	Hemi	even	18.25	1	24.83	1.54	−0.641	stationary	stationary	none
	Phiaris palustrana	Hemi	odd	46.13	2	60.71	2.23	−0.673	increasing	decreasing	better
	Phiaris schulziana	Uni	all	398.81	2	35.98	3.21	−0.635	decreasing	increasing	worse
	Rhopobota naevana	Uni	all	12.35	1	23.77	1.05	−0.583	stationary	stationary	none
	Sparganothis rubicundana	Uni	all	41.97	2	50.28	3.32	−0.962	stationary	increasing	worse
Pyralidae	*Zeiraphera griseana*	Uni	all	33.94	2	30.99	1.41	−0.590	stationary	decreasing	better
	Eudonia murana	Uni	all	17.23	2	55.71	2.54	−1.022	stationary	decreasing	better
	Gesneria centuriella	Uni	all	11.74	2	63.12	2.15	−1.234	decreasing	increasing	worse
	Udea decrepitalis	Hemi	even	3.63	3	63.00	1.41	−0.832	stationary	stationary	none
	Udea decrepitalis	Hemi	odd	25.38	2	65.93	2.92	−1.022	stationary	stationary	none
	Udea inquinatalis	Hemi	odd	16.75	2	74.81	2.32	−1.102	decreasing	stationary	worse
Lasiocampidae	*Poecilocampa populi*	Hemi	even	50.35	2	59.63	3.08	−0.563	increasing	stationary	better
	Poecilocampa populi	Hemi	odd	156.25	2	76.13	2.85	−1.311	increasing	decreasing	better
	Trichiura crataegi	Uni	all	14.42	3	85.74	1.76	−1.215	stationary	stationary	none
Geometridae	*Dysstroma citrata*	Uni	all	218.12	3	56.95	4.98	−0.069	increasing	stationary	better
	Dysstroma truncata	Uni	all	11.48	4	62.84	1.45	−1.010	increasing	mixed	.

Table 1 (continued)

Family	Species	Voltinism	Years analyzed	Average annual count	Final variables	Model R-Sqd	R_{max}	Rapid DD (Slope)	Current trend	Expected response	Difference
	Elophos vittaria	Hemi	even	9.94	1	66.59	3.23	−1.256	decreasing	stationary	worse
	Elophos vittaria	Hemi	odd	90.25	1	36.78	3.39	−0.668	stationary	stationary	none
	Entephria caesiata	Uni	all	844.33	1	26.90	3.27	−0.518	stationary	stationary	none
	Epirrita autumnata	Uni	all	5324.76	1	51.88	5.58	−0.603	decreasing	stationary	worse
	Eulithis populata	Uni	all	571.18	3	52.16	4.10	−0.439	stationary	stationary	none
	Eulithis testata	Uni	all	8.88	3	50.27	1.39	−0.297	stationary	stationary	none
	Eupithecia intricata	Uni	all	46.67	1	24.52	1.25	−0.478	stationary	stationary	none
	Eupithecia pusillata	Uni	all	55.61	2	31.16	1.42	−0.258	stationary	stationary	none
	Hydriomena ruberata	Uni	all	27.45	3	49.67	1.25	−0.168	stationary	stationary	none
	Macaria brunneata	Uni	all	32.79	3	59.88	1.65	0.554	increasing	stationary	better
	Macaria loricaria	Uni	all	8.64	4	63.55	1.55	0.430	increasing	stationary	better
	Operophtera brumata	Uni	all	115.45	3	70.18	2.91	−0.966	stationary	stationary	none
	Scopula ternata	Uni	all	62.33	4	68.26	3.00	−0.903	stationary	stationary	none
	Selenia dentaria	Uni	all	26.97	1	37.30	1.86	−0.197	stationary	stationary	none
	Thera obeliscata	Uni	all	16.09	1	33.40	1.49	−0.652	stationary	stationary	none
	Xanthorhoe decoloraria	Uni	all	17.33	3	48.73	2.05	−0.499	stationary	decreasing	better
Noctuidae	*Lithomoia solidaginis*	Uni	all	144.21	3	41.98	4.19	−0.443	increasing	stationary	better
	Syngrapha interrogationis	Uni	all	41.91	1	20.79	1.64	−0.379	stationary	stationary	none
	Xestia alpicola	Hemi	even	4.41	2	66.24	1.50	−0.992	stationary	stationary	none
	Xestia alpicola	Hemi	odd	263.56	2	70.71	4.94	−0.602	stationary	stationary	none
	Xestia laetabilis	Hemi	odd	36.06	2	78.71	4.06	−0.946	stationary	stationary	none
	Xestia speciosa	Hemi	odd	34.81	3	80.78	2.04	−0.394	stationary	increasing	worse
	Xestia tecta	Hemi	even	11.06	1	28.85	0.98	−0.327	stationary	increasing	worse
	Xestia tecta	Hemi	odd	550.88	3	78.91	5.36	−0.493	stationary	stationary	none

ecological variables on population change (Hunter *et al.*, 1997). Models were of the form:

$$R_t = X_t - X_{t-1}$$
$$= \alpha_1 X_{t-1} + \alpha_2 X_{t-2} + ... \alpha_D X_{t-D} + \beta_1 C_{t-1} + \beta_2 C_{t-2} + ... \beta_D C_{t-D}$$

where R is per capita rate of increase at a given time, t, $X = \log_e$ of moth abundance, the α's are the strength of the density-dependent effects on various time lags (D), and the β's are the strength of a number of different climatic factors (C) acting on various time lags (Price & Hunter, 2005). All of the climatic variables described under Climate Data (above) were tested for inclusion in time-series models. We used the corrected Akaike's information criterion (AICc) to select among competing models (Forchhammer *et al.*, 1998) using a forward stepping procedure. The AICc values provide a measure of parsimony by which to choose models with the maximum information gain for the minimum number of model variables. Forward stepping means models began with only an intercept, and that additional terms were added only if they significantly increased explanatory power under AICc. In addition, new variables were not permitted to enter models if their covariance with previously entered variables exceeded 0.5. In all cases, the maximum time lag investigated in our models was 3 years, i.e. the maximum lag for which ecological meaning can be easily inferred (Royama, 1992). Because of the well-established autocorrelation between per capita rates of increase and abundance at time t, the statistical significance of rapid density dependence was estimated independently using a randomization technique (Pollard *et al.*, 1987). Final model parameters, including the intrinsic rate of increase, R_{max}, and the strengths of density dependence, were estimated by maximum likelihood (Redfern & Hunter, 2005).

Associations between moth life-history traits and temporal trends

Life-history characteristics of moth species (listed in Table S2) were obtained from numerous publications on Lepidoptera, including high-standard determination guides and comprehensive revisions of separate taxa, and from consultations with specialists. Two points in our classification of life-history traits deserve special attention. First, only moth species whose larvae started feeding in autumn and then continued feeding the following spring were considered as hibernating in the larval stage. Second, we established the borderline between early pupating and late pupating moths based on leaf expansion and aging. In the majority of woody plants and shrubs in our study area, leaf expansion starts in the last week of May to early June and ceases by late June to early July. Only moth species that completed larval development by this time were considered as pupating early in the season.

We used categorical data modeling (Proc Catmod, SAS 9.2 for Windows) to compare the frequencies of current population trajectories (stationary, increasing or decreasing) among moths grouped by categorical life-history traits (Table S2). In each case, we compared our data with the null hypothesis of equal frequency of population trends among life-history groups (larval diet, pupation strategy, etc.). In addition, based on the results of time-series models (above) we repeated this analysis, but using the frequencies of population trajectories predicted under climate change (as opposed to current population trajectories). Predicted trajectories were assessed from the direction of significant correlations between moth per capita rates of increase and climate change variables in the time-series models. We used general linear models (Proc GLM, SAS 9.2 for Windows) to compare wing lengths (Table S2) of moths categorized both by current population trajectory and trajectories predicted under climate change. Finally, we also used general linear models to compare the demographic traits estimated from time-series models (R_{max}, average abundance and strength of density dependence) among moths grouped by their current and predicted population trajectories.

Results

Climatic change

Between 1978 and 2009, the mean and median annual temperatures at the Värriö station were −0.51 °C and −0.70 °C, respectively. Average annual temperatures increased during this period by 1.96 °C, i.e. 0.06 °C yr^{-1}. Six of the 13 climate variables that we selected for our study were correlated significantly and positively with study year (Fig. 1; Table S3). Average daily maximum temperatures in spring, fall, and winter all increased over time. Likewise, average daily minimum temperatures in fall and winter increased over time. Finally, winter precipitation increased during the course of the study period. In addition, spring precipitation (increasing over time) and annual snow depth (decreasing over time) exhibited marginally nonsignificant correlations with sample year (Table S3). Hereafter, we refer to the climate variables that varied systematically with year as 'climate change variables.'

Maximum and minimum temperatures within each season during the study period were strongly correlated with one another (r values ranged from 0.90 to 0.95, $n = 32$ years, $P < 0.0001$ in all cases). Because maximum and minimum temperatures can have very different effects on insect physiology and responses to climate (Dennis & Sparks, 2007; Speight *et al.*, 2008), both were included in the variable set for potential inclusion in time-series models (below). However, we never allowed maximum and minimum temperatures during the same season to enter the same time-series model because of their strong covariance.

Temporal trends in moth abundance

Among the 65 univoltine moth species, 38 exhibited stationary abundances, 21 were increasing over time and 6 were decreasing. Moth species with increasing
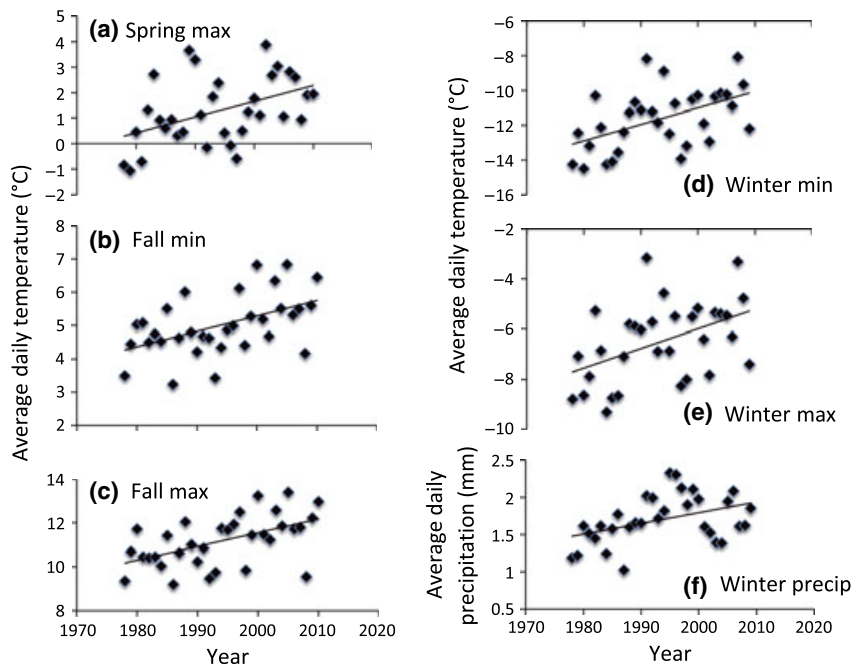
Fig. 1 Climate variables that underwent systematic change during 32 years of study in a subarctic forest in Finnish Lapland. Data represent average daily values of (a) spring maximum temperature, (b) fall minimum temperature, (c) fall maximum temperature, (d) winter minimum temperature, (e) winter maximum temperature, and (f) winter precipitation. Statistical information on the regressions is provided in Table S3.

abundances were therefore over three times more common than were those with decreasing abundances. Among the 15 hemivoltine moth species, 8 exhibited stationary abundances, 5 were increasing over time and 2 were decreasing. Overall, 26 moth species (33%) showed evidence of population increases while eight species (10%) showed evidence of population decreases (Table 1), with significantly more species increasing than decreasing ($\chi^2 = 9.53$, df = 1, $P < 0.01$).

Results of time-series analysis

Time-series models explained an average of 53.1% of variation in moth per capita rates of increase, with final models including from one to five variables each (median = 2 variables per model) (Table 1). Fourteen of 65 univoltine moth species (21.54%) showed evidence of delayed density dependence (time lag t−2), whereas only one out of 15 hemivoltine species (6.67%) showed evidence of delayed density dependence. Delayed density dependence was 6 times more common within macrolepidoptera than within microlepidoptera (42% and 7% of species, respectively; $\chi^2 = 12.1$, df = 1, $P = 0.0005$). All remaining moth species showed evidence of rapid density dependence. No species exhibited lags in density dependence greater than t−2 and there were no significant delayed (t−2 or longer)

effects of climate variables on moth per capita rates of increase.

Despite the relatively high frequency of moth species that were increasing in abundance over the study period, moth per capita rates of change were often associated negatively with the climate variables that were changing systematically over time (Table 1). For example, the per capita rates of change of fully 35% of microlepidoptera were associated negatively with climate change variables (Fig. 2). In contrast, the per capita rates of change of 16% of microlepidoptera were positively associated with climate change variables, and 9% of species exhibited mixed results (models contained both positive and negative associations with climate change variables). In comparison with microlepidoptera, macrolepidoptera exhibited far fewer associations between per capita rates of change and climate change variables. Rates of change of 64% of macrolepidoptera species were unaffected by climate change variables.

Summaries of associations between climate variables and moth per capita rates of increase are provided in Fig. 3a (microlepidoptera) and Fig. 3b (macrolepidoptera). Among the microlepidoptera, the most common associations are frequent negative correlations between fall and winter temperatures and moth per capita rates of increase. Notably, 16% of species retain positive
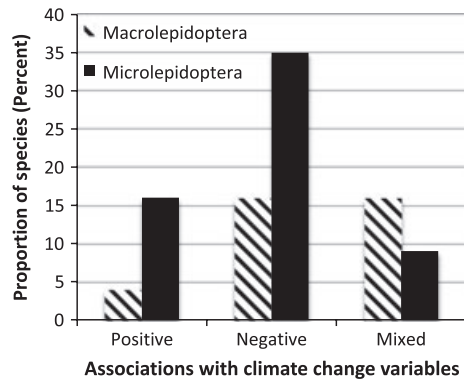
Fig. 2 Frequencies (percent) of macrolepidoptera (hatched bars) and microlepidotera (solid bars) species exhibiting positive, negative, or mixed associations between their per capita rates of change and climate change variables. Data are for 80 species of Lepidoptera sampled over 32 years in a subarctic forest in Finnish Lapland.

correlations between per capita rates of change and 'study year' after effects of climate have been included in models, suggesting that additional ecological factors that are changing systematically over time may be contributing to systematic changes in moth population growth rates.

Among the macrolepidoptera, there were frequent correlations between summer temperature and moth per capita rates of change (Fig. 3b). However, summer temperature is not among the climate variables that show systematic change over time at our study site. In contrast, macrolepidoptera may be affected negatively by declining snow depth. While the decline in snow depth over time is marginally nonsignificant, 20% of macrolepidoptera species in our study have per capita rates of change that are positively correlated with snow depth (Fig. 3b) and may therefore suffer under climate change if snow depth declines.

Associations between temporal dynamics and life-history traits

We found no associations between the life-history traits of moths (as described in Table S2) and their current population trajectories (Table 2). Likewise, moth life-history traits were generally unrelated to the predicted responses of their per capita rates of change to climate change variables (Table 2). However, the per capita rates of change of moths whose larvae fed on resources other than living vascular plants (e.g., litter, lichen, etc.) were much more likely to be associated negatively with climate change variables than were those of moths whose larvae fed on living vascular plants ($\chi^2 = 8.41$, df = 3, $P = 0.038$, Fig. 4).
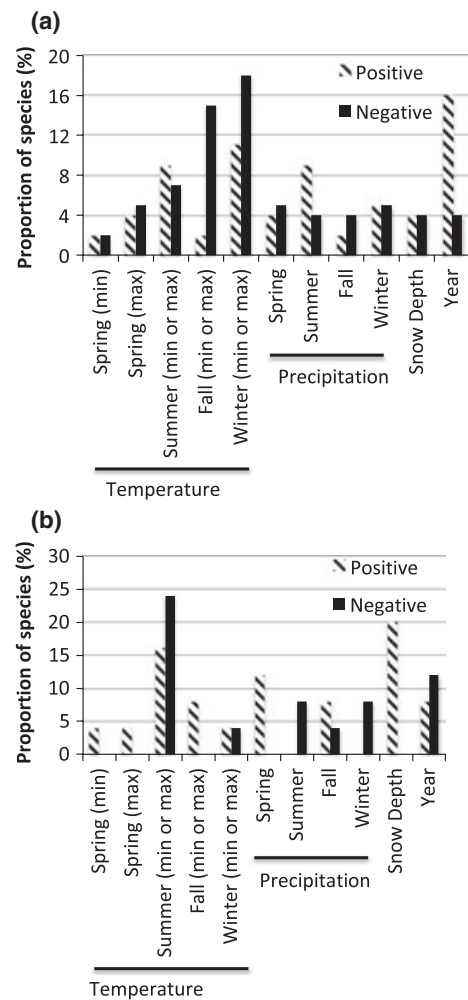

Fig. 3 Frequencies (percent) of (a) microlepidoptera and (b) macrolepidoptera species that show positive, negative, or no associations between their per capita rates of change and climate variables in a subarctic forest in Finnish Lapland. Data reflect associations in time-series models of 32 years of population change (Table 1). Data are provided separately for average daily minimum (min) and maximum (max) temperatures in spring because only spring maximum temperatures were increasing systematically over time.

We found no associations between the demographic traits of moths in our study and their current temporal trajectories in abundance (stationary, increasing or decreasing)(R_{max}: $F_{2,87} = 0.44$, $P = 0.644$; Average Abundance: $F_{2,87} = 0.65$, $P = 0.523$; Strength of Density Dependence: $F_{2,87} = 1.25$, $P = 0.291$). Likewise, we found no associations between their predicted responses to climate change variables and their demographic traits (R_{max}: $F_{3,86} = 0.52$, $P = 0.669$; Average Abundance: $F_{3,86} = 0.51$, $P = 0.676$; Strength of Density Dependence: $F_{3,86} = 2.33$, $P = 0.080$).

Table 2 Statistical associations between life-history traits and moth population trajectories sampled over 32 years in a subarctic forest in Finnish Lapland. Life-history traits and population trends are provided for each moth species in Table S2 and Table 1, respectively. Current trends refer to observed population trajectories (stationary, increasing or decreasing), whereas Expectations refer to associations (none, positive, negative, mixed) between moth per capita rates of change and climate change variables in time-series models. Significant associations are provided in bold

Trait	Current trends	Expectations
Pupation time		
Chi-Sqd	1.05	0.5901
df	2	3
P-value	0.59	0.902
Overwintering stage		
Chi-Sqd	3.64	0.54
df	4	6
P-value	0.456	0.997
Larval food		
Chi-Sqd	0.85	**8.41**
df	2	3
P-value	0.653	**0.038**
Feeding guild		
Chi-Sqd	3.66	4.77
df	6	9
P-value	0.723	0.854
Host plant life form		
Chi-Sqd	1.88	4.71
df	4	6
P-value	0.758	0.582
Dietary breadth		
Chi-Sqd	1.42	1.84
df	4	6
P-value	0.841	0.933
Pupation site		
Chi-Sqd	5.15	6.19
df	4	6
P-value	0.272	0.402
Wing span		
F-Value	0.65	2.42
df	2,80	3,79
P-value	0.523	0.072

Fig. 4 Frequencies (percent) of Lepidoptera species that show positive, negative, or mixed associations between their per capita rates of change and climate change variables in a subarctic forest in Finnish Lapland. Larval host plants are categorized as either living vascular plants (hatched bars) or other food sources (litter, lichen, etc.) (solid bars). Moth abundances were estimated over 32 years by light trapping.

increasing is perhaps surprising, given concerns about negative ecological effects of climate change at high latitudes or high elevations (Parmesan, 2006; Parry et al., 2007). Climate appears to be changing rapidly at Värriö, with significant increases in spring, fall, and winter temperatures, and in winter precipitation (Fig. 1), providing ample potential for ecological effects on organisms and their populations.

It is possible, of course, that climate change has either neutral or beneficial effects on northern latitude Lepidoptera (Fox, 2013). Range expansion and increased abundance of species with more typically southern distributions may add to the species pool and abundance of moths at northern latitudes (Warren et al., 2001). Such effects have been observed in northern parts of the UK (Conrad et al., 2006; Salama et al., 2007; Morecroft et al., 2009). Warmer temperatures may allow Lepidoptera to encounter and use plant species that were previously unavailable to them, so further facilitating range expansion (Pateman et al., 2012). In addition, the growing season in northern Europe has increased by as much as 3.6 days per decade during the last 50 years (Walther et al., 2002), increasing the productivity of high-latitude environments (Xu et al., 2013) and allowing southern species to complete their development in more northern regions (Bale et al., 2002).

However, our data do not suggest that climate change per se has had a positive influence on a majority of moth populations at Värriö. Rather, the per capita growth rates of moths were more often associated negatively (26% of species) than positively (11% of species) with climate change variables (Table 1). An additional 8% of species had per capita rates of change associated

Discussion

Despite strong evidence of population declines in Lepidoptera reported in most other studies (Hunter et al., 1997; Woiwod & Gould, 2008; Fox, 2013), we observed more cases of population increase (33% of moth species) than of population decrease (10% of moth species) at Värriö in Finnish Lapland. Moreover, at our study site, the populations of fully 57% of moth species were stationary over the 32 years of study. That the populations of 90% of moth species are either stable or
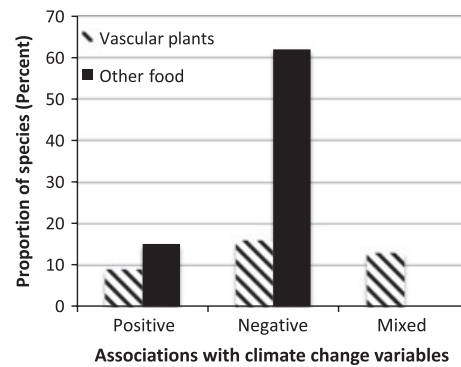
positively with some climate change variables but negatively with others, providing mixed expectations for population trends. The per capita growth rates of 55% of moth species were unrelated to climate change variables (Table 1). Unfortunately, in this analysis, we cannot distinguish between direct effects of climate on moths and indirect effects mediated by factors such as changes in natural enemies, host plants, or other factors.

We had expected that life-history or demographic traits might provide clues to understanding variation in moth population dynamics under climate change. However, we found no compelling evidence that these traits were associated meaningfully with current population trends, or those expected under climate change (Table 2). Overall, the per capita rates of change of microlepidoptera were more likely to be associated negatively with climate change variables than were those of macrolepidoptera (Fig. 2). Given that we found no association between wing length and climate change variables (Table 2), this difference cannot be explained based on size alone. However, we are unaware of any consistent ecological differences between these groups of moths that might explain their differential associations with climate change variables.

We also noted that the per capita rates of change of moths whose larvae feed on litter, lichen, and mosses (i.e. on resources other than living vascular plants) were much more likely to be associated negatively with climate change variables than were those of moths whose larvae feed on living vascular plants (Fig. 4). Recent increases in grazing pressure by reindeer are causing substantial reductions in the availability of ground vegetation and lichen in the forests of Finnish Lapland (Den Herder et al., 2003; Suominen et al., 2003), and may be responsible for negative associations between some moth species and climate change variables. This pattern supports the recent suggestion that litter and lichen feeding species, which remain relatively understudied in comparison to foliar-feeding Lepidoptera, merit increased attention from ecologists (Kozlov et al., 2010).

In previous studies, habitat specificity, limited dispersal, and host plant specificity have been associated frequently with population declines in butterflies, beetles, and hover flies (Sullivan et al., 2000; Warren et al., 2001; Kotze & O'hara, 2003; Koh et al., 2004; Kotiaho et al., 2005; Mattila et al., 2011; Stefanescu et al., 2011; Slade et al., 2013). For example, the specificity of larvae for host plants, overwintering stage, and flight period length are all significant predictors of distribution change and extinction risk in geometrid moths in Finland (Mattila et al., 2008). However, single traits may not always be the best predictors of insect responses to climate change (Mattila et al., 2006), particularly if those traits interact with each other in complex ways (Mattila et al., 2009). In addition to our study, others have been unable to find compelling links between insect life-history traits and population trajectories of Lepidoptera. For example, life-history traits correlate only weakly with population trends of butterflies in the California central valley (Forister et al., 2011) and of subarctic moths in other parts of Finland (Kozlov et al., 2010). Apparently, life-history traits are not always a strong predictor of responses to climate change or land use change in Lepidoptera.

Overall, populations of moths at Värriö are performing much better than might be expected given the high frequency of negative associations between moth per capita rates of change and climate change variables. We can investigate this further by comparing, species by species, current moth population trends with those expected from time-series models (see column labeled "Difference" in Table 1). We found that 43% of moth populations were performing better than might be expected from the relationships between their per capita rates of change and climate change variables; 17% of moth populations were performing worse than expected and 40% of moths were performing as expected.

We interpret these data to suggest that a high proportion of moth species at Värriö are responding primarily to ecological variables that are not immediately associated with climate change variables. Although our time-series models were commonly quite predictive, explaining an average of 53.1% of moth per capita rate of change (Table 1), many unmeasured ecological factors are probably contributing to population growth rates and current population trends. Time-series models are generally not mechanistic, relying upon correlations between demographic rates and measured variables (Royama, 1992; Boggs & Inouye, 2012). However, they have proven very useful in assessing species responses to climate change (Kausrud et al., 2012; Yan et al., 2013) and associations between climatic variables and population dynamics (Forchhammer et al., 1998; Price & Hunter, 2005). Simultaneously, time-series models of insects have also established the importance of other ecological factors, including effects of natural enemies and competition for limiting resources (Hunter et al., 1997; Hunter, 1998; Redfern & Hunter, 2005) on per capita rates of increase. Data were not available to explore the potential effects of these additional factors on moth dynamics at Värriö.

Understanding the underlying mechanisms by which climate drivers influence population growth rates is important for our ability to predict the population trajectories of species under climate change (Benton et al., 2006; Boggs & Inouye, 2012), especially when climate

drivers have both direct and indirect effects on organism performance (Sibly & Hone, 2002; White, 2008; Hansen *et al.*, 2013). For example, snow melt date has multiple effects on the population dynamics of the montane butterfly *Speyeria mormonica*, with both direct effects on the butterflies and additional indirect effects mediated by other members of the community (Boggs & Inouye, 2012). In addition, insect population growth may be related more to variation in weather patterns than to general trends of increase or decrease in temperature or precipitation. For example, increasing variability in precipitation promotes extinction of the checkerspot butterfly, *Euphydryas editha bayensis* (Mclaughlin *et al.*, 2002). Similarly, Rocky Mountain populations of the butterfly *Parnassius smintheus* respond negatively to extremes of warm or cold weather during winter rather than to average warming or cooling trends (Roland & Matter, 2012). Variation in climate can also affect negatively the natural enemies of insect herbivores, potentially releasing herbivore populations from regulation and causing increases in herbivore abundance (Stireman *et al.*, 2005).

However, a key result from our work is that dynamic ecological variables that appear unrelated to climate change may mask more subtle effects of climate change on the performance of organisms. For example, eight of our study species have increased in abundance over the last three decades during which time their per capita rates of increase were associated negatively with climate change variables (Table 1). In some sense, this may be good news, because negative impacts of climate change can be over-ridden by other ecological forces. However, it also means that simple temporal changes in population abundance cannot always be used to estimate effects of climate change on the dynamics of organisms.

While our study shows that the populations of most moth species at Värriö are either stable or increasing, a majority of studies of moth populations have reported recent declines in abundance. The strong evidence for systematic and widespread declines in UK moth populations has been reviewed recently (Fox, 2013). Both intensive studies at Rothamsted, UK (Woiwod & Gould, 2008) and extensive studies throughout a network of UK sites (Conrad *et al.*, 2004, 2006) provide compelling evidence of moth population declines at local and regional scales. Overall, about 66% of 337 species analyzes showed significant population declines between 1968 and 2002 (Conrad *et al.*, 2006). However, some moth species showed increases in abundance over the same period, particularly in northern areas (Conrad *et al.*, 2004). Likewise, among the dramatic and pervasive declines in moth populations in the Netherlands, some species are increasing strongly (Groenendijk & Ellis, 2011). Similarly, the butterfly fauna in the central

valley of California is undergoing more rapid population decline at lower elevation than at higher elevation, where some populations are actually increasing (Forister *et al.*, 2011). Yet northern latitudes are not free from declines in Lepidoptera. Historical records suggest declines in the distributions of geometrid and noctuid moths in Finland (Mattila *et al.*, 2006, 2008) and high extinction rates of moths in Sweden (Franzen & Johannesson, 2007).

There seems little doubt that habitat loss, habitat fragmentation, and climate change have all contributed to declines in the populations of some Lepidoptera (Warren *et al.*, 2001; Fox, 2013). For populations at the northern edge of their climatic range, climate warming may facilitate population growth and range expansion (Bale *et al.*, 2002), whereas habitat loss and overgrazing by ungulates may oppose such changes (Den Herder *et al.*, 2003; Suominen *et al.*, 2003). The overall effects on species assemblages would therefore reflect the balance of these opposing forces. At least for some butterfly species in the UK, negative effects of habitat loss appear to outweigh any beneficial effects of climate change on range expansion (Warren *et al.*, 2001). Similarly, in northeastern Spain and Andorra, declines in butterfly populations may be more closely associated with habitat modification than with climate change (Stefanescu *et al.*, 2011). Likewise, low elevation populations of butterflies in the central valley of California may be declining because of changes in land use and host plant availability rather than effects of climate change (Forister *et al.*, 2011). However, warming trends appear to be shifting species ranges up in elevation (Forister *et al.*, 2010), generating increases in both species richness and abundance at higher elevation. In combination, these and other studies illustrate that changes in habitat and climate interact strongly to influence the diversity and dynamics of Lepidoptera assemblages (Morecroft *et al.*, 2009; Forister *et al.*, 2010, 2011; Fox, 2013).

While range limitation can impose serious constraints on high-latitude populations under climate change (Parmesan, 1996, 2006; Parmesan *et al.*, 1999), some other studies in northern latitudes are consistent with our findings. For example, a study of 42 moth species at the Kevo Subarctic Research Station in Finland reported that 72% of species exhibited stationary time series while 14% were increasing and 14% were decreasing (Kozlov *et al.*, 2010). While there was no attempt in that study to associate population dynamics with climate change variables, there was no evidence to support systematic declines in moth abundance during recent decades.

In summary, our data provide an interesting puzzle. Overall, moth populations at Värriö are largely stable or increasing, yet the climate is clearly changing and climate change variables are more often associated

negatively than positively with moth per capita rates of increase. These patterns suggest that some other ecological factor(s) may be over-riding any potentially deleterious effects of climate change on moth population trends. In time-series models, estimates of per capita rates of change integrate the effects of multiple direct and indirect effects on population change, highlighting the need for future mechanistic studies of the trends reported here. Because of the isolated nature of our field site in Värriö, which is 250 km north of the Arctic Circle and 100 km from the nearest major road, anthropogenic changes in land use are essentially zero. What other factors may compensate for the potential negative impacts of increasing temperature and precipitation on moth populations that we observed in time-series models? One possibility is that natural successional processes in the plant community are favoring stability or increases in the populations of a majority of moth species. Such effects would have to be over and above any effects of plants on moths that are driven by climate change variables, which we already account for in our time-series models. Although we have not monitored plant succession quantitatively over this period, qualitative observations suggest increases in tree and shrub density at the expense of herbs (JI, unpublished data). Likewise, rates of tree growth, the altitude of the tree line, and plant phenology have all changed at Värriö during the last 30 years (JB, unpublished data). Our data collection occurred at a single research site, which limits our ability to generalize or to associate the dynamical patterns that we observed at Värriö with spatial variation in ecological factors such as plant successional stage. Whether driven by changes in the plant community, or by other ecological factors, our data illustrate that potentially negative impacts of climate change on Finnish subarctic moths at Värriö appear buffered, at least for now, by other ecological forces.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Counts of moths each year from a sub arctic forest in Finnish Lapland. Data represent the totals of individuals caught per year from 11 light traps. Please request the authors' permission before downloading or using these data, as they are still being used for research purposes.

Table S2. Summary of life-history traits of abundant moths trapped in Värriö Strict Nature Reserve, northern Finland, between 1978 and 2009.

Table S3. Correlation statistics (r = correlation coefficient with study year, P-value = probability) providing evidence of systematic climate change between 1978 and 2009 in a subarctic forest in Finnish Lapland. Significant correlations are in bold while marginal correlations are underlined.