

# Climate Change and Range Shifts in Two Insect Defoliators: Gypsy Moth and Nun Moth – a Model Study

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Environmental factors influenced by global climate change determine the distribution ranges of organisms. Especially ectothermic animals are expected to shift their distribution ranges northwards in the next hundred years or so. In this study simulations made with CLIMEX-modelling software were used to predict the future distribution ranges of two Central European serious forest pest species: the nun moth (*Lymantria monacha* L. (Lepidoptera: Lymantriidae)) and the gypsy moth (*L. dispar* L.). The software calculates an ecoclimatic index based on the life cycle requirements of a species and thus represents the probability of a viable population to exist at a certain location. Three different climate warming scenarios were considered: temperature increase of 1.4, 3.6 and 5.8°C. Simulations generated with the current climate conditions corresponded well to the current distributions of the species. The climate warming scenarios shifted the northern boundary of the distribution for both of these species north by c. a. 500–700 km. Also the southern edge of the ranges retracted northwards by 100–900 km. The results of this study are in agreement with the results of empirical studies on other species. Being serious pest species, these species pose a potential threat to silviculture and therefore, have to be considered in the planning of forest management practices.

**Keywords** CLIMEX, insects, forest pests, *Lymantria monacha*, *Lymantria dispar*, poleward shift, geographical range

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## 1 Introduction

Climate change will alter the distribution of many species in different taxa (Hickling et al. 2005) and poikilothermic animals, whose distribution is ultimately determined by climatic factors (Andrewartha and Birch 1954) have been noted to respond quickly to changing climate. With the mean temperature increase of  $\sim 0.6^{\circ}\text{C}$  over the past century and projected increases in the future (IPCC 2001), climate change has been shown to have effects on ecosystems worldwide (Walther et al. 2002). It has been recognized that global warming affects the individual species and communities in a form of range shifts and extinctions (Parmesan et al. 1999, Walther et al. 2002, Root et al. 2003, Battisti 2004, Battisti et al. 2005). Especially increasing winter temperatures have been proposed to be the key factor affecting range shifts in insects by reducing winter mortality (e.g. Ungerer et al. 1999, Veteli et al. 2005, Battisti et al. 2005). As a result of this temperature increase the ranges of species could expand poleward and in the mountainous areas also upward in elevation because the number of insect species is inversely related to latitude and elevation from the sea level (Sutherst 1991, Speight et al. 1999, Broadmeadow 2002, Hickling et al. 2005).

Furthermore, the greater volume, speed and frequency of international trade have increased the risk that defoliators could inadvertently be transported into new areas (MacLeod et al. 2002). One pathway into regions where defoliators do not already occur is timber trade (Liebhold et al. 1995). Thus, climate change and increasing global timber trade could both result in an increase in the introduction of alien invasive species. At the same time effects of defoliators, wood borers and bark beetles could become more detrimental due to prolonged growing season leading to multivoltinism, absence of extreme temperatures in winter that diminish population levels and possible shifts to novel host plants (Liebhold et al. 1995; Ayres and Lombardero 2000, Volney and Fleming 2000, Battisti 2004, Veteli et al. 2005, Battisti et al. 2006, Stastny et al. 2006).

The populations of many forest defoliators could increase into outbreak levels under warmer climate (Virtanen et al. 1995, Schlyter et al. 2006,

Williams and Liebhold 2002, Veteli et al. 2005) when also stress level of forest stands may be higher. This can be seen as a risk because, for example, an outbreak of the Siberian silk moth (*Dendrolimus sibiricus* Chetverikov) resulted in the death of 3 million forest hectares in Western Siberia in 1954–1957 (Isaev and Krivosheina 1976). If the outbreak areas of this insect would shift to the north it may remarkably change the forest dynamic in Siberia (Usher 2005) and in Canada (Volney and Fleming 2000). There are defoliators which are able to defoliate large forest areas also in Europe. For example, Nun moth, *Lymantria monacha* L. (Lepidoptera: Lymantriidae), and Gypsy moth, *L. dispar* L., are considered to be serious pest species in southern and central Europe. With the projected climate change, these species may pose a threat to current more northern ecosystems. Both species are already present in the fauna of northern Europe.

This study aims to simulate how climate change could affect on the range and distribution of two important lepidopteran forest defoliators: Nun moth (*Lymantria monacha*) and Gypsy moth (*L. dispar*). The analysis is emphasized on their potential to be significant defoliators in Northern Europe as a result of climate change.

## 2 Material and Methods

### 2.1 CLIMEX Software and Climate Data

CLIMEX 1.1 software was used to generate distribution simulations of two Lymantriid species and to estimate the possible distributions of these insects in changing climate. CLIMEX 1.1 holds weather data for monthly long-term average maximum and minimum temperature, rainfall and relative humidity from 2031 meteorological stations world wide from 1931 to 1960. 285 of them are situated in Europe. Additional weather data was added into CLIMEX meteorological database from ten different meteorological stations in Finland from year 1980 to 1990. After addition the total number of meteorological stations world wide was 2041 and for Europe 295. Additional weather data was gathered by Finnish meteorological institute.

CLIMEX can estimate a species potential geographic distribution, and its relative abundance in any region (Sutherst and Maywald 1985). CLIMEX can predict species potential distribution through weather parameters of its current habitat range, or directly by the species biological parameters such as minimum, maximum and optimum temperature for development. On the basis of biological parameters of the species, CLIMEX generates a map for the potential geographical distribution of the species by counting a ecoclimatic index (EI). EI is a numerical value for climatic suitability and relative abundance of the species. CLIMEX calculates EI from an annual growth index, describing conditions favourable for population growth together with stress factors that limit population growth during unfavourable season, and further, includes stress indices in the following manner:

$$EI = \left[ \frac{100}{52} \sum_{w=1}^{52} (TI_w \times MI_w \times DI_w) \right] \times \left[ \left( 1 - \frac{CS}{100} \right) \left( 1 - \frac{HS}{100} \right) \left( 1 - \frac{DS}{100} \right) \left( 1 - \frac{WS}{100} \right) \right]$$

Growth index counts for weekly temperature index ( $TI_w$ ), moisture index ( $MI_w$ ) and diapause index ( $DI_w$ ), where  $w$  is the week of the year. Each of the stress indices are calculated on weekly basis and expressed as a sum over the year as annual heat (HS), cold (CS), wet (WS) and dry stress indices (DS), all indicative of the climatic requirements of the species.

Temperature index consist of the lower temperature threshold (DV0), the lower and upper optimum temperatures (DV1 and DV2), and the upper temperature threshold (DV3). Further the number of degree-days (PDD) required to complete a generation cycle is used in modelling (Sutherst 1999). The assumption that soil moisture is the dominant factor which determines microclimatic conditions is the base of the Moisture index (MI). Four parameters are used in the calculations; lower and upper soil moisture threshold (SM0 and SM3) and the lower (SM1) and upper (SM2) bounds of optimum range. Diapause index is composed of diapause induction day length (DPD0), diapause induction temperature (DPT0), diapause termination temperature (DPT1) and diapause development days (DPD). In calculations param-

eter (DPSW) for winter diapause is also used. The stress indices used in this study are Heat stress (HS), Dry stress (DR) and Wet stress (WS). For adjusting parameters thresholds (TTHS, SMDS and SMWS) were determined. Outside these values stress accumulates at certain rate which is determined by stress rate parameters (THHS, HDS and HWS).

The equation and the theory behind it are more thoroughly described in Sutherst and Maywald (1985) and in Sutherst et al. (2000).

EI values range from 0 to 100, describing climatic suitability of the location for the species. At an EI value of 0 a species cannot establish a viable population at the location. Values over 20 indicate a very favourable climate for the species (Sutherst and Maywald 2005). More detailed description of EI values can be found e.g. in Vera et al. (2002) and Hoddle (2004). They considered EI values of 0 as unsuitable, 1–10 marginal, 11–25 favorable and  $\geq 26$  very favorable for establishment of a permanent population at a given location.

## 2.2 Climate Change Scenarios

CLIMEX is used in this study to predict the potential distributions of species as a result of climate change using IPCC climate change scenarios. The globally averaged surface temperature is projected to increase by 1.4 to 5.8°C by the year 2100. Calculations are based to SRES emission scenarios A1, A2, B1 and B2 (IPCC 2001). In this study, potential geographical ranges are simulated using three different temperatures varying within the limits of A1 and B2 scenarios. The temperatures used are: 1.4 (A1), 3.6 and 5.8°C (B2).

## 2.3 Study Organisms

Nun moth (*Lymantria monacha*) is a medium large black and white lymantriid moth reaching occasionally into outbreak densities in its core distribution areas in Eurasia (Bejer 1986, Jensen 1991, Coghlan 1994, Maksimov, S. 1999). It is highly polyphagous, feeding on species belonging to genera *Quercus*, *Salix*, *Carpinus*, *Tilia*, *Fagus*, *Picea* and *Pinus*. The distribution of *L. monacha* includes most parts of Europe and extends to

Middle Asia (Fig. 1). The species also exists in China, Japan and in isolated populations in South-East Asia.

Gypsy moth (*L. dispar*) is native to Eurasia, and has two strains, the European gypsy moth (EGM) and the Asian gypsy moth (AGM). Females of EGM are flightless, but those of AGM are capable of flight. Individuals of both strains are medium large black and white, but they can be distinguished by genetic markers (Garner and Slavicek 1996). Both strains can form populations reaching occasionally in outbreak densities in their core distribution areas in central Europe (Altenkirch 1986), Asia (Gninenko and Orlinskii 2003) and especially in North America (Liebhold et al. 2000), where the species has caused severe forest defoliations. It is considered to be one of the most serious forest pests in North America (Montgomery and Wallner 1988), and is also under close watch in New Zealand (Matsuki et al. 2001, Brockerhoff pers. com.), where serious concern is given to the matter of forest insect invasions (Brockerhoff et al. 2006). It is extremely polyphagous, feeding on a very wide variety of trees and low plants. The distribution area covers most part of Europe and Asia, and in North America its current distribution includes the northeastern states of USA and corresponding areas in Canada (Fig. 2). It is extinct in the British Isles since 1907 (Carter 1984).

#### 2.4 CLIMEX-Parameterization

Parameters used to estimate potential distributions of *L. monacha* and *L. dispar* are shown in Table 1. Parameter values were derived from literature and final fitting was done through estimation on the basis of the species' current distributions and seasonal phenologies in Europe (Distribution maps of insect pests 1955, Schwenke 1978, Distribution maps of insect pests 1981, Carter 1984, Marttila et al. 1996, Hulden et al. 2000, Hydén et al. 2006) as iterative geographic fitting procedure. Various methods have been used for model validation for CLIMEX simulations. Visual validation, the iterative geographic fitting procedure, which is used in this study, is suggested by the model creators (Sutherst and Maywald 1985, Maywald 1985 and Sutherst and Maywald 2005) and has

been used by several authors (e.g. Samways et al. 1999, Rafoss and Sæthre 2003, Yonow et al. 2004, Paul et al. 2005). Climate change scenarios have been validated with catch data of the modeled insect and comparing it to EI values which present the relative abundance of the insect (Rafoss and Sæthre 2003, Venette and Cohen 2006). Risk analysis for possible species introduction validation has been done by comparing the EI values of current known distribution and EI values of potential distribution by MacLeod et al. (2002). In this study, we relied on geographic fitting since for Europe there is no available abundance data with uniform standardized sampling effort for the studied species. Moisture requirements for both of the species are poorly known. As a result of this the parameter values for moisture were set so that they would not limit the species distributions strictly.

#### 2.5 Model Validation and Sensitivity Analyses

Parameter values of each of the indices in baseline simulation (Table 1) were subjected to sensitivity analyses to evaluate impact and magnitude of impact to EI value changes. During sensitivity analyses the parameter values of baseline simulation were kept constant and only one parameter was adjusted at a time. The simulation was re-run after each of the parameter changes. After re-run a mean value of EI for European weather stations were calculated for a diagram to measure sensitivity of different parameters. Temperature parameters DV0, DV1, DV2, DV3 and PDD were adjusted, respectively with DV value changes of -2, -1, 1 and 2 and PDD value changes -50, -25, 25 and 50 from base simulation in Table 1. Moisture parameters SM0, SM1, SM2 and SM3 were adjusted, respectively with value changes of -0.002, -0.001, 0.001 and 0.002 from base simulation. Diapause parameters DPD0, DPT0, DPT1 and DPD were adjusted, respectively with DPD and DPT value changes of -2, -1, 1 and 2 and DPD value changes -20, -10, 10 and 20 from base simulation.

Cold Stress parameters TTCS were adjusted with -2, -1, 1 and 2 and THCS with -0.002, -0.001, 0.001 and 0.002 changes, respectively

**Table 1.** CLIMEX-parameters for estimating the potential distribution of Nun moth (*Lymantria monacha*) (*LM*) and Gypsy moth (*L. dispar*) (*LD*).

Index	CLIMEX-parameter	<i>LM</i>	<i>LD</i>
Temperature (TI)			
	DV0 – Limiting low temp.	10	10.4
	DV1 – Lower optimal temp.	16	16
	DV2 – Upper optimal temp.	23	25
	DV3 – Limiting high temp.	28	32
	PDD – Minimum degree-days above DV0	480	500
Moisture (MI)			
	SM0 – Limiting low moisture	0.003	0.003
	SM1 – Lower optimal moist.	0.01	0.01
	SM2 – Upper optimal moist.	2.5	2.5
	SM3 – Limiting high moist.	3	3
Diapause (DI)			
	DPD0 – Diapause induction day length	12	10
	DPT0 – Diapause induction temp.	11	11
	DPT1 – Diapause termination temp.	6	8
	DPD – Diapause development days	70	90
	DPSW – Indicator for summer or winter diapause	0	0
Heat stress (HS)			
	TTHS – Heat stress temp. threshold	29	36
	THHS – Heat stress temp. rate	0.003	0.003
Dry stress (DS)			
	SMDS – Dry stress threshold	0.003	0.003
	HDS – Dry stress rate	0.002	0.002
Moisture Stress (WS)			
	SMWS – Wet stress threshold	2.5	2.5
	HWS – Wet stress rate	0.002	0.002

from base simulation. Heat Stress parameters TTHS were adjusted with  $-2$ ,  $-1$ ,  $1$  and  $2$  and THHS with  $-0.002$ ,  $-0.001$ ,  $0.001$  and  $0.002$  changes, respectively from base simulation. Dry Stress (SMDS, HDS) and Wet Stress (SMWS and HWS) parameters were adjusted with  $-0.002$ ,  $-0.001$ ,  $0.001$  and  $0.002$  changes, respectively from base simulation.

## 3 Results

### 3.1 Distribution

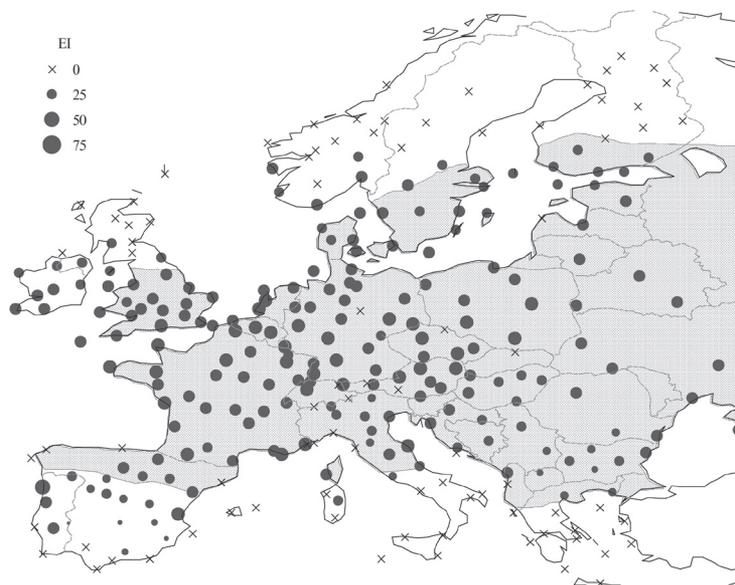
#### *Lymantria monacha*

The potential distribution of *L. monacha* defined by climate extends to North- and South-America, southern parts of Africa, Australia and to New-Zealand. In addition, the potential range extends in Asia wider than the current distribution. According to EI-values, the climate is most suitable for *L. monacha* in South- and Middle-Europe, and through Asia. Potential range in Europe defined by climate is shown in Fig. 1. In core distribution areas, EI values are greater than 30, which mean very favourable climate conditions for *L. monacha*. Southern distribution line is determined by heat stress. Potential range extends up to middle Fennoscandia, where the simulation gave an EI result varying between 18 and 23 (Fig. 1).

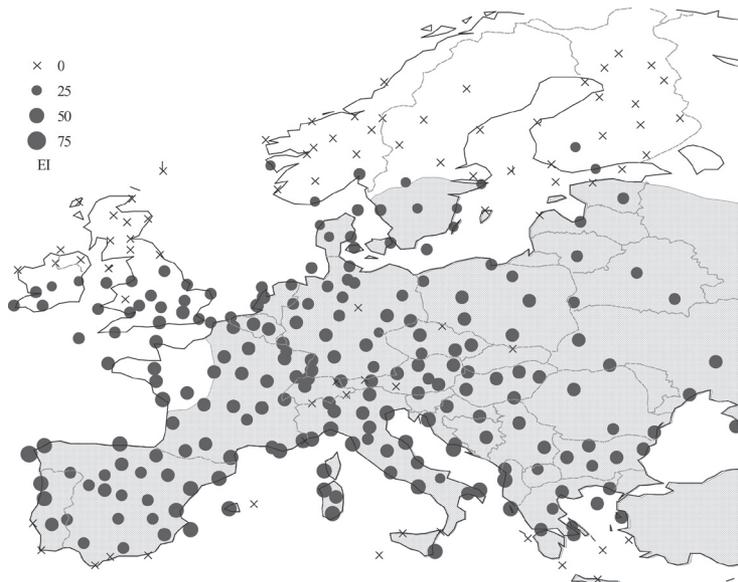
The EI values increase at northern locations with projected increase  $1.4^{\circ}\text{C}$  compared to the simulations without climate change scenarios. Potential range extends remarkably more to the north, with a minor decrease in EI value when moving northwards. EI values near the northern edge of range are 21–28 (Fig. 3). The distribution margin in the southern part of range in Europe remains unchanged or in some areas shifts northwards (Fig 3).

With the projected temperature increase of  $3.6^{\circ}\text{C}$ , the potential range in North Europe expands beyond the Arctic Circle (Fig. 4). EI values in the northern areas increase or remain unchanged, when compared to the simulation with a projected increase of  $1.4^{\circ}\text{C}$ . Results show that under warmer climate conditions, Fennoscandia will become more favourable for *L. monacha*. The southern distribution margin shifts to the higher latitudes. As a whole, range does not expand but shifts partially into the new areas.

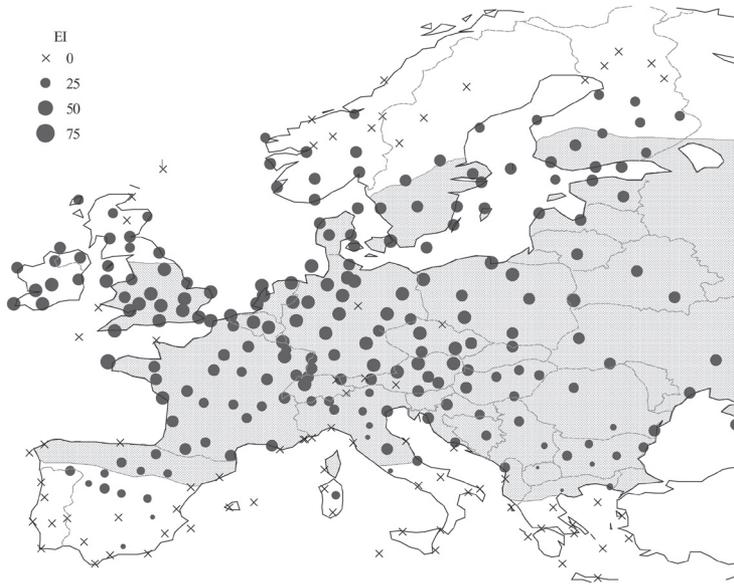
In the most extreme simulation with projected increase of  $5.8^{\circ}\text{C}$ , EI values increased only at a few locations (Fig. 5) compared to the  $3.6^{\circ}\text{C}$  simulation (Fig. 4). EI commonly decreased or remained unchanged in comparison with the projected increase of  $3.6^{\circ}\text{C}$ . EI values varied from 19 to 35 in Northern Fennoscandia. The southern



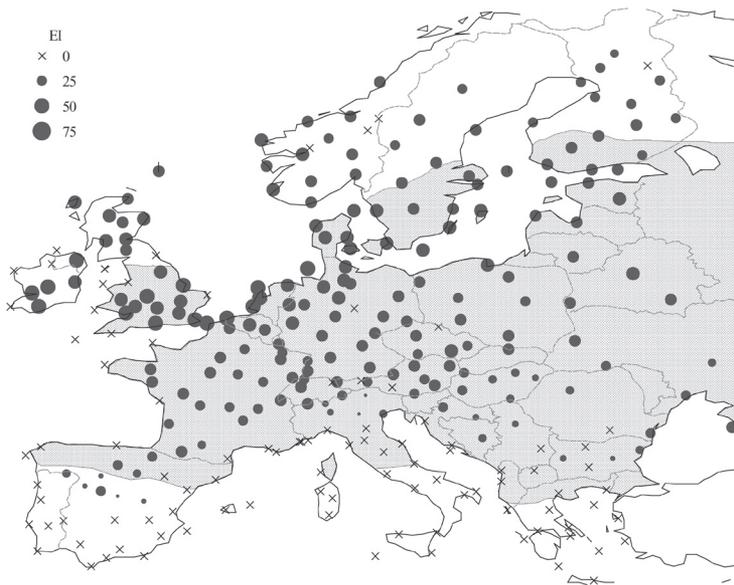
**Fig. 1.** The distribution of Nun moth (*Lymantria monacha*) (Distribution maps of insect pests 1955, Schwenke 1978, Carter 1984, Marttila et al. 1996, Hulden et al. 2000, Hydén et al. 2006) and predicted distribution by CLIMEX. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. monacha*.



**Fig. 2.** The distribution of Gypsy moth (*Lymantria dispar*) (Schwenke 1978, Giese and Scheider 1979, Distribution maps of insect pests 1981, Carter 1984, Marttila et al. 1996, Hulden et al. 2000, Hydén et al. 2006) and predicted distribution by CLIMEX. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. dispar*.



**Fig. 3.** Predicted distribution of Nun moth (*Lymantria monacha*) by CLIMEX in Europe using average global temperature increase of 1.4°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. monacha*. Shaded area represents current distribution (For references: see Fig. 1).



**Fig. 4.** Predicted distribution of Nun moth (*Lymantria monacha*) by CLIMEX in Europe using average global temperature increase of 3.6°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. monacha*. Shaded area represents current distribution (For references: see Fig. 1).

line of distribution area moved furthermore to the higher latitudes, to the level of Austria and Switzerland. In Great Britain, potential ranges diminished considerably.

### *Lymantria dispar*

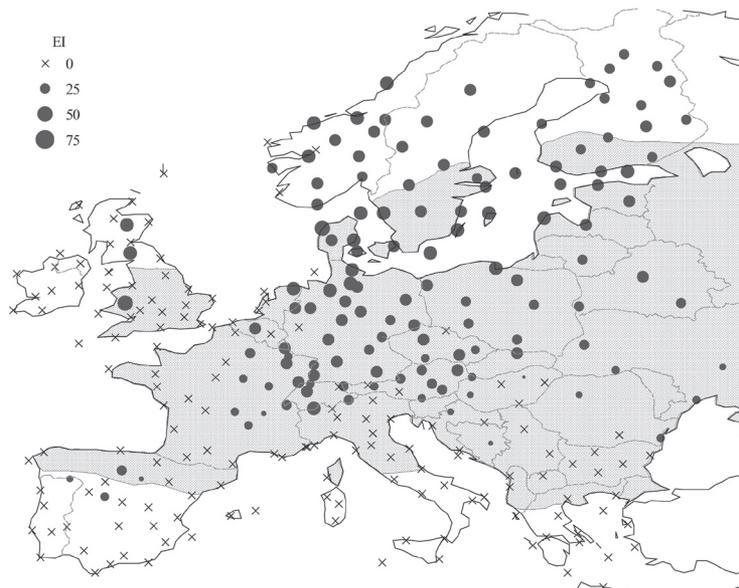
Simulation suggests that suitable areas for European strain of *L. dispar* are found to be wider than current distribution represents, particularly on the area of North- and South America, Africa, Australia and New-Zealand. The results are corresponding to the known distribution range of a *L. dispar* in Europe (Fig. 2). EI values are quite high throughout Europe varying around 30. When moving northwards, EI values decrease. This can be seen also in EI values of 16–20 on northern border of the range margin.

As a consequence of 1.4°C climate warming, the southern boundary of *L. dispar*'s range moves more to the north (Fig. 6). On a few southern locations, the EI value decreases to 0. The potential range in North Europe extends up to northern edge

of the Bay of Bothnia, which can be observed as EI values rising of up to 17–25.

The simulation with the projected increase of 3.6°C shows that, climatically suitable areas are found on even more northern areas (Fig 7). Now the potential range covers the northern Fennoscandia up to the Arctic Circle. EI values increase at all locations varying between 17 and 31.

In the simulation with projected increase of 5.8°C, the climate becomes even more favourable on the more northern locations (Fig. 8). EI values increased at all locations compared to simulations by the two other scenarios. Values decrease when moving from central Scandinavia to the north, but indices are also relatively high at northern locations, for example 27 at the Bay of Bothnia, and 21 in Sodankylä (near Arctic Circle). The southern boundary moves northward remarkably, in comparison to the simulation with projected temperature increase of 3.6°C (Figs. 7 and 8). This can be observed on the areas of Italy and Spain where most locations become unsuitable to maintain stable populations.



**Fig. 5.** Predicted distribution of Nun moth (*Lymantria monacha*) by CLIMEX in Europe using average global temperature increase of 5.8°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. monacha*. Shaded area represents current distribution (For references: see Fig. 1).



**Fig. 6.** Predicted distribution of Gypsy moth (*Lymantria dispar*) by CLIMEX in Europe using average global temperature increase of 1.4°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. dispar*. Shaded area represents current distribution (For references: see Fig. 2).



**Fig. 7.** Predicted distribution of Gypsy moth (*Lymantria dispar*) by CLIMEX in Europe using average global temperature increase of 3.6°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. dispar*. Shaded area represents current distribution (For references: see Fig. 2).



**Fig. 8.** Predicted distribution of Gypsy moth (*Lymantria dispar*) by CLIMEX in Europe using average global temperature increase of 5.8°C. Black circles indicate Ecoclimatic Indices (EI) at meteorological stations. Crosses indicate an EI of 0. Larger circles represent higher EI values and more favourable climatic conditions for *L. dispar*. Shaded area represents current distribution (For references: see Fig. 2).

### 3.2 Sensitivity Analyses

#### *Lymantria monacha*

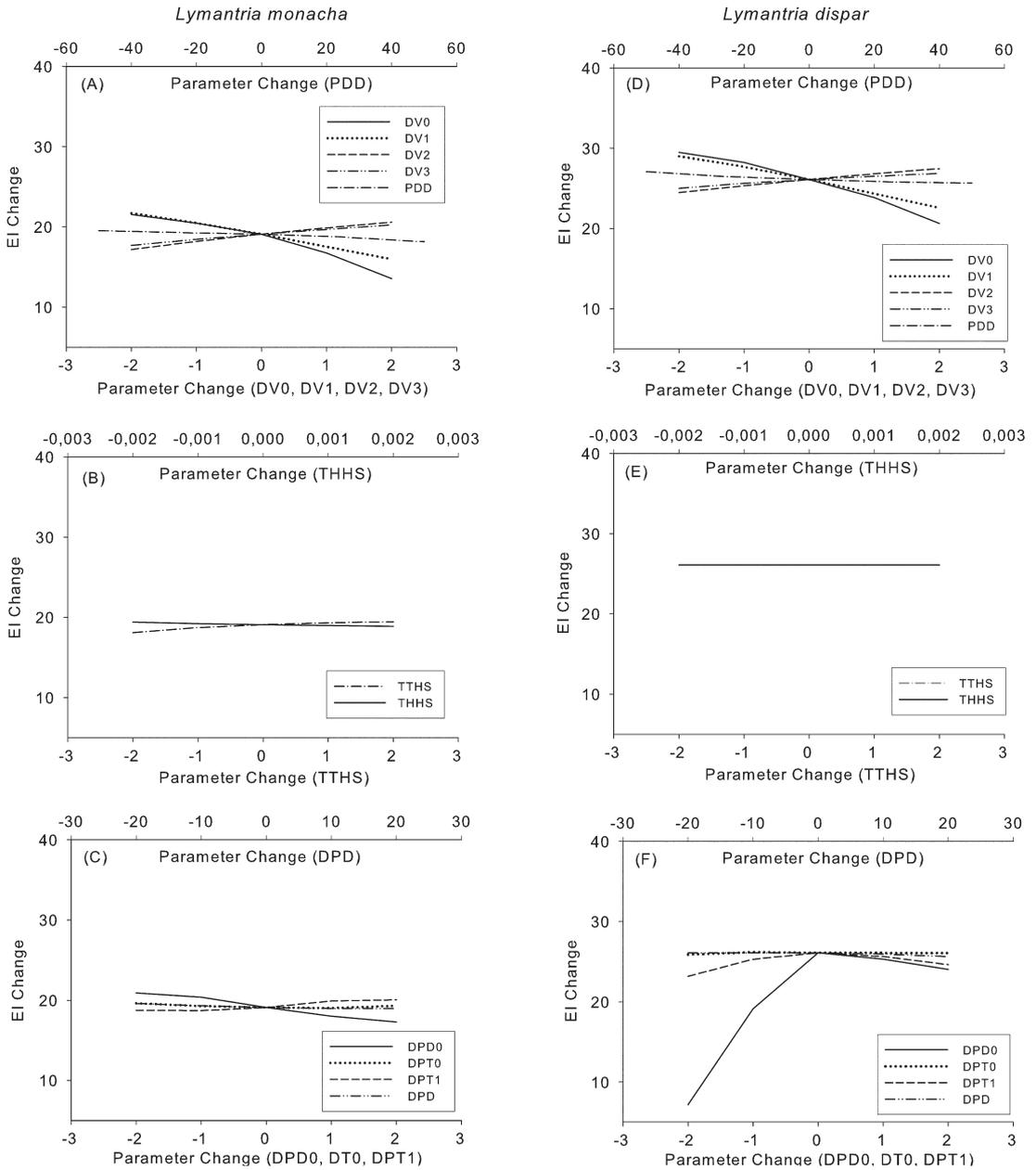
Our baseline simulation for potential distribution of *L. monacha* was highly sensitive to changes in DV0 (Fig. 9), the limiting low temperature-parameter. When DV0 was set to -2 from baseline simulation (Table 1), the average EI for European weather stations rose from the baseline prediction 19.09 to 21.55. Raising the DV0 had more extensive effects than lowering it. With DV0 raise of 2, the EI average dropped to 13.54 having the most profound effect on EI values than other parameters. Changes in DV1 to -2 and 2 from baseline simulation had similar effects, but not as strong as changes in DV0. The average of EI changed to 21.71 and 15.97 from baseline simulation, respectively. Only modest sensitivity was detected in changes of DV2 and DV3. With DV2 changes of -2 and 2, the average EI changed to 17.18 and 20.59 from baseline simulation, respectively. DV3 changes of -2 and 2 altered

average EI value to 17.69 and 20.25 from baseline simulation, respectively. Changes in PDD, the Minimum degree-days above DV0-parameter had only minor effects on average EI. With changes of -50 and 50 of PDD, EI value changed to 19.54 and 18.14, respectively.

Diapause and heat stress parameters DPD0, DPT1, TTHS had modest effect on average EI value, while DPT0, DPD and TTHS had only minor effects (Fig. 9). Changes in soil moisture and wet stress parameters had no effect on EI values.

#### *Lymantria dispar*

The baseline simulation for potential distribution of *L. dispar* was most sensitive to changes in DPD0 (Fig. 9), the diapause induction day length-parameter. When DPD0 was set to -2 from baseline simulation (Table 1), the average EI for European weather stations dropped from the baseline prediction 26.11 extensively to 7.19 having



**Fig. 9.** Sensitivity analysis of CLIMEX-simulations of *L. monacha* and *L. dispar* as change of EI: (A) Temperature (DV0, DV1, DV2, DV3, PDD), (B) Heat Stress (TTHS, THHS) and (C) Diapause parameters (DPD0, DPT0, DPT1, DPD) of *L. monacha*. (D) Temperature (DV0, DV1, DV2, DV3, PDD), (E) Heat Stress (TTHS, THHS) and (F) Diapause parameters (DPD0, DPT0, DPT1, DPD) of *L. dispar*. For abbreviations refer to text and Table 1.

the most profound effect on EI values than other parameters. Raising the DPD0 had only moderate effect, with raise of 2 the EI average dropped to 24.03. Other diapause parameters DPT0, DPT1 and DPD had only minor or moderate effects on average EI. Change in DPT0 to -2 and 2 from baseline simulation were 25.89 and 26.10, with DPT1 change of -2 and 2 were 23.18 and 24.63, respectively.

The simulation for *L. dispar* was also highly sensitive to changes in DV0 and DV1 (Fig. 9), much like the simulation of *L. monacha*. The average EI rose to 29.49 when DV0 was set to -2 from the baseline simulation (Table 1). With DV0 raise of 2, the EI average dropped to 20.61. When DV1 was changed by -2 and 2, the average EI changed to 29.00 and 22.56 from baseline simulation, respectively. DV2 and DV3 were only minor or moderately sensitive to -2 and 2 changes from the baseline simulation. The average of EI changed to 24.48 and 27.45 with DV2 and with DV3 to 25.00 and 26.85, respectively. Changes in PDD had only minor effects on average EI. With changes of -50 and 50 the EI value changed to 27.08 and 25.65, respectively. Soil moisture, heat stress, dry stress and wet stress parameters had no effect on average EI value (Fig. 9).

## 4 Discussion

This study shows that predicted climate change is going to affect the distributions of *L. monacha* and *L. dispar* (EGM) by causing a range shift towards the pole. There is a very good fit with the observed and predicted distribution of both species studied here. Parameterization of the factors causing distribution patterns was successful, and the results of potential distributions correspond well to known core distribution areas for both of these species (Figs. 1 and 2). Therefore, despite being a climate based model not including biotic factors, such as host plant range, predators and parasites and so forth, CLIMEX seems to be a reliable method to predict also the possible changes in distribution ranges.

However, several concerns have been raised for studies made by climate matching, which are based on the assumption that the current distribu-

tion corresponds to suitable climatic conditions for a species (Logan et al. 2003). The predictive power of these models decreases rapidly with the number of parameters used to predict the distribution. Thus, the number of them needs to be kept as low as possible. Critique has been presented against this methodology by many researchers (e. g. Davis et al. 1998; Samways et al. 1999), while others claim that, when adequate data for species studied are missing, this method may be the only choice available (Baker et al. 2000).

Matsuki et al. 2001 have used CLIMEX to estimate the potential risk of establishment of Asian strain of gypsy moth (AGM) (*Lymantria dispar*) in Australia and New Zealand. They used published data on temperature thresholds and visual fitting of AGM distribution to set the parameters accordingly. Oval temperature requirements were set according to Rubtsov (1938) and Mason and McManus (1981), larval and pupae requirements by Abdullaev (1967), Barteneva et al. (1974) and Leonard (1981) in their study. Degree-day parameter was set by combining observations by several authors (Benkevich 1955, Idrisova 1977, Lyamtsev 1983). Soil moisture requirements were set according to observations on effects of rain by Leonard (1981) and Campbell (1981) and drought by Hérard and Drea (1981) in study by Matsuki et al. (2001). The simulation by Matsuki et al. 2001 does not correspond with the current distribution of the European strain of gypsy moth (EGM). In their prediction the northern boundaries of distribution exceed well over five to six hundred kilometers to north probably by too low lower temperature thresholds for development. The gypsy moth is only migratory in Fennoscandia except in Denmark and southern Sweden and only larval imports and flying males have been found (Marttila et al. 1996). Our simulation is based on distributional data and estimates of seasonal phenology in Europe fitted in CLIMEX parameters and therefore more reliable prediction for European strain of the gypsy moth. What comes to the differences between observed and simulated distributions in Figs. 1 and 2, they can be explained by lack of available host-plants and discontinuities in habitats allowing dispersal.

The highest poleward range shift was c.a. 500 km for both of these species in the simulation (B2-scenario). Most evident this was in *L. monacha*

which also has a more northern distribution in Europe. The summer and winter temperatures are not likely to increase in an equal manner. In the boreal zone, winter temperatures are expected to rise more than the summer ones (IPCC 2001). Even though we did not consider the winter and summer temperature changes separately, as Crozier and Dwyer (2006) did in their analysis with *Atalopedes campestris* (Lepidoptera: Hesperidae), the range shift was remarkably similar than in their study. These range shifts are also remarkably similar to empirical findings of Parmesan et al. (1999). They analysed geographical ranges of butterfly species and found that of 35 analysed species northern boundaries of 22 species shifted northwards by 35 to 240 km and 2 shifted southwards during the last century. Also, an analysis of 51 species of British butterflies showed that 11 species have expanded in the northern part of their distributional range (Hill et al. 2002). Other data supporting the hypothesis that especially winter warming is driving insect range expansion to the north was found also by Walther et al (2002), Crozier (2004) and Battisti et al. (2005).

The processes for these margin changes in ranges may be both ecological and evolutionary. If abiotic factors, such as temperature, allow, habitat breadth can be increased as well as dispersal tendencies, which may result in extraordinary fast dispersal into new areas cross habitat disjunctions that would have expressed barriers to dispersal (Thomas et al. 2001). For the studied species, the poleward shift could be relatively slow, since they are quite sedentary occasionally reaching outbreak densities in core areas of their distribution (Schwenke 1978, Bejer 1988, Maksimov, S. 1999). However, the rates of local extinctions and colonizations in the margins of their range may be quite fast (e. g. Parmesan et al. 1999, Thomas et al. 2001).

For example, despite being a quite sedentary species, the dispersal ability of *L. dispar* is quite impressive, even though the females of EGM do not fly (Johnsson et al. 2006). According to Liebhold et al. (1992) of range margin can shift approximately 20 km/year. Yearly spread rate of *L. dispar* is extensive compared to its dispersal capabilities. Adult females are flightless but newly hatched larvae can disperse on silk threads blown by wind, but according to Sharov et al. (1999)

the spread by larvae, distances under 120 m/year which larvae normally disperse by wind cannot explain the rapid yearly spread of this species in North America. They suggested that inadvertent transportation of different life stages by human is the most important route for rapid of spread *L. dispar*. With warming climate the sedentary gypsy moth would probably widen its distribution range in Europe by inadvertent transportation as in North America and would colonize new more northern habitats.

Both of the studied species are extremely polyphagous and can lay eggs practically anywhere without the risk of the newly hatched larvae finding no food. Gypsy moth can feed on more than 700 different species of broadleaved and coniferous trees (Barbosa 1978, Liebhold et al. 1995, Matsuki et al. 2001). Nun moth can live on many coniferous and broadleaved Eurasian species and develops to maturity also on several North American tree species (Keena 2003), but outbreaks are observed in mainly on *Picea abies* and *Pinus sylvestris* stands (Jensen 1991, Coghlan 1994, Maksimov 1999). These host tree genera and species for both of the species cover much of the Europe and lack of host species would not prevent dispersion of gypsy and nun moth towards north with warming climate.

Range shifts observed in our simulations do not necessarily mean that these species could establish themselves in outbreak densities in the margins of their range due to limiting climatic factors. Near the coldest edges of their range these, ectothermic animals are restricted by thermal sum and are usually found on warm places such as sheltered hill slopes facing south (e.g. Thomas et al. 1999). In Central Scandinavia, extreme winter temperatures limiting these species are usually not met but the summer is too short to reach adequate thermal sum to complete the developmental cycle, and thus maintain stable populations.

According to our simulations, climate warming at the northern boundary for *L. monacha* is favourable up to 3.6°C. Beyond that, an increase in mean temperature decreases EI values, probably due to heat stress. For *L. dispar* the change is favourable also in the most extreme simulation of a 5.8°C increase. In their laboratory study Williams et al. (2003) found that elevation of temperature by 3.5°C shortened the development

of *L. dispar* by 7.5 to 8 days. As in consequence, warmer and prolonged summers will have positive effects on the growth of the gypsy moth at its northern limits. Also, winter minimum temperatures are likely to affect the population dynamics of these species to, especially, in preventing the occurrence of outbreak densities near the northern edge of range boundaries (e. g. Virtanen et al. 1995, Veteli et al. 2005).

The southern limit for these temperate species moved northward, which is suggested by study of Thomas et al. (1999) and shown with other species by Parmesan et al. (1999) and Battisti et al. (2005). Heat stress may be the dominant factor contributing to this at least in the case of *L. monacha*. Heat stress can affect these species in various ways, e.g. by affecting maintenance and termination of diapause, as well as synchrony with hosts (Battisti 2004). In case of *L. dispar* this shift to the north generally happens due changes which affect to diapause phase, most probably winter survival of eggs at low temperatures (Tauber et al. 1990, Sharov et al. 1999, Veteli et al. 2005). Temperatures may be too high for successful development during diapause phase or alternatively temperatures are not low enough for induction or appropriate development of diapause. This is in line with findings of Keena (1996) who noted that at higher temperatures between 15°C to 20°C the development time of diapause increases and also greater proportion of eggs did not hatch due to increased metabolism, though she also stated that the non-diapausing Asian strain of *L. dispar* could survive in areas where winter temperatures do not go under 20°C. For *L. dispar*, the increase in mean temperature is more advantageous than for *L. monacha* due to its wider optimum temperature range and the capability of multivoltinism without diapause by Asian strain. In addition *L. dispar* tolerates high temperature outside of its optimum range, which *L. monacha* does not.

Possible changes in precipitation patterns may also have effects on the distribution of these species through altering distribution and abundance, as well as quality, of suitable host plants. Heat and dry stress have been shown to affect plants by altering allocation of resources thus having substantial effects on their growth, yield and chemical defence (e.g. Ismail and Hall 1998,

Veteli et al. 2007). The effect of these changes are more difficult to predict, but it may well be that plants become more vulnerable to defoliators (e.g. Veteli et al. 2007). Hale et al. (2005) showed that dry stress affects negatively the growth of *L. dispar*-larvae on *Populus*. However, it is highly likely that the effect of dry stress, as well as heat stress, is species specific.

Our simulations are based on climatic factors only. The CLIMEX software does not allow us to consider possible changes in bottom-up or top-down regulation of the populations; these factors include e.g. resource availability, diseases, parasites and predators. However, due to the observed range shifts for many other species in published literature, we can be quite sure that the ranges of these two species will also shift polewards in the near future. Warming of the climate and the good dispersal abilities of Lymantriid moths assures this.

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## References

- Abdullaev, Y. 1967. Biological characteristics of the gypsy moth in the forests of Samarkand Province. In: Voprosy zashchity rasteniy, Tashkent. p. 80–82.
- Altenkirch, W. 1986. Die Nonne (*Lymantria monacha* L.) in Nordwestdeutschland 1977–1980. Journal of Pest Science 59(4): 67–74.
- Andrewartha, H.G. & Birch, L.C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois. 782 p.
- Ayres, M.P. & Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. The Science of the Total Environment 262(3): 263–286.
- Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod A. & Walters, K.F.A. 2000. The

- role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture, Ecosystems & Environment* 82(1): 57–71.
- Barbosa, P. 1978. Host plant exploitation by the gypsy moth, *Lymantria dispar*. *Entomologia Experimentalis et Applicata* 24(3): 228–237.
- Barteneva, Y., Gostjunin, I. & Persidskaya, L. 1974. The effect of temperature on the feeding rate of gypsy moth larvae. In: *Nauchnyye trudy Moskovogo lesotekhnicheskogo instituta. Voprosy zashchity lesa*. MLTI, Moskova: 93–96.
- Battisti, A. 2004. Forests and climate change – lessons from insects. *Forest@* 1(1): 17–24.
- , Sastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. & Larsson, S. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* 15(6): 2084–2096.
- , Stastny, M., Buffo, E. & Larsson S. 2006. A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biology* 12(4): 662–671.
- Bejer, B. 1986. Outbreaks of nun moth (*Lymantria monacha* L.) in Denmark with remarks on their control. *Journal of Pest Science* 59(5): 86–89.
- 1988. The nun moth in European spruce forests. In: Berryman, A.A. (ed.). *Dynamics of forest insect populations. Patterns, causes, implications*. Plenum Press. New York and London. p. 211–231.
- Benkevich V. 1955. The role of solar radiation in the heat balance of developing gypsy moth eggs. In: *Uchenyye zapiski Orekhovo-Zuyevskogo pedagogicheskogo instituta*. Moscow. p. 163–175.
- Brockerhoff, E.G., Liebholdt, A.M. & Jactel, H. 2006. The ecology of forest insect invasions and advances in their management. *Canadian Journal of Forest Research* 36: 263–268.
- Campbell, R. 1981. Population dynamics. In: Doane, C.C. & McManus, M.L. (eds.). *The gypsy moth: research toward integrated pest management*. USA Forest Service, Science and Education Agency, Animal and Plant Health Inspection Service. Technical Bulletin 1584: 65–86.
- Carter, D.J. 1984. *Pest Lepidoptera of Europe*. Series Entomologica 31. Dr. W. Junk, Dordrecht, Boston, Lancaster. 431 p.
- Coghan, A. 1994. Emergency rescue saves Poland's pine forests. *New Scientist* 144: 26.
- Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85(1): 231–241.
- & Dwyer, G. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist* 167(6): 853–866.
- Davis, A.J. Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783–786.
- Distribution Maps of Insect Pests. 1955. Pest: *Lymantria monacha* (L.). Series A, Map No. 60. Commonwealth Institute of Entomology. Queens Gate, London.
- Distribution Maps of Insect Pests. 1981. Pest: *Lymantria dispar* (L.). Series A, Map No. 26. Commonwealth Institute of Entomology. Queens Gate, London.
- Garner, K. & Slavicek, J. 1996. Identification and characterisation of a RAPD-PCR marker for distinguishing Asian and North American gypsy moths. *Insect Molecular Biology* 5(2): 81–91.
- Giese, R.L. & Schneider, M.L. 1979. Cartographic comparisons of Eurasian gypsy moth distribution (*Lymantria dispar* L.; Lepidoptera: Lymantriidae). *Entomological News* 90(1): 1–15.
- Gninenko, Y. & Orlinskii, A. 2003. Outbreaks of *Lymantria dispar* in Russian forests during the 1990's. *EPPO Bulletin* 33(2): 325–329.
- Hale, B.K., Herms, D.A., Hansen, R.C., Clausen, T.P. & Arnold, T. 2005. Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. *Oecologia* 31(11): 2601–2620.
- Hérard, F. & Drea, J. 1981. Agricultural research service sponsored public law 480 project in Morocco: 1972–1975. In: Doane, C.C. & McManus, M.L. (eds.). *The gypsy moth: research toward integrated pest management*. USA Forest Service Science and Education Agency Animal and Plant Health Inspection Service Technical Bulletin 1584: 317–321.
- Hickling, R., Roy, D., Hill, J., Fox, R. & Thomas, C. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12(3): 450–455.
- Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London. Series B-biological Sci-*

- ences 269(1505): 2163–2171.
- Hoddle, M.S. 2004. The potential adventive geographic range of glassy-winged sharpshooter, *Homalodisca coagulata* and the grape pathogen *Xylella fastidiosa*: implications for California and other grape growing regions of the world. *Crop Protection* 23: 691–699.
- Huldén, L., Albrecht, A., Itämies, J., Malinen, P. & Wetenhovi, J. 2000. Suomen suurperhosatlas (Finnish butterfly atlas). – Suomen Perhostutkijain Seura & Luonnontieteellinen keskusmuseo, Helsinki. 328 p. (In Finnish).
- Hydén, N., Jilg, K. & Östman, T. 2006. Nationalnyckeln till Sveriges flora och fauna. Fjärilar: Ädelspinnare – tofsspinnare. ArtDatabanken, SLU, Uppsala. 480 p. (In Swedish).
- Idrisova, N. 1977. Materials on the biology and ecology of the gypsy moth in Bashkirian ASSR. In: *Nasekomye – vrediteli lesov Bashkirii, Ufa*. p. 38–54.
- IPCC 2001. IPCC third assessment report, Climate change 2001: a synthesis report. Summary for policymakers. IPCC Plenary XVIII. Wembley, United Kingdom. p. 24–29.
- Isaev, A. & Krivosheina, N. 1976. The principles and methods of the integrated protection of Siberian forests from destructive insects. In: Tamm, C.O. (ed.). *Man and the boreal forest*. (Ecol. Bull. 21). Swedish Natural Science Research Council. Stockholm. p. 121–124.
- Ismail, A.M. & A.E. Hall. 1998. Positive and negative effects of heat-tolerance genes in cowpea. *Crop Science* 38: 381–390.
- Jensen, T. 1991. Integrated pest management of the nun moth, *Lymantria monacha* (Lepidoptera: Lymantriidae) in Denmark. *Forest Ecology and Management* 39(1): 29–34.
- Johnson, D.M., Liebhold, A.M. Tobin P.C. & Bjornstad, O.N. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* 444: 361–263.
- Keena, M.A. 1996. Comparison of the hatch of *Lymantria dispar* (Lepidoptera: Lymantriidae) eggs from Russia and the United States after exposure to different temperatures and durations of low temperature. *Annals of the Entomological Society of America* 89(4): 564–572.
- Leonard, D. 1981. Bioecology of the gypsy moth. In: Doane, C.C. & McManus, M.L. (eds.). *The gypsy moth: research toward integrated pest management*. USA Forest Service, Science and Education Agency, Animal and Plant Health Inspection Service. Technical Bulletin 1584: 9–29.
- Liebhold, A., Halverson, J. & Elmes, G. 1992. Quantitative analysis of the invasion of gypsy moth in North America. *Journal of Biogeography* 19(5): 513–520.
- , MacDonald, W.L., Bergdahl, D. & Mastro, V.C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. *Forest Science Monographs* 30. 49 p.
- , Elkinton, J., Williams, D. & Muzika, R. 2000. What causes outbreaks of the gypsy moth in North America? *Population Ecology* 42(3): 257–266.
- , Gottschalk, K., Muzika, R., Montgomery, M., Young, R., O’Day, K. & Kelly, B. 1995. Suitability of North American tree species to the gypsy moth: a summary of field and laboratory tests. USDA General Technical Report NE-211, USDA Forest Service, Delaware, Ohio, USA. 34 p.
- Logan, J.A., Régnière, J. & Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1(3): 130–137.
- Lyamtsev, N. 1983. Impact of weather on changes in gypsy moth density. In: *Molodye unchenyye k yubileyu instituta. Trudy SSSR VNIILM, Pushkino*. p. 188–194.
- MacLeod, A., Evans, H.F. & Baker, R.H.A. 2002. An analysis of pest risk from an Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European Community. *Crop Protection* 21(8): 635–645.
- Maksimov, S. 1999. On factors responsible for population outbreaks in nun moth (*Lymantria monacha* L.). *Russian Journal of Ecology* 30(1): 47–51.
- Marttila, O., Saarinen K., Haahtela, M. & Pajari, M. 1996. Suomen kiitäjät ja kehääjät. Kirjayhtymä. 384 p. (In Finnish).
- Mason, C. & McManus, M. 1981. Larval dispersal of the gypsy moth. In: Doane, C.C. & McManus, M.L. (eds.). *The gypsy moth: research toward integrated pest management*. USA Forest Service, Science and Education Agency, Animal and Plant Health Inspection Service. Technical Bulletin 1584: 161–202.
- Matsuki, M., Kay, M., Serin, J., Floyd, R., & Scott, J.K. 2001. Potential risk of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australasia: effects of climatic conditions and suitability of native plants. *Agricultural and Forest Entomology* 3(4): 305–320.

- Montgomery, M.E. & Wallner, W.E. 1988. The gypsy moth: a westward migrant. In: Berryman, A.A. (ed.). Dynamics of forest insect populations. Patterns, causes, implications. Plenum Press. New York and London. p. 353–375.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579–583.
- Paul, I., van Jaarsveld, A.S., Korsten, L. & Hattingh, V. 2005. The potential global geographical distribution of Citrus Black Spot caused by *Guignardia citricarpa* (Kiely): likelihood of disease establishment in the European Union. *Crop Protection* 24(4): 297–308.
- Rafoss, T. & Sæthre, M.G. 2003. Spatial and temporal distribution of bioclimatic potential for the Codling moth and the Colorado potato beetle in Norway: model predictions versus climate and field data from the 1990's. *Agricultural and Forest Entomology* 5(1): 75–86.
- Rubtsov, I. 1938. Effect of constant and fluctuating temperatures on egg development in the gypsy moth (*Porthetria dispar* L.). *Zashchita rasteniy* 17: 25–38.
- Samways, M.J., Osorn, R., Hastings, H. & Hattingh, V. 1999. Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (*Coccinellidae*, *Chilocorus* spp.) worldwide. *Journal of Biogeography* 26(4): 795–812.
- Schwenke, W. 1978. Die Forstschadlinge Europas. Band III. Verlag Paul Parey, Hamburg U. Berlin.
- Schlyter, P., Stjernquist, I., Barring, L., Jönsson, A.M. & Nilsson, C. 2006. Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. *Climate Research* 31(1): 75–84.
- Sharov, A., Pijanowski, B., Liebhold, A. & Gage, S. 1999. What affects the rate of gypsy moth (*Lepidoptera: Lymantriidae*) spread: winter temperature or forest susceptibility? *Agricultural and Forest Entomology* 1(1): 37–45.
- Stastny, M., Battisti, A., Petrucco-Toffolo, E., Schlyter, F. & Larsson, S. 2006. Host-plant use in the range expansion of the pine processionary moth, *Thaumetopoea pityocampa*. *Ecological Entomology* 31(5): 481–490.
- Sutherst, R.W. & Maywald, G.F. 1985. A computerised system for matching climates in ecology. *Agriculture, Ecosystems and the Environment* 13: 281–299.
- , Maywald, G.F. & Russell, B.L. 2000. Estimating vulnerability under global change: modular modelling of pests. *Agriculture, Ecosystems and the Environment* 82(1–3): 303–319.
- Tauber, M., Tauber, C., Ruberson, J., Tauber, A. & Abrahamson, L. 1990. Dormancy in *Lymantria dispar* (*Lepidoptera: Lymantriidae*): analysis of photoperiodic and thermal responses. *Annals of the Entomological Society of America* 83(3): 494–503.
- Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D. & Webb, N.R. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology* 13(Suppl. 1): 55–64.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411: 577–581.
- Ungerer, M.J., Ayres, M.P. & Lombardero, M.J. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (*Coleoptera: Scolytidae*). *Journal of Biogeography* 26(6): 1133–1145.
- Yonow, T., Kriticos, D.J. & Medd, R.W. 2004. The potential geographic range of *Pyrenophora seminiperda*. *Phytopathology* 94(8): 805–812.
- Venette, R.C. & Cohen, S.D. 2006. Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. *Forest Ecology and Management* 231(1): 18–26.
- Vera, M.T., Rodriguez, R., Segura, D.F., Cladera, J.L. & Sutherst, R.W. 2002. Potential geographical distribution of the Mediterranean fruit fly, *Ceratitis capitata* (*Diptera: Tephritidae*), with emphasis on Argentina and Australia. *Environmental Entomology* 31(6): 1009–1022.
- Veteli, T.O., Lahtinen, A., Repo, T., Niemelä, P. & Varama, M. 2005. Geographic variation in winter freezing susceptibility in the eggs of the European pine sawfly (*Neodiprion sertifer*). *Agricultural and Forest Entomology* 7(2): 115–120.
- , Mattson, W.J., Niemelä P., Julkunen-Tiitto R., Kuokkanen K, Lavola A. & Kellomäki S. 2007. Do elevated temperature and CO<sub>2</sub> generally have counteracting effects on the phenolic phytochem-

- istry of boreal trees? *Journal of Chemical Ecology* 33(2): 287–296.
- Virtanen, T., Neuvonen, S., Nikula, A., Varama, M. & Niemelä, P. 1995. Climate change and the risks of *Neodiprion sertifer* outbreaks on Scots pine. *Silva Fennica* 30(2–3): 169–177.
- Volney, W.J.A. & Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. *Agriculture Ecosystems and Environment* 82(1–3): 283–294.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- Williams, R., Lincoln, D. & Norby, R. 2003. Development of gypsy moth larvae feeding on red maple saplings at elevated CO<sub>2</sub> and temperature. *Oecologia* 137(1): 114–122.
- Williams, D.W. & Liebhold, A.M. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4(2): 87–99.

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