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Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling

MICHIEL F. WALLISDEVRIES and CHRIS A.M. VAN SWAAY
De Vlinderstichting/Dutch Butterfly Conservation, PO Box 506, 6700 AM Wageningen, The Netherlands

Abstract

Global warming may explain the current poleward shift of species distributions. However, paradoxically, climatic warming can lead to microclimatic cooling in spring by advancing plant growth, an effect worsened by excess nitrogen. We suggest that spring-developing but thermophilous organisms, such as butterflies hibernating as egg or larva, are particularly sensitive to the cooling of microclimates. Using published data on butterfly trends in distribution, we report a comparatively greater decline in egg–larva hibernators in European countries with oceanic climates and high nitrogen deposition, which supports this explanation. Furthermore, trends in abundance from a nationwide butterfly monitoring scheme reveal a 63% decrease over 13 years (1992–2004) for egg–larva hibernators in the Netherlands, contrasting with a nonsignificant trend in adult–pupa hibernators. This evidence supports the hypothesis that these environmental changes pose new threats to spring-developing, thermophilous species. We underline the threat of climate change to biodiversity, as previously suggested on the basis of mobility, habitat fragmentation and evolutionary adaptation, but we here emphasize a different ecological axis of change in habitat quality.

Keywords: biodiversity, butterflies, climate change, habitat quality, microclimate, nitrogen deposition

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Introduction

The rate of biodiversity loss in invertebrates may well be higher than for the more widely studied vertebrates and plants (J.A. Thomas *et al*., 2004). Many of these cold-blooded organisms, such as butterflies, require body temperatures of 30–35 °C for optimal growth and development (Porter, 1982; Shreeve, 1992; Stoutjesdijk & Barkman, 1992). In the temperate zone, a warm microclimate is essential for these organisms (Shreeve, 1992; Stoutjesdijk & Barkman, 1992; J.A. Thomas *et al*., 1998, 2001; Bourn & Thomas, 2002; Parmesan, 2003; Roy & Thomas, 2003). Hence, it has been suggested that climatic warming drives the range expansion of many species at the cool margins of their range (Parmesan *et al*., 1999; C.D. Thomas *et al*., 2001; Warren *et al*., 2001; Hill *et al*., 2002; Parmesan & Yohe, 2003). This implies that macroclimate and microclimate are positively correlated. However, the link between microclimate and macroclimate appears, at best, to be weak (Geiger, 1961; Stoutjesdijk & Barkman, 1992; Kennedy, 1997). Therefore, macroclimatic warming in temperate regions does not necessarily result in a more favourable environment for butterflies. Here, we explore the hypothesis that, to the contrary, macroclimatic warming, especially in combination with excess nitrogen, can actually cause species to suffer from microclimatic cooling.

We propose the following mechanism for relating microclimatic cooling to butterfly decline. At the cool margins of their range, butterfly species hibernating as eggs or larvae and developing in spring, highly depend on the thermal energy they can collect to complete their larval development. Therefore, they can be expected to be particularly sensitive to microclimatic conditions. In early spring, the larvae feed on green plants but depend on direct sunlight and warm substrates to reach their optimal body temperature. At this time of year, warmest microclimates are found in short vegetation (Geiger, 1961; Stoutjesdijk & Barkman, 1992) and on dry substrates, such as dead leaves, that warm up rapidly in the sun. Tall and green vegetation, however, provides a moist and cool environment, evapotranspiration keeping the temperature of green leaves at a level comparable to the ambient air temperature (Geiger, 1961;

Correspondence: Michiel WallisDeVries, e-mail: michiel.wallisdevries@vlinderstichting.nl

Stoutjesdijk & Barkman, 1992). Microclimatic measurements have confirmed that solar irradiation substantially raises surface temperatures of dead plants and larvae of the butterfly *Melitaea cinxia* L. above those of green plants and air temperature (WallisDeVries, 2006). In contrast, species hibernating as adults or pupae are expected to be little affected by spring microclimates, as they have already completed their larval development.

There are two main reasons why microclimates could have become cooler over recent decades: global warming and nitrogen deposition. Global warming has advanced the onset of plant growth in spring (Gitay *et al*., 2002; KNMI, 2003; EEA, 2004a). Since 1990, the plant growing season in the Netherlands has advanced by 2 weeks and the number of plant growing days between January and May has increased by 23% compared with the two preceding decades (www.knmi.nl; KNMI, 2003). These changes are expected to cause a cooler, less favourable microclimate for larval development because dead vegetation is rapidly overgrown by green foliage. Plants begin to grow at about +5 °C and are less dependent on direct sunlight for their development than larvae (Stoutjesdijk & Barkman, 1992). In contrast, flight periods of butterflies in the neighbouring British Isles (Roy & Sparks, 2000) have advanced for just 3.3 days on average over two decades and the trend is only significant for three out of 35 species. This could suggest a weakening synchronization between plant growth and larval development due to climatic warming.

Nitrogen deposition from intensive agriculture, industry and traffic is likely to worsen the impact of climatic warming on butterflies. Anthropogenic nitrogen input enhances mineralization and biomass accumulation in grassland and heathland communities (Achermann & Bobbink, 2003). The increased accumulation of green plant material is expected to further increase microclimatic cooling, strengthening the unfavourable effect on the development of butterfly larvae in spring.

In summary, the hypothesized mechanism to explain the decline of butterflies is as follows. With climatic warming, spring comes earlier to plants, driven by ambient temperature, than to butterfly larvae, that rely much more on solar irradiation. Early plant growth is exacerbated by nitrogen deposition, causing cool microclimates by the time butterfly larvae would normally start to develop. Thus, climatic warming and nitrogen deposition combine to cause microclimatic cooling and, hence, the decline of spring-developing, thermophilous butterflies. Unfortunately, experimental data to test this mechanism are not available. Time series of microclimatic measurements at a sufficient number of sites are equally lacking. In this paper, we present a first test of the proposed mechanism, based on trends in the distribution and abundance of butterflies across regions differing in climate and nitrogen deposition.

Geographical variation in butterfly trends, with an effect of hibernation mode (egg–larva vs. adult–pupa), should be expected if increases in spring temperature and nitrogen deposition, through their effect on microclimate, do indeed affect butterfly population dynamics. Therefore, we assessed the impact of climate change and anthropogenic nitrogen deposition on butterfly status over an east–west gradient across temperate lowland Europe, with climates ranging from continental to oceanic. Along this gradient, the length of the plant growing season increases with spring temperature. Nitrogen deposition is low at the western and eastern ends of the gradient and highest in the centre.

Furthermore, we expect trends in butterfly abundance to diverge over time between hibernation modes, when subject to mild winter–spring temperatures and high nitrogen deposition. To test this hypothesis, we analysed trends in butterfly abundance in 13 years of monitoring data (1992–2004) from the Netherlands, a country with both a mild oceanic climate and high nitrogen deposition.

Materials and methods

We have developed our hypothesis of microclimatic cooling for grassland vegetation. Although the proposed mechanism might also apply to woodland conditions, microclimatic conditions might be affected differently in the shrub layer and tree canopy and cause different effects on typical woodland species. In this paper, therefore, we focus on butterfly species with host plants in the herbaceous vegetation layer (i.e. we consider species feeding on shrubs and trees separately).

Distribution and environmental data

Trends in butterfly distribution over a period of 25 years were taken from the *European Red Data Book* (Van Swaay & Warren, 1999) for nine countries from Belarus in the east to Ireland in the west. Species were classified as declining (decreasing or extinct) or not-declining (stable, fluctuating or increasing). Species with unknown trends were discarded. Alpine species were excluded to avoid confounding effects of altitudinal gradients. All species were classified according to their mode of hibernation (Bink, 1992; Pollard & Yates, 1993). The butterfly *Pararge aegeria* L. may hibernate as larva, but it was classified as an adult–pupa hibernator, because pupal hibernation predominates (Bink, 1992) and because its flexibility rather suggests a response to microclimatic cooling as adult–pupa than as egg–larva hibernator.

Data on mean daily temperature for the nine countries were obtained from main lowland stations for the period 1961–1990 (KNMI, 1998) and averaged over the months January–May as an indication of weather conditions during the period of spring larval growth. Data on total nitrogen deposition (reduced and oxidized nitrogen in wet and dry deposition, expressed as N in mg m^{-2}) were obtained from www.emep.int (Tarrasón, 2003) to reflect anthropogenic impact on plant production (Achermann & Bobbink, 2003). Country averages were calculated from modeled nitrogen deposition values for 50 km × 50 km grid cells (Simpson *et al.*, 2003) over four periods (1980, 1985, 1990, 1995); only grid cells with $>70\%$ of their area in a selected country were used. Country averages for temperature and nitrogen deposition were not significantly correlated ($r = 0.24$, $P = 0.54$).

Multiple linear regression analysis was applied to explain the status of decline by January–May temperature, nitrogen deposition and hibernation mode. Butterfly family was included as a covariate to correct for phylogenetic factors. The large Nymphalidae family was subdivided into Satyrinae and other Nymphalidae. In order to avoid pseudoreplication, only one randomly selected country was included in the analysis for each species. Only species occurring in >4 countries were considered to obtain a representative sample for the whole study area. Status of decline was subsequently predicted for the other species × country cases on the basis of the obtained regression parameters. In doing so, two species groups were distinguished: species included in the regression dataset for other countries and species with a restricted distribution that were not included in the regression dataset.

Abundance data

Abundance data over the period 1992–2004 were obtained from the Dutch Butterfly Monitoring Scheme. They reflect butterfly numbers from weekly counts along more than 300 permanent transects (Pollard & Yates, 1993) distributed all over the Netherlands. Trends were calculated using time-series analysis with missing data, based on log-linear regression analysis (Van Swaay *et al.*, 2002). Average trends for species with different modes of hibernation were calculated as geometric means of index values for individual species. Species counted at <5 locations were excluded. A simultaneous analysis of hibernation mode, mobility effects and phylogeny (butterfly family) on trends was performed on the trend slopes of 29 species for which mobility estimates were available (Pollard & Yates, 1993).

Results

Butterfly decline across Europe

In total, 79 widely distributed species out of a total of 133 nonalpine butterfly species using host plants in herbaceous vegetation were included in the regression analysis; 63 of these hibernate as egg or larva, and 16 as adult or pupa (112 and 21 species, respectively, for the whole species set). As expected on the basis of the proposed influence of climate, the proportion of species hibernating as egg or larva in the native, regional butterfly fauna diminishes from the continent (84%) via the United Kingdom (73%) to the oceanic climate of Ireland, which is microclimatically cooler (63%; $\chi^2 = 6.5$, df = 2, $P = 0.039$).

Declines have occurred least in Ireland and Belarus and most frequent in Luxemburg, Germany, Belgium and the Netherlands (Fig. 1). The probability of being in decline increased with average spring temperature, nitrogen deposition and hibernation as egg or larva (Table 1; $R^2 = 0.370$, $P < 0.0001$). Hibernation mode, nitrogen deposition and average temperature correctly classified the status of decline in 80% of the species (35 declining and 28 nondeclining species; $\kappa = 0.59 \pm 0.09$). The model slightly overestimated the degree of decline: 10 species were wrongly expected to decline vs. six wrongly expected not to decline. Differences between butterfly families were not significant. Predictions of the status of decline were correct in 76% of the cases for the species in the regression analysis occurring in different countries ($\kappa = 0.52 \pm 0.04$; $P < 0.0001$,

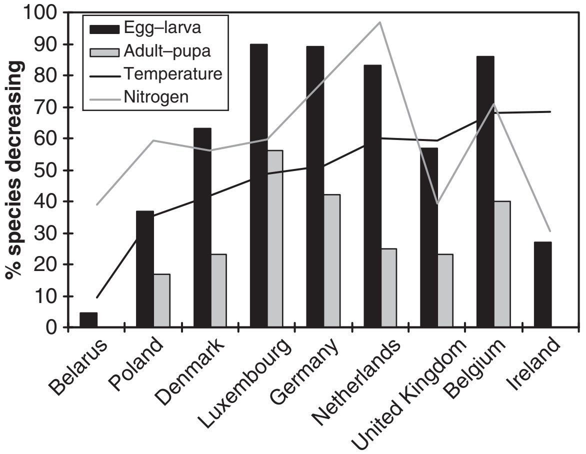

Fig. 1 Percentage of butterfly species of the two hibernation modes showing a long-term decrease in distribution along an east–west gradient in climate and nitrogen deposition. Indications of average winter–spring temperatures and nitrogen deposition are shown qualitatively by transformed values (temperatures °C × 10, nitrogen in mg m^{-2}/30).

Table 1 Logistic regression parameters estimating the change in distribution of 79 butterfly species in nine temperate lowland countries in Europe, as declining or not-declining

Term	Estimate ± SE	χ^2	P
Intercept	–8.71 ± 16.71	0.27	ns
Annual nitrogen deposition (N in mg m^{-2})	0.00202 ± 0.00063	10.31	0.0013
Hibernation mode (adult–pupa vs. egg–larva)	–1.32 ± 0.48	7.38	0.0066
Average daily temperature (°C)	0.63 ± 0.24	7.17	0.0074
Butterfly family			
Papilionidae-Satyrinae	–5.28 ± 83.03	0.00	ns
Pieridae-Satyrinae	0.33 ± 16.65	0.00	ns
Hesperiidae-Satyrinae	0.74 ± 16.62	0.00	ns
Nymphalidae-Satyrinae	1.69 ± 16.61	0.01	ns
Lycaenidae-Satyrinae	1.81 ± 16.62	0.01	ns

$N = 467$), and the predictions were correct in 73% of the cases for the 54 species with a more restricted distribution that were not included in the regression analysis ($\kappa = 0.43 \pm 0.08$; $P < 0.0001$, $N = 128$). Including 14 species feeding on shrubs and trees in the model significantly lowered the fit of the model ($R^2 = 0.262$) and introduced a significant lack of fit ($P = 0.0181$).

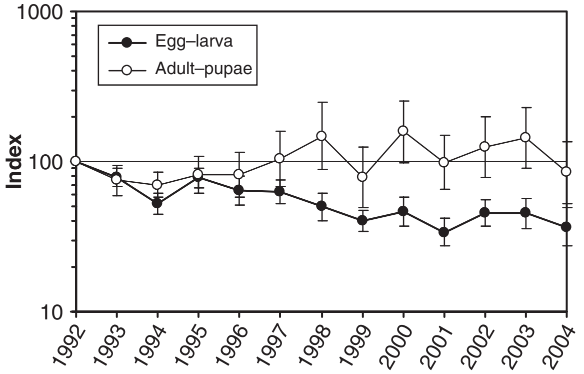

Fig. 2 Trends in butterfly abundance in the Netherlands for species hibernating as egg–larva ($N = 23$) or as adult–pupa ($N = 13$), based on the Dutch monitoring scheme. The abundance is indicated as an index (±SE) with a value relative to 100 in 1992, the year monitoring started.

Butterfly abundance in the Netherlands

Trends in butterfly abundance in the Netherlands were analysed for 23 egg–larva hibernating and 13 adult–pupa hibernating species that use host plants in herbaceous vegetation. The linear trend of log-transformed indices clearly differed between hibernation modes. Over the 1992–2004 period, there was a nonsignificant increase of adult–pupa hibernators (slope 0.0147 ± 0.0083, $F_{1,12} = 3.13$, $P = 0.1048$) compared with a significant decrease of 63% in the abundance of egg–larva hibernators (slope -0.0307 ± 0.0056, $F_{1,12} = 30.04$, $P = 0.0002$) (Fig. 2); regression coefficients were significantly different between the two groups ($P < 0.01$).

When differences in trend slopes for butterfly abundance were analysed including estimates of mobility, the effect of hibernation mode remained significant, as we expected ($P = 0.0107$). The effect of mobility was about as strong ($P = 0.0098$) but contrary to expectations, because the most mobile species showed a stronger decline than intermediately or least mobile species. Butterfly family, as a phylogenetic factor, did not explain any additional variation ($P = 0.41$).

Discussion

Microclimatic cooling as a threat to biodiversity

So far, other studies have related changes in butterfly distribution and abundance to macroclimate (Parmesan *et al.*, 1999; C.D. Thomas *et al.*, 2001; Warren *et al.*, 2001; Hill *et al.*, 2002; Parmesan & Yohe, 2003). This study is the first to examine the role of microclimate in determining trends in butterfly populations. In contrast with macroclimatic warming, our analysis supports the hypothesis of a cooling down of the microclimate in the herbaceous vegetation layer, with a generally negative impact on the population dynamics of spring-developing butterflies (i.e. species hibernating as eggs or larvae). The cooling is explained by an earlier start of plant growth in oceanic climates as a result of climatic change and anthropogenically increased nitrogen input. Microclimatic cooling has been tentatively advanced earlier to explain the decline of woodland butterflies with the demise of coppicing practices in Britain (Warren, 1995; Parmesan, 2003). Our study now substantiates that microclimatic cooling is much more than a regional problem of changing habitat management, but should be seen as a widespread environmental threat to a whole suite of species with a similar life history, including other thermophilous insects (Willott, 1997; Bourn & Thomas, 2002).

We considered only species with host plants in the herbaceous layer, because our proposed mechanism of microclimatic cooling might not work for species developing on woody plants higher up in the vegetation. Although there were not enough species from this group to perform a similar analysis, the reduced fit of the overall model when including them suggests that microclimatic cooling does indeed not apply to species feeding on shrubs and trees.

Robustness of the microclimatic cooling hypothesis

The apparent contradiction between our results concerning range contractions and studies reporting butterfly range expansions in Europe can be explained in several ways. Firstly, it should be pointed out that significant range expansions have occurred only in less than 25% of the species and, in general, range margins have neither moved southwards nor northwards (Hill *et al*., 2002). Secondly, the most significant range expansions northwards have occurred in species that hibernate as adults or pupae, such as *Polygonia c-album* L. and *Pararge aegeria* L. (Warren *et al*., 2001). Indeed, this group of species is also significantly overrepresented in the northward range shifts documented for Great Britain and northern Europe by Parmesan *et al*. (1999). We consider such species less vulnerable to microclimatic cooling since their larvae mainly develop in summer, when higher ambient temperatures allow optimal body temperatures to be reached more easily. Thirdly, expansions of habitat specialists among egg–larva hibernators, such as *Hesperia comma* L. and *Aricia agestis* DENIS & SCHIFFERMÜLLER (C.D. Thomas *et al*., 2001), occur on a much smaller scale and only in habitats with short vegetation of low productivity. In such high-quality habitats, especially under the comparatively low levels of nitrogen deposition in Great Britain and with appropriate habitat management, macroclimatic warming may also have resulted in microclimatic warming (Bourn & Thomas, 2002). This may also be true for reported range expansions in northern Europe (Parmesan *et al*., 1999), where nitrogen deposition is low as well. Differences in mobility between species might be expected to account for part of the observed trends (Warren *et al*., 2001), as could phylogenetic relationships. However, our analysis did not indicate an important role of these factors.

We believe that our primary conclusions will remain robust even when the wide variation in life cycles within each group of egg–larva or adult–pupa hibernators is taken into account. Both life-history types occur in all five main families of *Rhopalocera* butterflies. Indeed, including butterfly family in the analysis did not reduce the explanatory power of hibernation mode, temperature and nitrogen deposition. Thus, we are not discussing a phylogenetically isolated phenomenon. In a broader scientific context, we contend that life-history strategies and niche separation should be studied more closely as a function of microclimatic constraints.

Our grouping of hibernation modes could have been an oversimplification. However, similar results were obtained when distinguishing all four hibernation modes: the main contrast was that between egg–larva and adult–pupa hibernators. Evidently, experimental research is required to confirm our results under controlled conditions of climate and productivity.

Microclimatic cooling in a European perspective

Representation of the selected European countries in a spring temperature–nitrogen deposition plane (Fig. 3) shows the alarming situation for egg–larva hibernating butterflies in the Netherlands, Belgium and Germany. The aggravating effect of nitrogen deposition on their decline is clearly shown by the greater decline in the Netherlands and Belgium, where nitrogen deposition is high, compared with Great Britain and Ireland, with similar spring temperatures but low nitrogen deposition. Although nitrogen deposition in the Netherlands decreased by 27% over the period 1985–2000, the predicted lessening of butterfly decline has not taken place, because of the detrimental and compensatory effect of a simultaneous rise of spring temperatures.

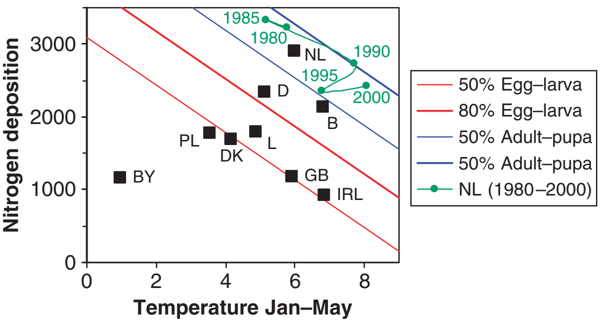

Fig. 3 Isoclines of butterfly decline and representation of the countries studied in relation to winter-spring temperature (°C) and nitrogen deposition (N in mg m^{-2}). Countries with abbreviated country names are shown in black squares. The development of winter–spring temperature and nitrogen deposition from 1980 till 2000 is shown for the Netherlands (green curve with dots at 5-year intervals). Isoclines of butterfly decline reflect 50% or 80% probabilities of predicted decline, depending on their hibernation strategy as eggs or larvae (red lines) or as adults or pupae (blue lines).

Conclusion

We conclude that despite macroclimatic warming, microclimatic cooling may drive the decline of insects relying on warm spring microclimates. This underlines the threat of climate change to biodiversity. This threat was previously suggested on the basis of mobility, habitat fragmentation and evolutionary adaptation (Warren *et al*., 2001; Hill *et al*., 2002; McLaughlin *et al*., 2002; Opdam & Wascher, 2004; C.D. Thomas *et al*., 2004), but we emphasize a different ecological axis of change in habitat quality. The problems of microclimatic cooling are worsened by the increase in plant production under anthropogenic nitrogen deposition. The effect of recent reductions in nitrogen emission (Tarrasón, 2003) is not expected to result in more favourable habitat conditions, because climatic warming has offset any improvement (see Fig. 3). Under these circumstances, the conservation of species that are vulnerable to microclimatic cooling requires additional attention to habitat management (J.A. Thomas *et al*., 1998, 2001; WallisDeVries, 2004) and renewed efforts to reduce anthropogenic emission of nitrogen and greenhouse gases. In Europe, the maintenance of low-productive seminatural grasslands (EEA, 2004b) could be essential for the preservation of butterflies and other organisms relying on warm microclimates.

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References

Achermann B, Bobbink R (eds) (2003) *Empirical Critical Loads for Nitrogen: Proceedings Expert Workshop*, 11–13 November 2002, Env. Doc. No. 164 Air, SAEFL, Berne, Switzerland.

Bink FA (1992) *Ecologische Atlas van de Dagvlinders van Noordwest-Europa*. Schuyt & Co, Haarlem, the Netherlands.

Bourn NAD, Thomas JA (2002) The challenge of conserving grassland insects at the margin of their range in Europe. *Biological Conservation*, **104**, 285–292.

EEA (2004a) *Impact of Europe's changing climate: an indicator-based assessment*. EEA Report No. 2/2004, European Environmental Agency, Copenhagen, Denmark.

EEA (2004b) *High nature value farmland: characteristics, trends and policy challenges*. EEA Report No. 1/2004, European Environmental Agency, Copenhagen, Denmark.

Geiger R (1961) *Das Klima Der Bodennahen Luftschicht*, 4th edn. Viehweg & Sohn, Braunschweig, Germany.

Gitay H, Suárez A, Watson RT, Dokken DJ (eds) (2002) *Climate change and biodiversity*. IPCC Technical Paper V, WMO, Geneva, Switzerland.

Hill JK, Thomas CD, Fox R *et al*. (2002) Response of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London B*, **269**, 2163–2171.

Kennedy AD (1997) Bridging the gap between general circulation model (GCM) output and biological microenvironments. *International Journal of Biometeorology*, **40**, 119–122.

KNMI (1998) *Wereld Klimaat Informatie WKI versie 2.00*. De Bilt, the Netherlands.

KNMI (2003) *De toestand van het klimaat in Nederland in 2003*. De Bilt, the Netherlands.

McLaughlin JF, Hellman JJ, Boggs CL *et al*. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences*, **99**, 6070–6074.

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285–297.

Parmesan C (2003) Conservation and biodiversity: butterflies as bioindicators for climate change effects. In: *Butterflies: Ecology and Evolution Taking Flight* (eds Boggs CL, Watt WB, Ehrlich PR), pp. 541–560. University of Chicago Press, Chicago.

Parmesan C, Ryrholm N, Stefanescu C *et al*. (1999) Poleward shifts in geographical ranges of butterflies associated with regional warming. *Nature*, **399**, 579–583.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pollard E, Yates TJ (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London.

Porter K (1982) Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos*, **38**, 308–312.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Roy DB, Thomas JA (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its margin. *Oecologia*, **134**, 439–444.

Shreeve TG (1992) Adult behaviour. In: *The Ecology of Butterflies in Britain* (ed. Dennis RLH), pp. 22–45. Oxford University Press, Oxford.

Simpson D, Fagerli H, Jonson JE *et al*. (2003) *Transboundary acidification, eutrophication and ground water level ozone in Europe. Part I. Unified model description*. EMEP/MSC-W Status Report 1/03, Meteorologisk Institut, Oslo, Norway.

Stoutjesdijk P, Barkman JJ (1992) *Microclimate, Vegetation and Fauna*. Opulus Press, Knivsta, Sweden.

Tarrasón L (ed.) (2003) *Transboundary acidification, eutrophication and ground water level ozone in Europe. Part II. Unified EMEP model performance*. EMEP/MSC-W Status Report 1/03, Meteorologisk Institut, Oslo, Norway.

Thomas CD, Bodsworth EJ, Wilson RJ *et al*. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Thomas CD, Cameron A, Green RE *et al*. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thomas JA, Bourn NAD, Clarke RT *et al*. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London B*, **268**, 1791–1796.

Thomas JA, Simcox DJ, Wardlaw JC *et al*. (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *Journal of Insect Conservation*, **2**, 39–46.

Thomas JA, Telfer MG, Roy DB *et al*. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.

Van Swaay CAM, Plate CL, Van Strien AJ (2002) Monitoring butterflies in the Netherlands: how to get unbiased indices. *Proceedings of Experimental and Applied Entomology NEV Amsterdam*, **13**, 21–27.

Van Swaay CAM, Warren MS (1999) *Red data book of European butterflies (Rhopalocera)*. Nature and Environment, No. 99, Council of Europe Publishing, Strassbourg, France.

WallisDeVries MF (2004) A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. *Conservation Biology*, **18**, 489–499.

WallisDeVries MF (2006) Larval habitat quality and its significance for the conservation of *Melitaea cinxia* in northwestern Europe. In: *Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa* (eds Fartmann T, Hermann G) *Abhandlungen aus dem Westfälischen Museum für Naturkunde*, **68**, 281–294.

Warren MS (1995) Managing local microclimates for the High Brown Fritillary. In: *Ecology and Conservation of Butterflies* (ed. Pullin AS), pp. 198–210. Chapman & Hall, London.

Warren MS, Hill JK, Thomas JA *et al*. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Willott SJ (1997) Thermoregulation in four species of British grasshoppers (Orthoptera: Acrididae). *Functional Ecology*, **11**, 705–713.