How are insects responding to global warming?

Rosa Menéndez

Global average surface temperature has increased by around 0.6 ºC during the past century and will continue to rise in the future. Understanding how these changes in climate have affected biological systems has attracted a vast research effort during the last two decades. Here I review the existing empirical evidence of how insects have responded to these changes in climate, especially to the increases in temperature. Evidence provided here indicates that insects are good indicators of current human-driven climate change. They have responded to warming in all the predicted ways, from changes in phenology and distribution, to undergoing evolutionary changes albeit at the population level. Insects have also provided examples of how biodiversity and community structure is affected by current climate change. However, there are still many unknowns in our understanding of the detrimental and beneficial effects of climate change to biological systems. Future research needs to consider other climatic factors, geographic and taxonomic bias and the effect of individual responses on species interaction.

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Introduction

Global average surface temperature has increased by around 0.6 ºC during the past century, with the 1990s being the warmest decade. Temperature changes vary geographically, greater at higher latitudes; and within the year, greater during the coldest months (Houghton et al. 2001). There is now a consensus that anthropogenic emissions of CO_2 and other greenhouse gases are ultimately responsible for these changes in climate (Houghton et al. 2001). The Third IPCC report predicts that temperatures will continue to rise during the next century, with increases of up to 5.8 ºC by the year 2100 (Houghton et al. 2001). Understanding how these human-induced changes in climate have affected individual species and communities and will do in the near future, has attracted a vast research effort during the last two decades. Consequently, we have started to gain significant evidence of the ecological impacts of current warming on a broad range of organisms with diverse life-history traits and geographical distributions (reviewed in Hughes 2000, McCarty 2001, Peñuelas & Filella 2001, Walter et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Badeck et al. 2004, Lovejoy & Hannah 2005, Parmesan 2006). Insects comprise 54 % of all known species and occupy every terrestrial habitat (Schowalter 2000), so exploring the responses of insects to climate change will provide us with a good understanding of how climate change is affecting biological systems.

The aim of this paper is to provide an overview of the impact that current global warming is already having on insect communities. My intention is to illustrate, with empirical examples, the type of responses that have been observed. I will also explore the ways individual responses are affecting biodiversity and the composition of natural communities. I am concentrating on direct effects of rising temperatures as this has received more attention than other abiotic factors such as precipitation, CO_2, UVB, and the evidence is more conclusive.

Why should we expect an effect of climate change on insects?

Insects are among the groups of organisms most likely to be affected by climate change because climate has a strong direct influence on their development, reproduction, and survival (Bale et al. 2002). Moreover, insects have short generation times and high reproductive rates, so they are more like to respond quicker to climate change than long-lived organisms, such as plants and vertebrates. Warming can potentially affect several aspects of insect life-cycle and ecology, especially those directly controlled by energy availability variables such as degree day (accumulative temperature needed for development). Consequently, potential responses include changes in phenological patterns, changes in habitat selection, and expansion and contraction of geographic and altitudinal ranges (Fig. 1).

The fossil record provides good evidence that insects have responded to past changes in climate. Beetle remains clearly illustrate that species shifted their geographic ranges during the Quaternary in response to the glacial/interglacial climatic oscillations (Coope 1995). Several carabid species living today only in the boreal regions of Europe, were present in the British Isles when the ice sheets covered most of northern and central Europe. Conversely, many dung beetle species restricted today to the south of Europe were living in the British Isles during the thermal maximum of the Last Interglacial, when the climate of Britain was considerably warmer than it is today (Coope 1995).

Species responses are expected to be idiosyncratic depending on the flexibility of different life-history characteristics. Bale et al. (2002) proposed that different growth rate and diapause requirements may influence distributional responses to climate change. Fast growing, non-diapausing species or those which are not dependent on low temperature to induce diapause, will respond to warming by expanding their distributions. In contrast, slow growing species which need low temperatures to induce diapause (such as boreal and mountain species in the northern hemisphere) will suffer range contractions. Thus, climate change will affect species ranges, with expansion in some species and contractions in others, which in turn will lead to changes in regional and local diversity (Fig. 1).

Climate change can also affect insects in indirect ways, where the insect responds to climate-induced changes mediated by other factors. These other factors may include interaction with other species (competition, predation and parasitism) or for herbivorous insects, host plant.

Finally, warming may affect the structure of existing communities because individual responses will inevitably alter species interactions, leading to changes in the composition of natural communities (Fig. 1).

Empirical evidence of insects responding to current climate change

Phenological changes

Phenological changes are probably the best documented responses to recent climate change and have been detected for a wide range of organisms from plants to vertebrates (Root et al. 2003, Root & Hughes 2005). Empirical evidence is also common within the uniramian taxa. Under a rise in temperature insects will pass through their larval stages faster and will become adults earlier. Thus, observed responses include both an advance in the timing of adult emergence and an increase in the length of the flight period. In this regard, Lepidoptera are by far the best documented group. Changes in butterfly phenology have been reported in the UK (Roy & Sparks 2000), with species advancing their flight periods by around 2–10 days for every 1 ºC increase in temperature. This has resulted in an extended flight period, especially for multivoltine species. In Spain butterflies have advanced their first appearance between one and seven weeks in a period of 15 year (Stefanescu et al. 2003) and by around eight days per decade in California (Forister & Shapiro 2003). In both cases phenological changes were correlated with the amount of warming experienced during the same time period. Several species of Microlepidoptera in The Netherlands (Ellis et al. 1997) and Odonata in the UK (Hassall et al. 2007) have also experienced considerable temporal shifts in their phenology to earlier in the year.

Aphids are another group for which long term datasets are available, due no doubt to their agricultural importance as pests. Early adult emergence and an early arrival of migratory species have been reported in the UK for this group (Zhou et al. 1995, Harrington 2007).

Although evidence for other groups of insects is rare, this is probably due to a lack of data more than to a lack of response. Gordo & Sanz (2005) observed a common phenological response in four unrelated species of insects (a butterfly, a bee, a fly and a beetle). During the last 50 years all four species showed significant temporal changes in their first appearance date. In all cases their appearance earlier in the year was correlated with the increase in spring temperature observed in the area during the same time period.
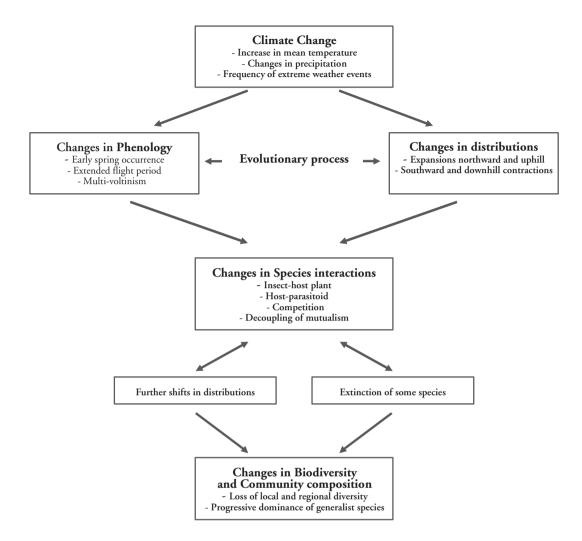
Fig. 1. Potential effect of climate change on individual insect species and ways through which individual species responses could lead to changes in biodiversity and community composition (modified from Hughes 2000).

Thus phenological responses are likely to be widespread within all groups of insects; especially at higher latitudes and elevations where temperature has increased and is predicted to increase more than in other parts of the world (Houghton et al. 2001). There are not enough data yet to prove these predictions because information on phenological changes from different latitudes (especially southern and tropical areas) and from different altitudes is not available. However, Parmesan (2007) reported a significant increase in the strength of advancement of spring events in the northern hemisphere with increasing latitude, although latitude explained only 4% of overall variation of phenological changes.

Distributional shifts

Climate is an important determinant of geographic range for many species (Andrewartha & Birch 1954). Consequently warming is expected to force species to shift their distributions by expanding into the new climatic areas and by disappearing from areas that have become climatically unsuitable (Hughes 2000). Shifts in distributions will occur, in part, by range expansion at the cool, upper altitudinal and latitudinal limits, and by contractions at the warm, lower altitudinal and latitudinal limits of species' ranges. Numerous cases of recent distributional shifts have been recorded for a variety of taxa from around the world (Pounds et al. 2005, Wilson et al. 2005,

Table 1. Empirical evidence of latitudinal and altitudinal range shifts reported for insect species.

| Latitudinal shifts | | Altitudinal shifts | |
North expansions	South contractions	Uphill expansion	Downhill contractions
Lepidoptera (Europe)[1]	Lepidoptera (Europe)[1]	Lepidoptera (Czech Republic)[9]	Lepidoptera (Sierra de Guadarrama, Spain)[12]
Lepidoptera (UK)[2]	Lepidoptera (UK)[2, 8]	*Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) (Alps, Italy)[10]	*Euphydryas editha* (Boisduval, 1852) (N. America)[4]
Lepidoptera (Finland)[3]	*Euphydryas editha* (Boisduval, 1852) (N. America)[4]	*Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) (Sierra Nevada, Spain)[11]	*Erebia epiphron* (Knoch, 1783) (UK)[8]
Euphydryas editha (Boisduval, 1852) (N. America)[4]		Odonata (UK)[7]	*Parnassius appollo* (Linnaeus, 1758) (Alps)[13]
Atalopedes campestris Boisduval, 1852 (N. America)[5]		Neuroptera (UK)[7]	
Arctia caja (Linnaeus, 1758) (UK)[6]		Coleoptera (UK)[7]	
Odonata (UK)[7]		Heteroptera (UK)[7]	
Neuroptera (UK)[7]		Orthoptera (UK)[7]	
Coleoptera (UK)[7]			
Heteroptera (UK)[7]			
Orthoptera (UK)[7]			

References: 1, Parmesan et al. 1999; 2, Hill et al. 2002; 3, Mikkola 1997; 4, Parmesan 1996; 5, Crozier 2003; 6, Conrad et al. 2002; 7, Hickling et al. 2006; 8, Franco et al. 2006; 9, Konvicka et al. 2003; 10, Battisti et al. 2005; 11, Hódar & Zamora 2004; 12, Wilson et al. 2005; 13, Descimon et al. 2006.

Hickiling et al. 2006 and those reviewed in McCarty 2001, Walther et al. 2002, Parmesan & Yohe 2003, Parmesan 2006). Table 1 summarises the evidence reported for insect species. Again Lepidoptera is the insect group most intensively studied. Movements of the entire species' ranges have been found in butterflies in both North America and Europe, where species shifted their ranges northward and to high elevations as a result of warming (Parmesan 1996, Parmesan et al. 1999, Warren et al. 2001, Hill et al. 2002, Konvicka et al. 2003, Wilson et al. 2005). Other groups of insect have shown similar responses. The best information comes from the UK, where the distribution of several groups of insect has been intensively recorded during the last 30 years. Many beetles, butterflies, dragonflies, grasshoppers and aquatic bugs have moved northwards and to higher elevations during a period of warming (Hickiling et al. 2006).

Although long-term distributional data are not available for lower latitudes and from tropical areas, movements of tropical species into more temperate areas have been reported. Five dragonflies from Cuba and the Bahamas have successfully established in Florida in 2000 (Paulson 2001). Species from North Africa are also moving into Spain and France. The African Monarch butterfly (*Danaus chrysippus* [Linnaeus, 1758]) established its first population in southern Spain in 1980 (Haeger 1999), since then the species has established multiple populations along the east cost of Spain reaching as far north as Catalonia (García-Barros et al. 2004). The dragonfly *Trithemis annulata* Palisot de Beauvois, 1807, a widely distributed species in Africa, has expanded into the Mediterranean area colonising the Iberian Peninsula in 1981, Corsica in 1989 and France in 1994 (Bonet-Betoret 2004).

A clear trend emerging from Table 1 is that range expansions have been recorded more often than range contractions. However, this pattern can be attributable partially to failure to detect declines with the available data (Thomas et al. 2006). When distributions are recorded at a coarse scale, only one population needs to be established in a region to detect expansions but the extinction of all populations from a region is needed to detect contractions.

Table 1 also showed that there is still a considerable geographic bias in the available evidence, with almost completely absence of data from South America, Asia or Africa.

Evolutionary changes

Until recently there was the conception that evolutionary change will rarely be a response to current

climate change because the fossil record shows that species shifted their distributions rather than staying and evolving locally (Coope 1995) during the Pleistocene glaciations (but see Davis & Shaw 2000). However, the two types of response already described in previous sections (phenological and distributional responses) are likely to involve both ecological and evolutionary processes (Davies et al. 2006). Climate change will alter selection pressures within populations because most populations are to a reasonable degree adapted to their local environment. Thus, traits that confer high fitness in the existing climate might not be as successful in the new climatic conditions, so evolutionary responses might take place.

The potential of evolutionary changes is great among insects, as they grow fast, have short generation times and high reproductive rates meaning populations may adjust rapidly to the new environmental conditions. Therefore, it is not surprising that most empirical evidence of evolutionary changes comes from insect species (Parmesan 2006, Thomas 2005).

Adaptations to climate change have been observed in the core of species' ranges involving an increase in the frequency of pre-existing warm-tolerant genotypes. Well studied cases are chromosomal-inversion polymorphisms in several *Drosophila* species (*D. melanogaster* Macquart, 1843, *D. robusta* Sturtevant, 1916 and *D. subobscura* Collin, 1936), which change with latitude and are related to climatic factors. During periods of warming the frequencies of warm-adapted genotypes have considerably increased within existing populations in several geographic areas (Europe: Rodríguez-Trelles & Rodríguez 1998, Balanyá et al. 2006; Australia: Umina et al. 2005; North and South America: Levitan 2003 Balanyá et al. 2006).

Within existing populations many species have also altered their phenology, probably by phenotypic plasticity. However, true evolutionary responses in the timing of the life cycle have also been reported. Mosquito larvae of the pitcher-plant mosquito, *Wyeomyia smithii* (Coquillett, 1901), in the United States enter an overwintering state at an earlier date in the northern latitude than in the south, and this is genetically heritable within populations. When mosquito larvae were reared in controlled environment in the lab in 1972 and 1996, populations from northern areas (30 and 40°N) initiated diapause nine days later in 1996 than in 1972. So the delay in the life cycle can be attributed to an evolutionary response to the increased length of the growing season (Bradshaw & Holzapfel 2001).

Evolutionary changes imposed by climate change have been involved in changes in habitat and host-plant preferences, both at the core and the edge of the species' range. In two butterfly species (*Euphydryas editha* (Boisduval, 1852) in North America and *Aricia agestis* (Denis & Schiffermüller 1775) in Britain) climate warming has induced evolutionary changes by altering the frequency of populations with different host plant preferences (Singer & Thomas 1996, Thomas et al. 1996, Thomas et al. 2001).

Distributional shifts are also likely to be accompanied by evolutionary changes because expanding populations will contain genotypes that are more successful as colonisers (Haag et al. 2005). Consequently evolution towards greater dispersal has been observed in expanding populations of several species of insects that are shifting their ranges as a result of climate change (Hill et al. 1999a, 1999b, Hughes et al. 2003, Simmons & Thomas 2004).

It is clear that local evolutionary processes are taking place as a result of climate change, but there is no evidence so far of evolution at the species level. It remains to be seen if genetic shifts as the ones presented here will be enough to prevent predicted species extinctions (Thomas et al. 2004).

Changes in species interactions

The observed changes in phenological patterns and distributions of individual species are likely to have altered species interactions within communities. As the magnitude of response differs between species the potential for disruption of existing species interactions is huge (Visser & Lambrechts 2004). Interactions that involve two or more trophic groups, such as plant-herbivore, plant-pollinator and host-parasitic interactions are likely to suffer the largest mismatch (Harrington et al. 1999).

This aspect is still poorly explored but there are already a few good empirical examples that illustrate how current warming is altering species interactions. Visser & Both (2005) reviewed phenological changes of interacting species, some of which involved insects. Two such cases are plant-insect interactions: moth-host plant and butterfly-nectar resource. The results indicated that insects have advanced their phenology faster (early eggs hatching and early migration return date) than their resources (budburst and flowering). The other four cases involve prey-predator interactions (insect-bird), and again insects have advanced more (peak of abundance) than their predators (laying date and migration arrival of birds). Thus, in all cases, phenological changes imposed by climate change have resulted in a mismatch between interacting species.

Distributional changes are also expected to bring about changes in species interactions because species are expanding at different rates and expanding species will begin to overlap with others with which
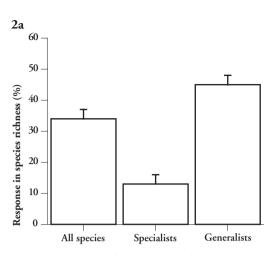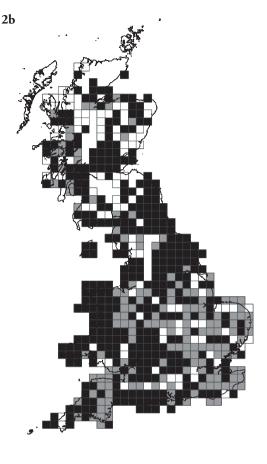
2a

2b

Fig. 2. Responses of British butterfly species richness to climate change. (a) Percent of expected diversity change (observed diversity change/predicted diversity change) that has taken place between 1970 and 1999 (means ± SEs, n = 609 squares). Predicted changes based on climate models (for more details see Menéndez et al. 2006). (b) Changes in species composition, black: squares where species richness of generalists has increased more than specialists, grey: squares where specialists increased more than generalists and white: squares were both groups change the same.

previous interaction may have been limited or non-existent. The Pine processionary moth, *Thaumato-poea pityocampa* (Denis & Schiffermüller, 1775), is a common pest of Mediterranean pine woodlands. In the Sierra Nevada mountains (South Spain) the moth has expanded to higher elevations during the last 20 years as a result of increasing mean temperature. During its expansion the species has encountered a new host, relic populations of the Andalusian Scots pine (*Pinus sylvestris* (L.) var. *nevadensis* H. Christ.) from the last glaciation. In warmer years defoliation has increased considerably in high elevation, from 5% to 25% in populations above 1700 m (Hódar & Zamora 2004). In this case climate-driven range expansion has created a new interaction with potentially devastating consequences for an endemic mountain species already threatened by direct effects of climate change.

Thus, empirical evidence suggests that mismatches are the rule rather than the exception. The detrimental consequences of these mismatches on the persistence of individual species and on biodiversity as a whole needs to be urgently investigated.

Species extinctions
It has been suggested that climate change will become a major factor involved in species extinction (Thomas et al. 2004). Mountain species and those restricted to high latitudes will be most likely to go extinct as a result of warming. These species are adapted to cold conditions so they will be forced to move uphill and to higher latitudes as the climate warms. But, even if they are able to move, they will eventually run out of habitable areas and will inevitably go extinct. As mentioned before, species decline is difficult to detect. However, there is already some evidence that northern and montane species in the northern hemisphere have taken the path to extinction as a result of warming. Four butterflies with northern distribution in Britain have disappeared from lower latitudes and altitudes during the last 25 years, with climate change having been responsible for at least half of the population extinctions (Franco et al. 2006). In the central mountains of Spain, Wilson et al. (2005) reported that lower elevation limits of 16 mountain butterflies have increased in altitude by around 212 m as a result of warming.

This represents an average reduction in habitable area by one-third, with predictions up to 70% loss of habitable area for these species in the near future (assuming 1 °C increase in temperature).

Extinctions are also difficult to attribute to climate change because of the potential for other drivers of extinction, such as habitat loss and invasive species. However, even if extinction is directly caused by another factor, warming may have played a trigger role. To my knowledge, extinctions of insect species due to indirect effects of warming have not yet been reported. However, the decline of birds in tropical mountains could be a good example where climate change has been driving species toward extinction through climate warming's effect on an invasive species of insect (LaPointe et al. 2005). Around 40% of the endemic forest birds in the Hawaiian Islands have become extinct in the past century. Many factors contributed to that but there is a growing consensus that introduced mosquito-borne avian malaria has been responsible for many of these extinctions. Birds have mainly survived in areas above 1600m in altitude because the mosquito, as well as the transmission of the disease, is limited by the low temperatures at these higher altitudes. Increases in temperature predicted for the future will reduce the disease-free area available in most of the islands with drastic consequences for the remaining populations of these birds.
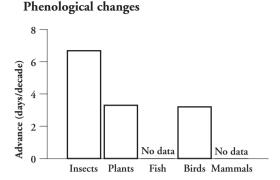
Community level changes

The empirical evidence provided so far tells us that species are responding to climate change in many different ways, leading to changes in species interactions. The cascading of these individual responses to affect the structure and composition of communities seems inevitable. In the northern hemisphere, communities will be invaded by expanding species associated with warmer conditions and will lose existing species that have colder tolerances. This type of changes has been reported for freshwater invertebrates in France (Daufresne et al. 2003). Downstream thermophilic invertebrate taxa have replaced upstream cold-water taxa, during a period when the water temperature has increased 1.5°C.

Because range expansion and contractions are happening at a different rate, distributional shifts will also affect biodiversity. A good example of how climate change is affecting biodiversity and community composition is provided by Menéndez et al. (2006). Sixty-five percent of the butterfly species found in Britain reach their northern limit in this region and they have responded differently to climate change. The average species richness of butterflies in Britain has increased since 1970, during a period when climate warming would lead us to expect increases. However, the increase in species richness has been much slower than predicted by climate, only one-third of the predicted increase has taken place (Fig. 2a). Species richness of butterflies across Britain is determined by both climate and habitat variables (host-plant richness and habitat diversity) but the relative contribution of these factors differ between habitat specialist and habitat generalist butterflies (Menéndez et al 2007). Species richness of specialist butterflies is dependent on the diversity of habitat/resources available to them, as well as on their physiological responses to climate. In contrast, the diversity of generalists and species with widespread habitats appears to be set predominantly by climate. As a result the lag in response to climate change is mainly due to specialist butterflies (Fig. 2a); they have been unable to colonise new climatically suitable areas further north due to loss and fragmentation of their habitats (Warren et al. 2001). Because the number of generalist species has increased more than the number of specialists, local butterfly assemblages have become dominated by generalist butterflies (Fig. 2b). Thus, individual responses to climate change of species with different biological traits have resulted in changes in the composition of communities.
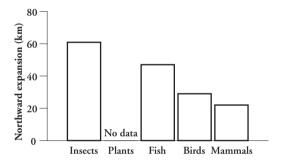
Altitudinal shifts of butterflies in central Spain have also brought about changes at the community level. In this case species richness has decreased, as would be expected in a warmer area, and changes have followed climate closely (Wilson et al. 2007). Butterfly communities with similar species compositions shifted uphill 293 m consistent with an upward shift of 225 m in the mean annual isotherms. Changes in species richness and composition reflect the loss of mountain species from lower elevations. The few colonisations by species with lower altitudinal distributions have not compensated the loss of mountain species. It is estimated that species richness has probably declined in ninety percent of the region and that communities are now becoming dominated by widespread species.

Conclusions: insects as bio-indicators of climate change

Insects have proved to be good bio-indicators of human-driven changes in the environment, such as pollution and habitat loss and fragmentation (McGeoch 1998). Evidence provided in this review indicates that insects are also good indicators of current human-driven climate change. They have responded to warming in all the predicted ways, from changes in phenology and distribution to

Phenological changes

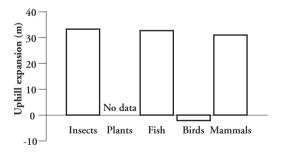## Latitudinal changes

Altitudinal changes

Fig. 3. Mean responses to climate change for several groups of organisms in the UK during the last 30 years. Phenological changes data from: insects (Hassall et al. 2007, Root et al. 2003, Roy & Sparks 2000), plants (Spark et al. 2000) and birds (Crick & Sparks 1999). Data for latitudinal and altitudinal changes are from Hickiling et al. 2006.

undergoing evolutionary changes, albeit at the population level. The response has also been stronger than in other groups of organisms typically considered as bio-indicators, such as plants, birds and mammals (Fig.3). Insects have also provided examples of how biodiversity and community structure are affected by current climate change.

We still, however, have a long way to go in understanding the detrimental and beneficial effects of human-induced climate change to biological systems. Areas of research that need more attention in the future include:

1. Reducing the geographic and taxonomic bias. Most evidence comes from North America and Europe but little is known about effect of climate change in other parts of the World. Only a few groups of insect have been studied in the context of climate change (butterflies, moths, dragonflies and aphids) and we have almost no information from the most diverse groups (e.g. beetles). This is a difficult task because detecting responses to climate change require good quality historical data at a large spatial scale (e.g. latitudinal shifts) which are not available for many areas and taxonomic groups. Hickling et al. (2006) found similar qualitative results when comparing less studied groups with those for which good quality data were available in Britain. This result suggests that incomplete datasets from other geographic areas and other taxonomic groups could be suitable for analysis after all.

   Moreover, altitudinal and phenological changes may be easy to explore for a variety of insects at local or regional scales by re-examining previously well studied systems.

2. Species interactions have been largely ignored and this is crucial to provide reliable predictions for the future. In particular phenological mismatches between insects and plants (plant-herbivore and plant-pollinator interactions) will have important consequences for ecosystem functioning and need to be explored urgently.

   Many species will shift their distribution and become part of new communities. In this regard, available information on species invasions may prove to be valuable in understanding the effect of the new arrivals, especially the information on non-target effects of introduced biological control agents (Ward & Masters 2007).

3. The impact of other factors such as changes in levels of CO_2, changes in precipitation patterns and extreme events, as well as the interactions between them could be very important and need detailed investigation. Stireman et al. (2005) demonstrated that increasing climatic

variability reduced the level of parasitism of caterpillars, which in turn may increase the frequency and intensity of herbivore outbreaks.

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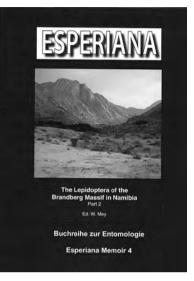
Book review

Wolfram Mey (editor), 2007. **The Lepidoptera of the Brandberg massif in Namibia, Part 2.** Esperiana Memoir 4: 1–304. Delta Druck u. Verlag, Schwanfeld, Germany.
ISBN 3–938249–07–2, hardback. Price € 99.–

We received only this volume for review, but it cannot be seen separately from the first part, published in Esperiana Memoir 1 (2004). Together these volumes treat the complete Lepidoptera fauna of the Brandberg Massif in Namibia. This is based on three expeditions to this massif by the editor and some others. The editor has managed to find specialists for most families to identify the collected species and describe what was new. In this volume 20 chapters, written by 11 authors, treat those families that weren't covered in volume 1 and for some families in volume 1, additional data are given. Together these two volumes provide what is nowadays often indicated as an "all taxa inventory", although for the Lepidoptera only. Such treatments are, even for this order, very rare. Usually many groups of so-called Microlepidoptera are left out by lack of specialists. Mey tries to fill the gaps where there is no specialist himself. This is for instance the case for the Pyralidae: Phycitinae. Here the concept of morphospecies is used, and most species remain unidentified and receive names such as *Ancylosis (Ancylosis)* spec. A, or even ? genus, spec. 2. Still, all these species are illustrated, both adult habitus and genitalia, and in this way the information has been made available for future studies.

Of all the tropical fauna's, the African Lepidoptera are probably the least studied, thus it is no surprise that these books deal with a wealth of new and unknown material. In an epilogue the total number of species per family is given, in all 611 species are treated. Although not a very high number for a tropical fauna, it remains an impressive undertaking.

With so many authors, it is no surprise that the chapters show differences, especially in the way of illustrating genitalia. Remarkable chapters are those on the poorly known Cecidosidae (by Mey), a thorough treatment of the Psychidae (Sobczyk & Mey) and the poorly known Metarbelidae (Lehmann).

The colour photographs of the adults are in general good, although one would wish a little more uniformity in for instance the scale lines (some are completely without any indication of size), and some Scythrids have disturbing labels still on the background.

For the study of African Lepidoptera, these volumes are indispensable, and all lepidopterists with a general interest in the order should have these volumes, which show a very special fauna of a remarkable area.

Erik van Nieukerken