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REVIEW

Direct impacts of recent climate warming on insect populations

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Abstract

Effects of recent climate change have already been detected in many species, and, in particular, in insects. The present paper reviews the key impacts of global warming on insect development and dispersal. The effects of climate change appear to be much more complex than a simple linear response to an average increase in temperature. They can differ between seasons and bioclimatic regions. Earlier flight periods, enhanced winter survival and acceleration of development rates are the major insect responses. Differential response of insects and hosts to warming up might also lead to disruption of their phenological synchrony, but adaptive genetic processes are likely to quickly restore this synchrony. In a number of cases, warming results in removing or relocating the barriers that limit present species' ranges. It is also likely to facilitate the establishment and spread of invasive alien species. Finally, knowledge gaps are identified and future research interests are suggested.

Key words: adaptation, alien species, climate warming, phenology, range distribution.

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INTRODUCTION

Climate change involves simultaneous and complex changes of many environmental variables, but primarily air temperature (Trenberth *et al.* 2007). Mean global temperature has increased by approximately 1 °C since the pre-industrial era in Europe, with an acceleration during the past decades where 8 out of the 10 years between 1996 and 2007 were among the warmest years since 1850 (EEA 2008). Simultaneously, concentration of CO₂ has increased by 30% from pre-industrial concentrations and is still rising. Based on various climate scenarios, the mean global temperature could increase by 1.8–4.0 °C for the period 2090 to 2099 relative to 1980 to 1999 (Meehl *et al.* 2007). Simultaneous changes in rainfall regimes and in frequency of extreme climatic events are also predicted.

Climatic parameters are known to have a direct effect on insect population dynamics through the modulation of survival, development rates, fecundity and dispersal (Messenger 1959; Andrewartha & Birch 1984). Long-term data recorded in China over more than 1000 years was recently analyzed and it was revealed that locust outbreaks are closely associated with drought/flood frequencies and low temperature (Stige *et al.* 2007; Zhang *et al.* 2009). Indirect climatic effects via hosts, competitors and natural enemies have also been shown (Price *et al.* 1980; Herms & Mattson 1992). The ongoing climate change is thus likely to induce significant responses from insect species. Signs of such responses have already been detected in recent years (Ayres & Lombardero 2000; Hughes 2000; Harrington *et al.* 2001; Bale *et al.* 2002; Hill *et al.* 2002; Crozier 2003; Parmesan & Yohe 2003; Battisti *et al.* 2005; Parmesan 2006; Menéndez 2007; Battisti 2008; Netherer & Schopf 2010). According to the Intergovernmental Panel on Climate Change (IPCC), if conditions change beyond the tolerances of species, they might respond by shifting the timing of life-cycle events, shifting range boundaries or the density of individuals, changing morphology, reproduction or genetics, or go extinct (Rosenzweig *et al.* 2007). Although quantitative changes in a number of factors such as humidity, intensity and periodicity of rainfall, solar radiation, elevated CO₂, O₃ and ultraviolet light levels could be involved (Hunter 2001; Newman 2005; Stireman *et al.*

2005; Asshoff & Hättenschwiler 2006), most of these published studies essentially document the effects of increasing temperatures. Insects are essentially ectothermic organisms with their physiological processes displaying a high degree of sensitivity to ambient temperatures (Beck 1983). Therefore, they are likely to respond very quickly to an increase in temperature (Logan *et al.* 2003). Temperature thresholds often delimit one or more boundaries of a species' geographic range (Andrewartha & Birch 1984). For example, as climatic isotherms have moved northwards 120 km on the average during the past century, 63% of the non-migratory European butterflies have extended their distribution by 35–240 km northwards (Parmesan *et al.* 1999). The 4th IPCC report mentioned the advanced emergence of butterflies, the extinction of some species, the increase in egg-laying for other species, genetically-based changes in morphology and other life-history traits, the expansion of damaging forest insects such as bark beetles in the USA and pine processionary moths in Europe, but also changes in the range of vector-borne diseases (Rosenzweig *et al.* 2007). Climate warming appears to have an increasingly important role in triggering increases in population abundance of native species (DeLucia *et al.* 2008), but also in facilitating the establishment and further spread of introduced alien species (Walther *et al.* 2009). Such changes are particularly obvious at higher altitudes and latitudes, and might result in a larger impact of herbivores (Wolf *et al.* 2008). However, the data accumulated so far suggest that the effect of climate change is much more complex than a simple, linear response to an average increase in temperature, and it is likely to differ between regions (Walther *et al.* 2002; Hickling *et al.* 2006; Deutsch *et al.* 2008). Moreover, Musolin *et al.* (2010) point out that insect responses to global warming are likely species-specific (or even population-specific) in nature (e.g. changes in distribution, phenology, abundance, population structure and dynamics), magnitude (from organisms to local and global communities) and strength (from undetectable or no responses to dramatic) (Bale *et al.* 2002; Parmesan 2007). Even within the same species or population, responses can differ, and sometimes be opposite, for different life-history traits as well as between seasons and bioclimatic regions (Battisti *et al.* 2006; Musolin *et al.* 2010; Robinet *et al.* 2010). Thus, the

entire life cycle of species should generally be taken into account to determine the overall disturbance (Visser & Both 2005). Therefore, even if some preliminary generalizations have been attempted about insect responses to global warming (e.g. about range modifications or phenological adaptations; Walther *et al.* 2001; Hickling *et al.* 2006; Parmesan 2007; Lawler *et al.* 2009), the effects of a future increase in temperature on insect communities are not so easy to predict (Helmuth 2009). Moreover, global warming simultaneously affects all the associated organisms (host plants, competitors, natural enemies, mutualists and symbionts), resulting in complex cascading effects on insect populations (Ayres & Lombardero 2000; Walther *et al.* 2002; Rouault *et al.* 2006; Hance *et al.* 2007; Bidart-Bouzat & Imeh-Nathaniel 2008; Netherer & Schopf 2010).

In this paper, we intend to present the major patterns of insect responses to the recent increase in temperatures, during the past few decades, considering the direct impacts of global warming on insect development and dispersal. We will finally suggest key knowledge gaps and future research interests.

EARLIER FLIGHTS AND ACCELERATION OF DEVELOPMENT RATES

In organisms for which population dynamics is mainly controlled by temperature, positive direct responses to an increase in temperature are expected as long as the stage-specific thresholds for development are not exceeded. Therefore, development rates are likely to be sped up. A first sign is an earlier occurrence of spring flights in insect species from temperate countries. For more than 70% of the butterfly species examined, the first flight has recently advanced in the UK (Roy & Sparks 2000), Spain (Stefanescu *et al.* 2003) and California (Forister & Shapiro 2003). In California, global warming (warmer and drier winters) explained 85% of variation in the first flight date. More generally, Harrington *et al.* (2007) predict that the first aphid occurrence in Europe will advance by 1 day, on the average, every 4 years under classical climate change scenarios for the future. Similarly, butterfly flight is predicted to occur 2–10 days earlier in the UK for every 1 °C increase (Roy & Sparks 2000).

In north-western North America, warmer temperatures have halved the time required to reproduce for the spruce beetle, *Dendroctonus rufipennis* Kirby, and have contributed to unprecedented damage to spruce forests (Berg *et al.* 2006). Polyvoltine species might profit as a result of this acceleration in cycle completion to produce one or more additional generations per year (Virtanen & Neuvonen 1999; Ayres & Lombardero 2000; Kiritani 2006; Gomi *et al.* 2007; Jönsson *et al.* 2009). Such processes have been observed in a number of insect groups, such as butterflies, bees, dragonflies and damselflies, flies and beetles (Gordo & Sanz 2005). For example, the life cycle, life-history traits and, hence, the spread of the invasive fall webworm, *Hyphantria cunea* (Drury), have been affected by recent climate change in Japan. The moth recently expanded its range, mainly towards the north of the country. This spread coincided with a shift from a bivoltine to a trivoltine life-cycle in at least a part of the range, together with significant changes in the length of the critical photoperiod for diapause induction (Gomi *et al.* 2007). A damselfly *Ischnura pumilio* (Charpentier), which was trivoltine in the southern part of its range in Europe but univoltine or semivoltine in the northern part, also tends to become more and more bivoltine in the latter range (Ott 2008). Similarly, the European spruce bark beetle, *Ips typographus* (L.), is changing voltinism in European mountain forests as a consequence of the disproportionately large warming at high elevations, and it might, therefore, have unprecedented outbreaks (Lange *et al.* 2006). For the future, models from Harrington *et al.* (2001) predict that an increase of winter and spring temperatures by 2 °C would allow some aphid species to produce 4–5 additional generations per year.

NEGATIVE EFFECTS ON HOST–INSECT PHENOLOGICAL SYNCHRONY?

Although an accelerated development potentially gives an important benefit for the insect species, this change in phenology might have some serious drawbacks. In insect herbivores, phenological synchrony between host plant development and insect life stages is often essential for developmental success (Van Asch & Visser 2007). It is especially true for host-specific insects

overwintering as eggs, such as a number of lepidopterans defoliating trees and shrubs, which need neonates hatching in spring to be precisely timed with plant budburst. Because the lower temperature thresholds for resuming development following winter might differ between the host plant and the associated insect, an increase in temperature is likely to affect their respective growth rates differently. Such a mismatch between vegetative budburst and hatching of larvae has already been observed over the past 2 decades for the system oak-winter moth, *Opheroptera brumata* (L.), where the egg hatch date has advanced more than the bud burst date of pedunculate oak (Visser & Both 2005). Similar observations have been made for sycamore and its associated aphid, *Drepanosiphum platanoides* Koch. (Dixon 2003). Winter and spring temperatures unusually warm for the period 1989–1991 might also have disrupted the strict synchrony previously existing between hatching of larch budmoth larvae, *Zeiraphera diniana* Guénée, and larch foliage availability (Esper *et al.* 2007). This could be a major reason of the unexpected collapse observed during the 1990s in the cycle of this insect, which was regularly outbreaking every 8–10 years in the Alps for hundreds of years (Battisti 2008). Further increase in temperature is predicted to induce long-term perturbations in the *Zeiraphera* larch system, with a possible induced shift of intense outbreak areas towards higher altitudes (Büntgen *et al.* 2009).

However, disrupted synchrony will lead to selection, and a response in phenology to this selection might lead to species genetically adapting to their changing environment. In the case of the winter moth cited above, Van Asch *et al.* (2007) show that egg-hatching reaction norms are heritable and that sufficient genetic variation exists to predict a rapid response to selection, leading to a restoration of synchrony of egg hatch with oak bud opening.

POSITIVE EFFECTS ON WINTER SURVIVAL AND CONSEQUENCES ON THE POTENTIAL LIMITS OF SPECIES RANGE

Under temperate latitudes, low temperature is usually a key factor constraining the range expansion through minimal thresholds required for the insect survival and development at the different stages (egg, larva, pupa and adult). For instance, the lower lethal temperature for the southern pine beetle *Dendroctonus frontalis* Zimmermann has been estimated at $-16\text{ }^{\circ}\text{C}$. Therefore, lower winter temperatures are limiting the beetle's northern distribution (Ungerer *et al.* 1999). In the past, beetle presence in southern USA effectively matched the areas where the probability of reaching this lethal temperature was low. However, since 2000, outbreaks have been observed at northern latitudes, where their probability was highly unlikely, first in New Jersey and Ohio (2001), and then in Maryland (2005). Tràn *et al.* (2007) show that these new outbreaks are directly related to a latitudinal shift in winter isotherms. Similarly, the unprecedented outbreak of mountain pine beetle *Dendroctonus ponderosae* Hopkins, currently affecting over 10.1 million hectares of lodgepole pine forests (*Pinus contorta* Dougl.) in British Columbia, Canada, partly relies on the occurrence of warmer winters. Warmer winters allow better beetle survival during overwintering (Kurz *et al.* 2008). A slight difference in cold tolerance could also explain the difference in the outbreak range expansion of 2 cyclic geometric moths, the winter moth, *Operophtera brumata*, and the autumnal moth, *Epirrita autumnata* (Borkhausen), in northern Scandinavia, the winter moth showing a larger decrease in egg mortality with increasing temperatures (Jepsen *et al.* 2008).

One of the best documented, most striking examples of the effect of climate warming on the release of thermal thresholds constraining species distribution is the pine processionary moth *Thaumetopoea pityocampa* (Den. & Schiff.). Originally Mediterranean, this insect is currently expanding its range distribution towards higher latitudes and altitudes (Battisti *et al.* 2005). This range expansion is clearly associated with better winter survival and enhanced feeding activity. Larval development occurs during winter and is limited by both a lethal temperature ($-16\text{ }^{\circ}\text{C}$; Battisti *et al.* 2005) and temperature thresholds allowing the nocturnal feeding uptake; that is, a daytime temperature higher than $9\text{ }^{\circ}\text{C}$ within the larval nest followed by a nighttime temperature higher than $0\text{ }^{\circ}\text{C}$ in the air (Battisti *et al.* 2005). If 1 of the 2 latter temperature conditions is not

satisfied, larvae starve in the nest and their survival and performances are reduced (Buffo *et al.* 2007). Climatic models based on these thresholds revealed the occurrence until the mid-1990s of a highly unfavorable area in the south of the Paris Basin (France), which constituted a barrier to latitudinal insect expansion. With the warming up observed in the area since 1996, the moth is no longer limited by unfavorable larval feeding conditions. It has succeeded in crossing this area and is expanding its range distribution northwards by 5.6 km per year (Robinet *et al.* 2007).

Thus, climate change might remove/relocate barriers that control spread and so allow for an expansion in areas where the species were previously kept in check by climatic factors (Walther *et al.* 2002; Battisti *et al.* 2005).

NATURAL DISPERSAL AND ACTUAL RANGE MODIFICATIONS WITH GLOBAL WARMING

Although climate warming could allow a species to extend its range, it might not be able to shift with its climatic envelope because of limited dispersal capabilities (Thomas *et al.* 2004). Increased temperatures might extend the flying period of insects and thereby enable them to become dispersed over greater distances (Ott 2008). For instance, migration patterns of the silver Y moth *Autographa gamma* (L.) (Lepidoptera: Noctuidae) to Britain are largely influenced by the changes in temperatures and rainfall in its overwintering sites of North Africa (Chapman *et al.* 2008). Following the heat wave that occurred in Europe during the summer of 2003, the distribution of the pine processionary moth has considerably extended at higher elevations in the Italian Alps. Battisti *et al.* (2006) show that the nights above the threshold temperature for flight take-off (14 °C) were over 5 times more frequent, and considerably warmer, at the range limit in 2003 than in an average year. Therefore, a larger proportion of female moths was allowed to disperse over long distances.

Indeed, a number of species belonging to different groups such as beetles, butterflies, dragonflies and grasshoppers have moved northwards and to higher elevations during the past 30 years (Hickling *et al.* 2006). Although most studies provide evidence of expansion, few species

have been reported to show no change in distribution or even a contraction of their southern range with global warming (see Menéndez 2007 for a review). Southerly distributed butterfly species in Britain tend to expand their range distribution northwards, whereas the most northerly distributed species have little opportunity to expand northward and most of them will probably decline (Hill *et al.* 2002). Even though a large variability is observed among species, Parmesan *et al.* (1999) show that the northern limit of European butterflies tends to shift northwards, whereas the southern limit remains stable in most cases. As an example for possible range contraction in the future, the nun moth *Lymantria monacha* (L.) is likely to suffer from too large an increase in temperatures because of negative effects on diapause termination (Vanhanen *et al.* 2007).

More generally, assuming that the growth period takes place during summer and the single diapause during winter, Bale *et al.* (2002) suggest that changes in the range distribution of the insect species could be roughly determined by a combination between the growth rate (slow or fast) and diapause requirement. They predict that: (i) fast growing, non-diapausing species are likely to be multivoltine and expand their ranges (e.g. anholocyclic aphids); (ii) fast growing species with a temperature-dependent diapause might contract their ranges (e.g. the lepidopterans *Inachis io* [L.], *Aglais urticae* [L.] and *Saturnia pavonia* [L.]); and (iii) slow-growing species with a temperature-dependent diapause will not maintain their ranges and will probably decline (e.g. *Lasiocampa quercus callunae* Palmer).

Even when a species is actually able to expand its distribution, another factor might affect its establishment. Indeed, when some individuals disperse into new areas, they are generally at low densities. If the population falls below a minimum population density, called the Allee threshold, it will likely go extinct naturally (Lande 1993; Liebhold & Tobin 2008). Many factors may generate Allee effects, such as a decrease in cooperation to find resources and avoid natural enemies, an increase of inbreeding and an increase of reproduction difficulties at low population density. In this regard, climatic factors might play an important role if they can increase the per capita reproductive output for any given population density. Invasive species with high mobility could more easily

follow the shift of the climate envelope and have the greatest potential for rapid expansion. However, in the case of Allee effects, they might fail to expand when they move to a large favorable area because of the dissemination of the population in space, and the decrease in the population density (Roques *et al.* 2008). The population growth rate could increase with climate change; so, Allee effects would not occur anymore and species with high dispersal capabilities could successfully invade new territories.

GLOBAL WARMING AND HUMAN-ASSISTED DISPERSAL, A NEW POSSIBILITY FOR SUCCESSFUL LONG-DISTANCE JUMPS AND INVASIONS

Long-distance jumps far beyond the natural range of an insect might not permit an establishment in most species because of the high probability of encountering unfavorable climatic conditions in the new area. However, climate warming has undeniably contributed to increase the probability of establishment of these long-distance dispersers beyond their natural distribution. An isolated but large colony of the pine processionary moth has recently been recorded in north-eastern France (Alsace), approximately 190 km from the current northern limits of the range (French Forest Health Department, pers. comm.). With respect to the colony size, it is likely that the colony founders had been introduced by the early 2000s, probably as moth pupae carried with the soil accompanying large pine trees translocated from southern areas as ornamentals. A retrospective analysis of the climatic conditions having occurred in the area showed that moth larvae had quite a null probability of surviving if introduced during the 1990s because of winter temperatures frequently under the lethal threshold. The warming up of the area since 2000 largely modified these conditions, resulting in a high probability of establishment of self-sustaining moth populations once accidentally introduced by humans (Robinet *et al.* 2010). Other Mediterranean insects, such as the praying mantis *Mantis religiosa* (L.) and the bush cricket *Meconema meridionale* A. Costa, are expanding their native range in southern Germany, but they are also found further north, far away

from their natural range, and these populations are also considered to be the result of accidental transport by humans (Ott 2008).

More generally, these observations apply to exotic alien species originating from regions warmer than the invaded one. Until recently, species introduced from warmer regions to temperate areas have been constrained by growing seasons that are too short, which has prevented several species from becoming naturalized. This is changing. Global warming is likely to provide new opportunities for introductions to areas where introduced species were not able to survive previously (Walther *et al.* 2009; Roques 2010). For instance, more than 400 out of the 1315 non-native insect species already established in Europe originated from areas with subtropical and/or tropical climates and appeared thus capable of surviving under European winter conditions, at least locally (e.g. along the Mediterranean coast, Roques *et al.* 2009). The recent arrival and establishment of several tropical species associated with palms is illustrative of this process. Since 1993, 31 palm pests have been recorded, among them a Castniidae moth from South America, *Paysandisia archon* (Burmeister), and the red palm weevil, *Rhynchophorus ferrugineus* (Olivier), from Melanesia. These 2 species stayed for some time in the western part of the Mediterranean basin but largely expanded from 2004 to 2007 to colonize the whole Mediterranean region (Roques 2010). More generally, the colonization of palms, eucalyptus and tropical legume trees planted in Europe significantly increased during the period 2000–2007 through the establishment of host-specific exotic insects, whereas that of broad-leaved trees remained stable and that of conifers decreased (Roques 2010). Former greenhouse inhabitants, such as 3 exotic scale species, *Diaspidiotus distinctus* (Leonardi), *Coccus hesperidum* L. and *Icerya purchasi* (Maskell), have also recently been found outdoors in Switzerland (Kenis 2006). Similarly, non-native biological control agents of greenhouse pests have started to establish outside the greenhouse environment, such as the predatory bug *Macrolophus caliginosus* Wagner (Hart *et al.* 2002) and the predatory mite *Neoseiulus californicus* McGregor (Hatherly *et al.* 2005) in the UK. There is also evidence of a

strong association between patterns of the emergence of invasive gypsy moth *Lymantria dispar* L. and annual climatic suitability in Ontario (Canada) (Régnière *et al.* 2009).

Expansion of native species or spread of alien insects into new areas with global warming is likely to cause serious economic or ecological hazards, affecting species inhabiting invaded areas. For example, 3 springtail species accidentally introduced into the Marion island perform better than indigenous springtails in the warmer and dryer climate that this sub-Antarctic island is presently facing (Chown *et al.* 2007; Slabber *et al.* 2007). The carabid beetle *Oofterus soledadinus* (Guérin) was accidentally introduced into the Kerguelen Islands (sub-Antarctic) from the Falklands at the beginning of the 20th century. However, it was not before the second half of the century that it started to spread, possibly due to increased temperature and lower precipitation (Chevrier *et al.* 1997). It has now invaded most regions and has become so abundant that it is threatening the native fauna. The southern green stink bug *Nezara viridula* (L.), formerly a sub-tropical species, has been expanding its range northward in temperate regions of Japan and Europe since the 1960s (Musolin 2007), probably because of reduced winter mortality resulting from milder winters. In the newly-invaded regions in Japan, *N. viridula* has become a major pest, outcompeting the indigenous *N. antennata* Scott (Tougou *et al.* 2009).

SUGGESTIONS FOR FUTURE RESEARCH

In most cases, the effects of climate change have been considered with regard to an increasing temperature mean. However, even if such a variable can be more easily manipulated for comparisons, its single use is likely to result in a number of biases. First, as previously mentioned, other important factors should be considered, including solar radiation, humidity, rainfall and levels of greenhouse gases. For instance, the establishment of the invasive Asian mosquito *Aedes albopictus* (Skuse) depends on temperature but also on photoperiod, humidity and rainfall (Eritja *et al.* 2005). Even though testing the effect of one factor in laboratory conditions is relatively easy, testing the effects of numerous factor combinations in the field is extremely complex, and

contradictory results are likely to appear (see Newman 2005 for the effects of an increase in CO₂ level). Investigating the possible synergistic effects between temperature and other potential driving factors is a real challenge for the future, especially through the development of large-scale field experiments.

Second, changes in temperature means do not completely reflect the changes in maximums and minimums that actually affect survival and development (e.g. considering higher and lower lethal temperatures for a given development stage). The temperature mean variability could have important effects in itself (Easterling *et al.* 2000; Walther *et al.* 2002). Insect populations are not facing a mean annual temperature but a year-to-year and day-to-day fluctuation of the weather conditions. From this point of view, an increase in temperature will not have the same significance when occurring in winter, spring or summer, and could even result in contradictory effects on insect populations. Moreover, the role of stochastic climatic anomalies is thus underestimated. Some species have an inherent ability to respond positively and permanently to rapid changes or fluctuations in climate. The pine processionary moth again provides a striking example for both these questions. Whereas the warm winters during 2000–2003 triggered larvae survival in the newly-colonized areas of the Paris Basin, the heat wave of summer 2003 killed a large part of the population in the same area (Robinet *et al.* 2010). Contradictorily, the high temperatures observed in the same summer 2003 positively resulted in a significant altitudinal shift of the moth in the Italian Alps (Battisti *et al.* 2006). Indeed, the moths were not at the same development stages in the 2 sites when the heat wave occurred. Adults are emerging earlier in the Paris Basin, and, therefore, extremely high, lethal temperatures affected egg-masses and first-instar larvae while these warm temperatures stimulated adult flight in the Alps. Similar adverse effects of warming according to season have been observed in the southern green stink bug, *Nezara viridula*. Although warming is strongly enhancing survival of adults in winter and accelerating development in autumn, it is negatively affecting nymphal development during summer (Musolin *et al.* 2010). This complexity has to be taken into account while attempting to predict the potential effects of global warming. As

Battisti *et al.* (2006) point out, an emphasis on long-term slow change in climatic variables might be insufficient in predicting species' responses to climate change, especially in light of the forecast rise in stochasticity of global climate dynamics.

Third, climate change affects the entire ecosystem, including host plants, competitors and natural enemies, but the responses probably differ among species and guilds, altering their interactions and the composition of the ecosystem (Petchey *et al.* 1999; Stenseth *et al.* 2002; Walther *et al.* 2002; Visser & Both 2005). As argued by Harrington *et al.* (2001), the concentration of studies on species obviously profiting from climate change might easily lead to the wrong conclusion that all insect pests will gain in importance. Altered environmental conditions will certainly bring about ambiguous consequences, involving positive, indifferent as well as negative responses of species. The disturbance of coevolved relationships might, for instance, be beneficial for the affected host plant, the herbivore species or neither of them. Some theoretical models have already been proposed to predict the changes in ecosystems (Berggren *et al.* 2009). It seems that the sensitivity to temperature could possibly increase with trophic level, but further investigation is needed to understand more deeply these changes in the field. For instance, no general pattern has emerged from the limited number of studies regarding the response of natural enemies to global warming. According to Roy *et al.* (2004), parasitoids and predators might simply respond to the population sizes and preferences of their hosts. However, some other case studies tend to show differential responses between natural enemies and insect hosts. The effectiveness of certain predators, such as ladybeetles, would increase in a warmer environment (Cannon 1998), and synchrony between parasitoids and host insects might be favored (Parmesan 2006). In contrast, climate warming would allow the host to better escape from natural enemies in the spruce budmoth, *Choristoneura fumiferana* (Clemens) (Fleming & Candau 1998), and from egg parasitoids in the expansion area of the pine processionary moth (Roques *et al.* 2005). Moreover, the interactions of these 2 trophic levels with the host plant have to be considered in order to obtain a correct picture. For example, Rouault *et al.* (2006) predict that reduced palatability of host tissue following drought

might lead to decreased development rates in defoliators and, subsequently, increase the duration of exposure to parasitoids. The development of more studies at the whole community level, that consider more than a single species, is of outstanding importance for a better understanding of the interactions between the different factors related to climate change.

Fourth, understanding the adaptive processes and the underlying genetic changes is essential for predicting long-term insect responses to climate change (Menéndez 2007). Sampling for genetic analysis should also be included in the collection scheme to investigate possible evolutionary changes. Bale *et al.* (2002) hypothesize that insect species can potentially respond to climate change through phenotypic flexibility or rapid evolutionary (genetic) responses to strong selection. For instance, the winter moth cited above was assumed to rapidly restore the disrupted synchrony with host plant development. More generally, when a species moves polewards as a consequence of climate warming, the day length becomes notably shorter. The northern populations of the pitcher plant mosquito, *Wyeomyia smithii* (Coq.), increased the length of its growing season and postponed the timing of its hibernation to counterbalance the shorter photoperiod (Bradshaw & Holzapfel 2008). Its critical photoperiod varies along the climatic gradient in North America, and this adaptation is actually driven by genetic features (Mathias *et al.* 2006).

Finally, in order to understand the mechanisms governing the response to climate change, it seems important to consider only a few relevant case studies among the numerous species that can be studied. For this purpose, it is important to keep on collecting data on the long term and update the distribution of the study species. Unfortunately, there is still little information on the precise distribution of most species in the world, and for the most well-known species, historical distribution maps are not always suitable or reliable for such studies. Therefore, we should improve technical methods to collect such data and obtain a good database to serve as a baseline for future studies.

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