



Plant–Insect Interactions in a Changing World

S. Pincebourde^{*1}, J. van Baaren[§], S. Rasmann[¶], P. Rasmont^{||},
G. Rodet[#], B. Martinet^{||} and P.-A. Calatayud^{**§§}

^{*}Institut de Recherche sur la Biologie de l’Insecte, UMR 7261, CNRS – Université François-Rabelais de Tours, Tours, France

[§]UMR–CNRS 6553 Ecobio, Université de Rennes 1, Université Bretagne-Loire, Rennes, France

[¶]University of Neuchâtel, Neuchâtel, Switzerland

^{||}University of Mons, Mons, Belgium

[#]AE, INRA, Avignon, France

^{**}UMR EGCE (Evolution, Génome, Comportement, Ecologie), CNRS-IRD–Univ. Paris-Sud, IDEEV, Université Paris-Saclay, Gif-sur-Yvette Cedex, France

^{§§}IRD c/o ICIPE, Nairobi, Kenya

¹Corresponding author: E-mail: sylvain.pincebourde@univ-tours.fr

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Abstract

Global change is resetting the spatial and ecological equilibrium of complex co-evolutionary relationships between plants and their insect herbivores. We review the mechanisms at play in the responses of plant–insect interactions to global changes, including increased temperature and atmospheric CO₂ concentrations, modification of land use and pollution. We distinguish between the direct effects of global changes on each partner from the indirect impacts on insects via the responses of plants. The indirect effects include a change in the nutritional quality of the plant tissues for herbivore insects, as well as a change in the microclimatic conditions at the leaf surface. Pollinators are involved in a close symbiotic relationship with their favourite plants, and any depression caused by climate stress can lead to pollination deficit. Pollinators are, indeed, quite sensitive to global changes. Furthermore, although species are connected by trophic links, all species respond differently to global changes. We highlight that more research is needed to elucidate the plant-mediated indirect effects of climate change on insects. Then, other human activities, such as land transformations and release of pollutants, are likely to modulate these links between climate and plant–insect relationships. We argue that predicting the net effect of global change on plant–insect relationships requires a comprehensive understanding of the mechanisms that modulate the interaction strength between the plants and the insects, rather than on focusing on each partner individually.



1. INTRODUCTION

Earth is experiencing rapid changes in both climatic conditions and landscape structure. CO₂ concentration in the atmosphere has risen from about 280 ppm during pre-industrial times to the current 397 ppm. The atmospheric CO₂ concentration is predicted to reach up to 600 ppm towards the end of the 21st century if the rate of fossil fuel combustion does not change (IPCC, 2014). As a consequence, global average temperature would increase from 1.7°C to 6°C by the year 2100 (IPCC, 2014). In addition, an increase in the frequency of extreme events is expected (Hance, van Baaren, Vernon, & Boivin, 2007). Meanwhile, European landscapes have undergone a simplification through agricultural intensification leading to the removal of hedges, groves, woods and natural grasslands, and tending to reduce the effectiveness of ecosystem services such as biological pests control (Thies et al., 2011). Thus, even if their combined influences on the

ecosystems are still poorly valued, there is increasing evidence that working on both landscape properties and climate aspects can greatly advance our understanding of their impacts on plant–insect interactions (Tougeron, van Baaren, Burel, & Alford, 2016). These changes in climate and landscapes are disrupting the energetic budget of plants, ultimately affecting their eco-physiological responses against insect herbivores. Therefore, global change is resetting the spatial and ecological equilibrium of complex co-evolutionary relationships between plants and their insect herbivores (Coley, 1998).

Humans disturb the ecosystems in which species live and evolve, leading to ecological and evolutionary consequences for plant–insect interactions (Mitter, Farrell, & Futuyma, 1991; Rundle & Nosil, 2005). Intentionally, humans create totally new environments, such as agriculture fields and cities, in which fauna and flora are subjected to new selection pressures. These new environments are maintained only through human actions. On the other hand, accidentally, humans disturb natural ecosystems due to proximity, needs, pollution and unexpected consequences of their actions. These effects can occur over large areas, at great distances from their anthropogenic origin. Humans are ingenious but they seem to be impotent when faced with the fact that all their innovations are accompanied with the emergence of new accidents (Virilio, 2005). Global climate change is probably the greatest accident. Overall, humans influence ecological processes in three ways: (1) by altering environmental conditions through modifications and transformations of the landscape, (2) by creating new niches in anthropized environments and (3) by rearranging ecological communities through species introduction or removal.

Since more than 500 million years ago, plants and insect herbivores have been engaged in an evolutionary arms race that has been the source of major diversification events (e.g., Currano, Labandeira, & Wilf, 2010; for a review see Chapters: Plant–Insect Interactions: a Paleontological and an Evolutionary Perspective and Evolution of Plant–Insect Interactions: Insights From Macroevolutionary Approaches in Plants and Herbivorous Insects by Kergoat, Meseguer, Jousselein, 2016), which has resulted in plants covering more than half of the biodiversity described today (Strong, Lawton, & Southwood, 1984). Due to their sessile nature, plants evolved sophisticated strategies to protect themselves from herbivore attacks, including structural and chemical means (Schoonhoven, van Loon, & Dicke, 2005). In turn, insects responded to this incredible chemical diversity by evolving detoxification mechanisms (Feyereisen, 1999; Heckel, 2014; for a review see chapter: From Plant Exploitation to Mutualism by Lieutier et al.,

2016), behavioural avoidance mechanisms (Dussourd & Denno, 1991) and temporal and spatial specialization for different plant organs (Jaenike, 1990). Because the equilibrium of the complex interactions between plants and insects depends on environmental conditions, current global change is likely to induce profound changes in the strength of the plant–insect interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008).

Species are linked by trophic links (see Chapters: Food Webs and Multiple Biotic Interactions and The Plant as a Habitat for Entomophagous Insects by Kaiser et al., 2016). In a given community, plants are attacked by herbivores which are themselves attacked by predators and parasitoids. Insect herbivores such as aphids contain different obligatory and facultative endosymbiotic bacteria (see chapter: Influence of Microbial Symbionts on Plant–Insect Interactions by Giron et al., 2016). In ecosystems, these multitrophic interactions are the result of a long co-evolutionary process that unfolds within a particular environment. Any modification occurring at one trophic level will have repercussions on the others. Indeed, each species of the multitrophic network has its own tolerance to temperature, CO₂ concentration or humidity. The preferendum may differ between species and trophic levels, causing various responses to climate change. For example, *Trichogramma chilonis* Ishii 1941 (Hymenoptera: Trichogrammatidae) has an optimal response at temperatures between 25°C and 35°C, whereas it is between 30°C and 35°C for its competitor *Cotesia vestalis* (Haliday, 1834) (Hymenoptera: Braconidae) (Reddy et al., 2002). During the quaternary period, global warming induced distribution shifts with different intensities and speed according to the species: the individual responses of each population or species produced new communities (Graham & Grimm, 1990). To predict the impact of climate change at the community level, it is therefore necessary to understand what will happen to every single species, at each trophic level (guild level), at the level of the synchronism between trophic levels and finally at the community level (Tylianakis et al., 2008).

A well-discussed case of how climate change might impact plant–insect interactions is the effect of environmental temperature. Global warming causes variation in the composition of the plants and their herbivore communities, particularly through differential colonization abilities from more sessile plants to more mobile animal herbivores (Burrows et al., 2011; Parmesan, 1996; Pateman, Hill, Roy, Fox, & Thomas, 2012; Pauli et al., 2012; Stange & Ayres, 2001), and also through shifts in phenological events such as the flowering date or emergence date of overwintering insects (Parmesan & Yohe, 2003). Such phenological mismatch should have

profound effects on the co-evolved plant–herbivore interactions (Harrington, Woiwod, & Sparks, 1999). These effects will be largely mediated by plant defence traits (Rasmann & Pellissier, 2015). Nevertheless, the magnitude and direction of change still remains to be fully elucidated, since the mechanisms at play are highly context dependent and variable (Zavala, Nability, & DeLucia, 2013; Zvereva & Kozlov, 2006).

Here, we review the mechanisms by which global climate change and human activities impact the way plants and insects interact with each other. We do not pretend to exhaustively cover the various effects of global change on plant–insect interactions (for a review see Björkman & Niemelä, 2015).

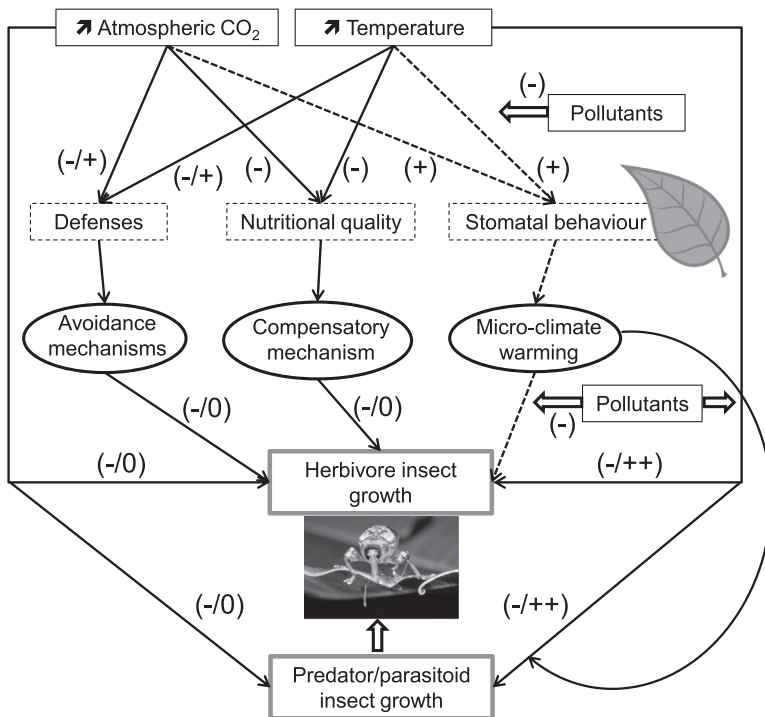


Figure 1 Diagram illustrating the complexity of the multiple interactions between some of the abiotic variables associated with global change (CO₂, temperature, pollution), some plant key processes (structural and chemical defences against herbivores, nutritional quality of plant tissues, stomatal ecophysiology), some herbivore insect responses (avoidance behaviour, compensatory responses) and the third trophic level, the predators and parasitoids. Signs (-/+ /0) indicate the possible effect, negative, positive or no effect, respectively. This diagram is not exhaustive, and other mechanisms may play a significant role.

Our aim is to emphasize the mechanisms behind the responses of plants and insects, and how they interact (Fig. 1). We specifically focus on the role of rising atmospheric CO₂ concentration and increasing temperature. The direct effects on both the plants and the insects are reviewed separately from the indirect effects of these factors on the insects via their influence on the plants. In particular, we highlight that more research is needed to elucidate the plant-mediated indirect effects of climate change on insects. Finally, we detail the effects of human activities on plant–insect relationships by focusing on land use and on pollution. We argue that predicting the net effect of global change on plant–insect relationships requires a comprehensive understanding of the mechanisms that modulate the interaction strength between the plants and the insects, rather than focusing on each partner individually.



2. DIRECT EFFECTS OF CLIMATE CHANGE ON PLANT–INSECT INTERACTIONS

2.1 The Plant Side: Impact of Climate Change on Plant Defence Mechanisms

The arms race between plants and insects has led to the evolution of plant mechanisms to minimize damage by insects (Futuyma & Agrawal, 2009; Mitter et al., 1991), including the deployment of chemical and physical defence traits (Schoonhoven et al., 2005). More specifically, plant resistance against herbivores is mediated by structural attributes, such as thick and tough epidermal layers, spines, trichomes, as well as toxic phytochemicals (also called secondary metabolites) that can inhibit, intoxicate and/or kill the herbivore (Schoonhoven et al., 2005). The main classes of secondary metabolites include the terpenoids, phenolics and alkaloids, and also other nitrogen- or sulphur-containing compounds such as the glucosinolates in the Brassicaceae or sugar-bound molecules such as the iridoids in the Plantagineae (Rosenthal & Berenbaum, 1991).

In addition to directly deploying physical and chemical defences, it has become a general agreement that plants can benefit from attracting predators near the site of herbivore attack (Dicke & Baldwin, 2010). More specifically, indirect defences involve the production of features that provide shelter (e.g., domatia), reward (e.g., extrafloral nectar) or information on herbivore presence, such as the release of volatile organic compounds (VOCs), for the natural enemies of herbivores (Kessler & Heil, 2011). These defence traits mediate herbivore–enemy interactions by increasing herbivore suppression,

and ultimately potentially increasing plant fitness (Romero & Koricheva, 2011; Schmitz, Hamback, & Beckerman, 2000).

While most of the variations in plant's defence arsenal are attributed to a variety of genetic, ontogenetic and phenologic components, including evolutionary history (Futuyma & Agrawal, 2009), plants also have to constantly cope with variations in environmental conditions, generally imposing a reshuffling of the carbon/energy balance, and thus the allocation between growth and defence (Coley, Bryant, & Chapin, 1985; Herms & Mattson, 1992). In the next section, we will discuss the general patterns emerging from several years of research on the two major climate change drivers – elevated CO₂ and temperature – on plant direct and indirect defences and how they might affect plant's resistance to herbivore attack.

2.1.1 Effect of Elevated CO₂ on Plant Defence and Resistance to Herbivore

The effect of elevated CO₂ on insect herbivores is mainly mediated by changes in plant chemistry (Cornelissen, 2011; Lincoln, Fajer, & Johnson, 1993). An overall conclusion drawn from summarizing the effect of CO₂ addition on plants suggests that changes in primary metabolism are in fact relatively predictable, whereas changes in plant's secondary metabolite production, and their corresponding effects on plant direct and indirect defences, are highly variable (Bidart-Bouzat & Imeh-Nathaniel, 2008), with subsequent strong variation in herbivore performance (Coviella & Trumble, 1999; Robinson, Ryan, & Newman, 2012). Elevated CO₂ typically increases the carbon:nitrogen ratio (Robinson et al., 2012). In addition, it has dramatic but variable impact on the general leaf secondary chemistry (Bidart-Bouzat & Imeh-Nathaniel, 2008; Cornelissen, 2011; Lindroth, 2010; Stiling & Cornelissen, 2007). Perhaps the only exception is the production of VOCs, which was consistently shown to increase in concentration in the headspace surrounding the plant under elevated CO₂ conditions (Peñuelas & Staudt, 2010). Nevertheless, such increase does not automatically translate into higher herbivore suppression by predators in the field, and again, context dependency applies when analyzing the community-wide impacts of elevated CO₂ (Facey, Ellsworth, Staley, Wright, & Johnson, 2014). This variation poses a clear challenge for developing credible predictions of how further CO₂ addition into the atmosphere will impact the plant resistance against herbivores. Therefore, one has to move away from the highly variable secondary metabolism and

look at other, more predictable traits. For instance, a relatively small literature which is rapidly gaining attention shows a direct effect of elevated CO₂ on plant hormones (phytohormones), such as jasmonic acid (JA) and salicylic acid (SA) (see below).

Plants attacked by herbivores generate specific hormonal cascades which ultimately elicit downstream changes in plant biochemistry and secondary metabolism through complex signalling networks (Browse & Howe, 2008; Wu & Baldwin, 2010). Both JA and SA are involved in the orchestration of plant defence after herbivore attack (Farmer, Alméras, & Krishnamurthy, 2003; Thaler, Agrawal, & Halitschke, 2010). Exposure to elevated CO₂ can modulate hormone production, which might explain some of the variations in the observed responses of allelochemicals (Ode, Johnson, & Moore, 2014; Zavala et al., 2013). To summarize, the emerging picture suggests that (1) elevated CO₂ down-regulates the constitutive herbivore-induced expression of several key genes associated with the JA pathway, resulting in an increased herbivore damage in field and laboratory conditions (Sun et al., 2011; Zavala, Casteel, DeLucia, & Berenbaum, 2008); (2) because of the inherent cross-talks between JA- and SA-signalling pathways (Thaler, Humphrey, & Whiteman, 2012), elevated CO₂ enhances induced defences derived from the SA-signalling pathway (Ghasemzadeh, Jaafar, & Rahmat, 2010), such as the pathogenesis-related protein (Sun et al., 2011) and (3) the differential responses among phytohormonal pathways provide new insights into how elevated CO₂ modulates plant defences against herbivory.

2.1.2 Effect of Elevated Temperature on Plant Defence and Resistance to Herbivore

Temperature affects the plant physiological processes, growth, reproduction and survival (Jamieson, Trowbridge, Raffa, & Lindroth, 2012; Julkunen-Tiitto, Nybakken, Randriamanana, & Virjamo, 2015). In addition, warming modifies the biosynthesis of plant secondary metabolites (Bidart-Bouzat & Imeh-Nathaniel, 2008; Loreto & Schnitzler, 2010). A general trend was reported for the responses of phytochemicals to enhanced temperature (Zvereva & Kozlov, 2006). Phenolics tended to decrease, whereas terpenes tended to increase at higher temperatures. However, any generalization remains difficult since several examples showed no, or even the opposite effects of elevated temperature on phenolic-based compounds, alkaloids, terpenoids, or glucosinolates (Bidart-Bouzat & Imeh-Nathaniel, 2008; Julkunen-Tiitto et al., 2015). When looking at the effect of increased

temperature on the production of VOCs, the picture seems to be clearer. VOC production generally increases with temperature up to the physiological maximum of the plant, beyond which enzymatic degradation inhibits emission (Guenther, Zimmerman, Harley, Monson, & Fall, 1993). The mechanisms of increased emission reside particularly on enhanced enzymatic activities, and increased VOC vapour pressure (Peñuelas & Llusà, 2003). Interestingly, Peñuelas and Llusà, (2003) suggested that increased VOC production should not only be related to enhanced biotic interactions (pollinator and/or predator attraction), which might be also less predictable (de Sassi, Staniczenko, & Tylianakis, 2012; Tylianakis et al., 2008), but also to an increased thermal tolerance for plants. In other words, increased temperatures favour VOC emissions, which in turn enable the plant to better withstand the heat stress.

Another approach for studying the effect of temperature changes on plant defences and plant–insect interactions is to use elevation gradients as natural source of variation in biotic and abiotic factors (Körner, 2007; Rasmann, Alvarez, & Pellissier, 2014; Rasmann, Pellissier, Defosse, Jactel, & Kunstler, 2014). Recent examples show that high-altitude adapted *Plantago lanceolata* L. or *Vicia sepium* L. genotypes produce lower levels of secondary metabolites (iridoid glycosides or VOCs, respectively). While such decline could be attributed to a reduction in herbivore pressure at high elevation, colder temperatures also inhibit iridoid glycoside production in *P. lanceolata* (Pellissier, Roger, Bilat, & Rasmann, 2014). A general decline in plant resistance at high altitude seems to be the rule (Pellissier et al., 2012; for exceptions see Rasmann, Alvarez, et al., 2014; Rasmann, Pellissier, et al., 2014). Specifically, we can hypothesize a general decline of plant defences at high elevation for the predominant plants in the community, while the rarest plants benefit from having their slow growing leaves well protected (Fine, Mesones, & Coley, 2004; Pellissier et al., 2016).

According to predictions, climate warming will reshuffle plant and herbivore communities along altitudinal gradients through high elevation colonization mismatch (Pauli et al., 2012). Therefore, we suggest that high elevation plants will be more exposed to herbivore pressure in the upcoming years (Rasmann, Alvarez, et al., 2014; Rasmann, Pellissier, et al., 2014). Plants' tolerance to such predicted increase in herbivory will be the outcome of several factors, including genetic (and epigenetic) variations, the ability to change their phenotype rapidly in the presence of herbivore attack (i.e. phenotypic plasticity), and ultimately the rate to which plants can adapt (Rasmann & Pellissier, 2015). In other words,

climate warming will indirectly impose a strong habitat-specific selection pressure on plants, in turn favouring evolution for novel defence syndromes at high elevation.

2.2 The Insect Side: Impacts of Climate Change on Herbivore Performance

2.2.1 Effect of CO₂ Addition on Insect Performance

The direct effect of changing CO₂ concentration in the atmosphere on the eco-physiology of insects has been largely overlooked till date. Recently, [Kerr, Phelan, and Woods \(2013\)](#) showed that the developmental rate of *Manduca sexta* Linnaeus 1763 caterpillars was only slightly affected when reared under high (above 1200 ppm) CO₂ concentrations. More importantly, rising atmospheric CO₂ concentration may be linked to changes in the acidification of insect body fluids. This may be especially true for the eggs that cannot ventilate like the larvae and adult stages, but can only exchange gases via passive diffusion ([Woods, Bonneau, & Zrubek, 2005](#)). Nevertheless, exposing *M. sexta* eggs to high CO₂ concentrations for several hours did not influence the pH in the egg yolk ([Kerr et al., 2013](#)). Undoubtedly, more experimental evidence is needed to generalize these findings.

Rising atmospheric CO₂ concentration may be more likely detrimental to insect species that already live in hypercarbic environments such as cambium miners, stem borers and insects that induce large galls ([Pincebourde & Casas, 2016](#)). These endophagous insects live deep into the plant tissues and gases diffuse slowly between outside the plant and the insect location. Therefore, an increase in atmospheric CO₂ concentration may slow down the diffusion of CO₂ outward, enhancing the risk of reaching dangerous asphyxiating levels ([Pincebourde & Casas, 2016](#)). Indeed, the hypercarbic conditions in the galleries of these insects coincide with hypoxia, i.e. low oxygen levels. But, again, a lack of knowledge on the direct physiological effects of CO₂ on insect herbivores precludes any firm conclusion.

Finally, changes in CO₂ could also affect the behaviour of insects. Particularly, several soil-dwelling herbivores utilize root-emitted CO₂ as a cue for finding their hosts ([Nicolas & Sillans, 1989](#)). Several species can be quite sensitive to variations in CO₂ levels, as they can detect CO₂ concentration increase as small as 0.003% and locate their host plant from a distance of 20 cm ([Doane, Lee, Klingler, & Westcott, 1975](#)). This peculiarity makes these insects especially sensitive to rising atmospheric CO₂ concentration.

2.2.2 Effect of Temperature on Insect Performance

Most insects are ectotherms and temperature variations were shown to directly influence their eco-physiology including: metabolic rate, growth, feeding rates and life-history traits, such as fecundity and longevity (Angilletta, 2009; Bale et al., 2002). Generally, the thermal response of insects follows the classic thermal performance curve. An insect can increase the performance above a threshold (minimal critical temperature, CT_{\min}) up to the optimal temperature, after which performance decreases sharply and reaches the upper threshold for performance (maximal critical temperature, CT_{\max}) (Angilletta, 2009). Therefore, a warming climate should generally improve the eco-physiological performance of insects, as long as the temperature does not surpass the temperature optimum, and does not reach the CT_{\max} . The ecological consequences of temperature-mediated improved performance include the expansion of species distribution ranges, as new thermal niches appear northwards (Parmesan, 2006; Parmesan & Yohe, 2003), and the increase of insect population outbreaks (Jepsen, Hagen, Ims, & Yoccoz, 2008). Understanding these processes, however,

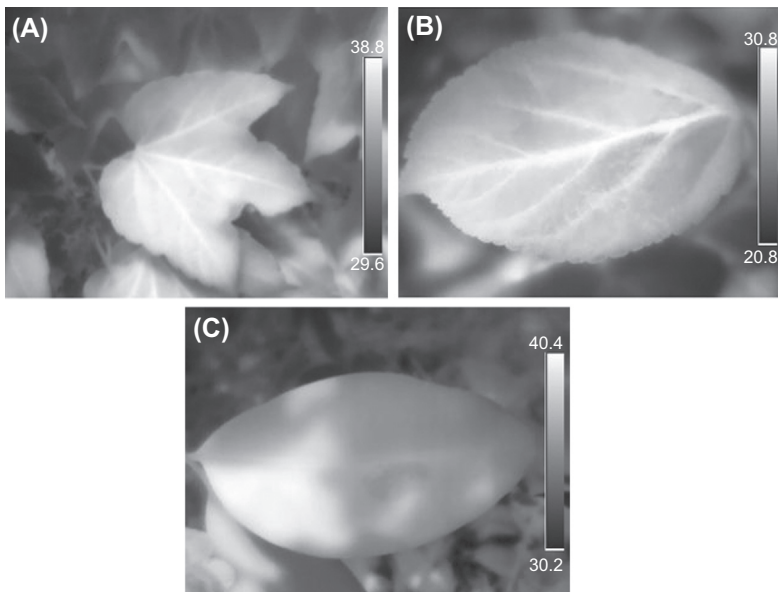


Figure 2 Thermographic images of leaf surfaces exposed to solar radiation for (A) grape ivy (France), (B) apple (France) and (C) *Clusia* sp. (French Guiana). During these measurements with an infrared camera, air temperature was 28.6°C, 24°C and 29.2°C, respectively.

necessitates clarifying the predictions of when and where the temperature falls above the optimal temperature and reaches the CT_{\max} of species (Sunday et al., 2014). Specifically, this requires the determination of the exact temperature experienced by insects at the leaf surface or within the leaf tissues (Pincebourde & Woods, 2012).

The temperature at the surface of plants can deviate from ambient air temperature (Fig. 2). For instance, the leaf temperature excess (i.e. temperature deviation between leaf surface and ambient air) can be up to 10°C in temperate plants (Cook, Dixon, & Leopold, 1964; Pincebourde, Sinoquet, Combes, & Casas, 2007) and even up to 20°C in alpine plants in full sunlight (Linacre, 1967). By contrast, in the arid ecosystem of Arizona (USA), *Datura* leaves are colder than the surroundings during the day (Potter, Davidowitz, & Woods, 2009). The developmental and tolerance thresholds of *Manduca sexta* eggs are adapted to the *Datura* leaf temperature patterns, as they would die if they experience the high desert ambient air temperature (Potter et al., 2009). Generally, the excess temperature of leaves decreases when ambient air increases (Linacre, 1967; Michaletz et al., 2015; Pincebourde & Woods, 2012). The shape of the relationships between leaf temperature and ambient air temperature, however, may depend on the plant system and on the spatial scale at which the process is investigated (Pincebourde, Murdock, Vickers, & Sears, 2016).

The degree to which leaf temperature influences insects depends on their body size. The main reason is purely physical: any organism small enough to remain totally embedded into the leaf boundary layer is subjected to leaf temperature directly (Kaspari, Clay, Lucas, Yanoviak, & Kay, 2015). By contrast, organisms larger than the leaf boundary layer mainly depend on the ambient conditions (Woods, 2013). Across their ontogeny, most herbivore insects experience leaf temperature fluctuation during the first stages of their development until they reach a body size, beyond which their thermal budget shifts as they are influenced by ambient air conditions. For example, early instars of the *Manduca sexta* caterpillar experience temperature about 5°C below ambient air at the *Datura* leaf surface, while the last larval stage reaches body temperatures that are several degrees above ambient air (Woods, 2013).

Understanding how warmer climates affect insects thus requires quantifying the effect of global warming on leaf surface temperatures. From an evolutionary perspective, the convergence of mean leaf temperature at all latitudes towards a value of $\sim 22^{\circ}\text{C}$ (Helliker & Richter, 2008) indicates that climate change may have a relatively small effect on leaf surface

temperature, as long as the whole plant can compensate. Nevertheless, it is not clear how global change will cause changes at the leaf surface, and several hypotheses were developed recently (Pincebourde & Woods, 2012). Depending on the level of adaptation to environmental fluctuations that are larger in the temperate zone compared to lower latitudes, the amplitude of warming may be buffered or by contrast be reported to the leaf surface temperature—more empirical research is needed. In addition, the ability of arthropods for behavioural thermoregulation could modify the leaf surface temperature pattern they experience (Pincebourde & Suppo, 2016). Spider mites, for example, make use of the within-leaf surface thermal heterogeneity to thermoregulate and keep track of the optimal temperature for their development (Caillon, Suppo, Casas, Woods, & Pincebourde, 2014). However, warming homogenizes leaf surface temperatures, thereby disrupting the behavioural thermo-compensation of mites, and ultimately leading them to overheat (Caillon et al., 2014).

2.3 Impact of Climate Change on Pollinators

Recently, climate change was pointed out as one of the major causes of regression of insect pollinator populations. While other groups may be involved, most of the pollination service is provided by the ~20,000 bee species (Michener, 2007; Proctor, Yeo, & Lack, 1996). Interestingly, these insects, and in particular bumblebees, generally show an elaborated endothermic behaviour, which allowed them to colonize a vast number of habitats (Heinrich, 1979; Owen, Bale, & Hayward, 2013). This specialized endothermy, however, exposes bumblebees to climate risks.

The modelling of eco-climatic envelope for bumblebee species indicated that many species will be significantly rarefied due to global warming (Rasmont et al., 2015). The climatic risk is more or less accentuated depending on the scenarios considered by IPCC (2007) (Fig. 3). In Europe, the distribution of 30, 47 and 53 species among the 69 bumblebee species will be reduced according to the scenario SEDG, BAMBU and GRAS, respectively (Settele et al., 2005). The population disruptions due to climate change can be severe. Specifically, for areas such as Madrid, Paris, London, and Helsinki, only one to three species can survive while several dozen species were present in the 20th century (Rasmont et al., 2015). By contrast, pollinators may find refuges in mountain areas which will conserve their current diversity. Therefore, population movements will likely determine the survival of these species. Comparable trends are expected for North America, except that the Northern margin of bumblebee distribution will

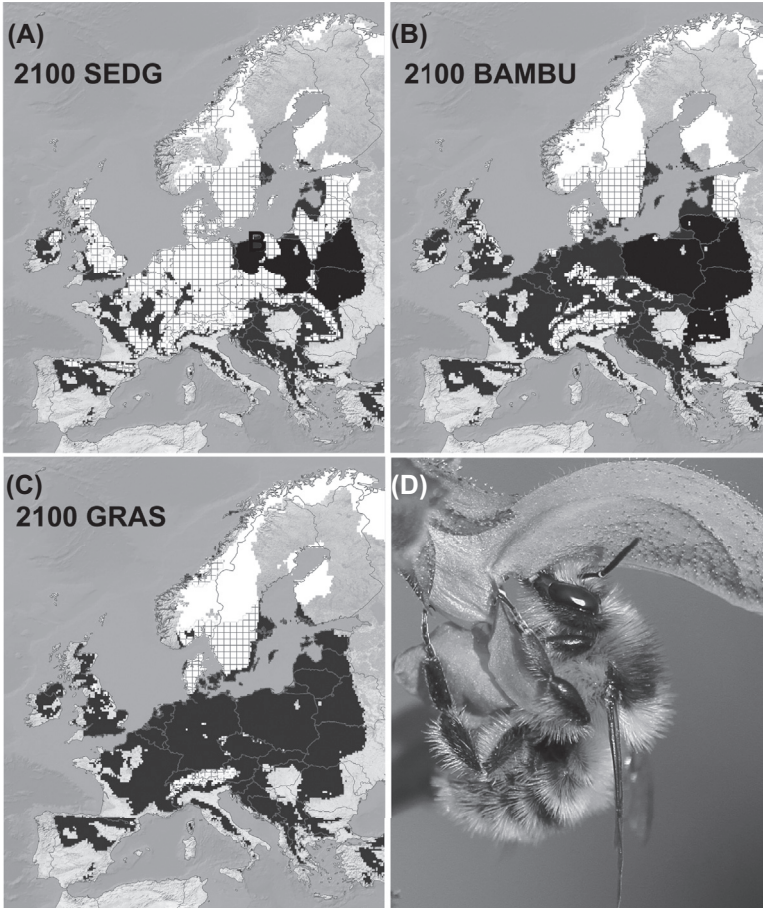


Figure 3 Projected suitable climatic area of *Bombus sylvarum* in 2100 in Europe. (A) SEDG scenario, (B) BAMBU scenario, (C) GRAS scenario and (D) *Bombus sylvarum* visiting a flower. Photo by J. Carteron. Areas in black will be lost; hatched areas will be conserved; areas in white will be gained. After Rasmont, P., Franzen, M., Lecocq, T., Harpke, A., Roberts, S.P.M., Biesmeijer, K., ..., Schweiger O. (2015). Climatic risk and distribution atlas of European bumblebees. *Biorisk*, 10, 1–246. <http://dx.doi.org/10.3897/biorisk.10.4749>.

not shift as much as the Southern limits (Kerr et al., 2015). North American taxa may have smaller dispersion ability than European species. Indeed, the postglacial history of species in Europe may have induced a strong selection of the most mobile taxa (Hewitt, 1999; Lecocq et al., 2013).

Some isolated mesoclimatic zones in southern European regions can play the role of ‘Noah’s Ark’ by becoming a source-bumblebee population for

this entire geographic region (Rasmont et al., 2015). Unfortunately, this perspective could be compromised by the genetic drift of the small surviving isolates. Indeed, the mechanism of sex determination in bumblebees may contribute to their decline in a warmer world. The male, normally haploid, is determined by the homozygosity of a small number of loci (Duchateau, Hoshiba, & Velthuis, 1994). During inbreeding, a large number of diploid males emerge with a drastically reduced fertility. Therefore, the monomorphism of these loci induced by genetic drift could depress the reproductive potential (Whitehorn, Tinsley, Brown, Darvill, & Goulson, 2009). Only large mountain areas, which will shelter large and genetically diverse residual populations, could ensure the survival of these pollinator species in the future.

The modelling studies of Kerr et al. (2015) and Rasmont et al. (2015) are mainly based on temperature averages. These models do not include extreme climatic events such as heat waves which will increase in frequency and duration in the next decades (Meehl & Tebaldi, 2004; Robinson, 2001) and which can cause local extinctions of some bumblebee species (Rasmont & Iserbyt, 2012). Martinet, Lecocq, Smet, and Rasmont (2015) showed that a typical heat wave temperature (40°C in temperate regions) rapidly kills the tested specimens (Fig. 4). Some bumblebee species, however, are more sensitive to thermal stress than others (e.g., arctic and top mountain species). Moreover, critical thermal limits vary according to altitudinal distribution of bumblebees (Oyen, Susma, & Dillon, 2016). By contrast, a species such as *Bombus terrestris* (Linnaeus, 1758) seems to tolerate well heat wave conditions. The particular thermal tolerance of this species may explain its recent Northward expansion in Europe despite the repeated heat waves (Martinet et al., 2016).

Some wild bee species are linked to hot and dry climates (Michener, 1979). For instance, the honeybee *Apis mellifera* Linnaeus 1758 or *Xylocopa varipuncta* Patton 1879 are able to fly in very hot conditions (Heinrich, 1979; Heinrich & Buchmann, 1986). Numerous wild bees are living in desert and other dry habitats, with their maximum diversity in these environments (Patiny & Michez, 2007). As of today, however, we have no evaluation of the thermal tolerance in these thermophilic taxa or on their resistance to climate change (Nieto et al., 2014, p. 84). For a small number of species, global warming is the best explanation for their northward expansion, e.g., *Xylocopa (Koptortosoma) pubescens* Spinola 1838 which is now present in Europe (Terzo & Rasmont, 2014).

Beyond the fate of pollinator insects during climate change, the question of pollination service is crucial. Both the plant and its pollinators may respond differently to climate change. For example, the large shift towards

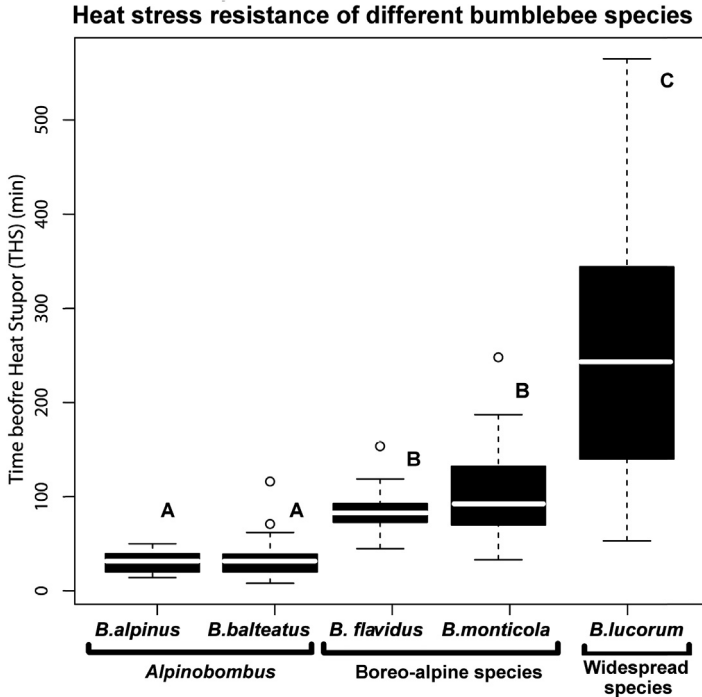


Figure 4 Boxplots of the time before heat stupor for six bumblebees species (*Bombus* sp.). (A) Arcto-alpine species: *Bombus alpinus* and *Bombus balteatus*, (B) boreo-alpine species: *Bombus flavidus* and *Bombus monticola* and (C) widespread species: *Bombus lucorum*. Circles are extreme values. After Martinet, B., Lecocq, T., Smet, J., & Rasmont, P. (2015). A protocol to assess insect resistance to heat waves, applied to bumblebees (*Bombus* Latreille, 1802). PLoS One, 10, e0118591.

the North of orchards relative to the small shift of the associated pollinators may generate an extensive pollination deficit area (Polce et al., 2014). In general, pollinators are involved in a close symbiotic relationship with their favourite plants, and any depression caused by climate stress can lead to pollination deficit (Franzén & Ockinger, 2012). This deficit can significantly reduce the reproductive potential of both domesticated and wild plants. In turn, this reduction can lower biodiversity by generating food deficiency for the species associated with these plants. This interaction chain still escapes our modelling capabilities.



3. INDIRECT EFFECTS OF CLIMATE CHANGE ON PLANT–INSECT INTERACTIONS

3.1 Plants Responses Matter for Insects

3.1.1 Impacts of Climate Change on the Plant Nutritional Quality for Herbivores

Rising atmospheric CO₂ concentration influences the development of herbivores indirectly by inducing changes in the plant nutritional quality (Lincoln et al., 1993). In general, plants growing in a CO₂-enriched atmosphere have higher levels of non-structural sugars, which are beneficial to insect herbivores (Bezemer & Jones, 1998). Nevertheless, higher CO₂ levels also lead to a lower concentration of proteins (Ehleringer, Cerling, & Dearing, 2002; Whittaker, 2001) and some amino acids (Docherty, Wade, Hurst, Whittaker, & Lea, 1997) in leaves. In addition, the concentration of secondary compounds, which are toxic to herbivore insects, increases in a CO₂-enriched atmosphere (Bidart-Bouzat, Mithen, & Berenbaum, 2005; Cornelissen, Stiling, & Drake, 2003; Stiling & Cornelissen, 2007). Therefore, the nutritional quality of plants is lower when grown under high CO₂ levels compared to current concentrations. Negative impacts of increasing CO₂ levels were also found on the development rate and survival of phytophagous insects (Smith & Jones, 1998; Whittaker, 2001). Herbivore insects may develop compensatory mechanisms by increasing their food intake quantitatively or by enhancing assimilation efficiency (Barbehenn, Karowe, & Chen, 2004; Stiling & Cornelissen, 2007). For example, leaf miner caterpillars compensate for the lower quality of their plant food by increasing the amount of leaf tissues eaten (Cornelissen et al., 2003; Salt, Brooks, & Whittaker, 1995). Compensatory mechanisms were not found in all species (Smith & Jones, 1998), however, and even when compensation occurs it does not cover all the negative impacts of low quality food (Hunter, 2001).

Temperature changes can also influence the nutritional quality of host plants. The net effect is highly plant species specific. A long-term increase in temperature induces a decrease in the water content of leaves (Williams, Norby, & Lincoln, 2000). In herbaceous, warming induces an increase in nitrogen concentration of plant tissues (Bezemer & Jones, 1998). By contrast, in woody species, warming negatively impacts the nitrogen concentration and increases the concentration of tannins (Dury, Good, Perrins, Buse, & Kaye, 1998). The concentration of sugar can also be affected by the increase in temperature (Morison & Lawlor, 1999).

Interactive effects of temperature increase and CO₂ concentration change were reported, but the net effect varies according to the insect–plant system (Zvereva & Kozlov, 2006). In some systems, only one of the two factors has an impact on the development rate of the insect, either negative (Williams et al., 2000) or positive (Buse & Good, 1996). In other systems, however, temperature and CO₂ interact such that the negative effect of one is suppressed by the positive effect of the second (Fajer, Bowers, & Bazzaz, 1991). Finally, in most cases, compensatory effects happen resulting in the compensation of the negative effect from one factor by the positive effect of the second (Johns, Beaumont, & Hughes, 2003; Johns & Hughes, 2002). Overall, the predicted negative effects of CO₂ elevation on herbivores are likely to be mitigated by temperature increase (Zvereva & Kozlov, 2006), but more experimental data are needed on different biological systems to generalize these findings (Robinson et al., 2012).

3.1.2 Cascading Effects of Changing the Plant Eco-Physiology on the Insect Microclimate

When feeding on their host plant, insects modify the plant tissues physically and/or physiologically. In turn, these modifications can induce shifts in the insect microclimate — an effect called the physical feedback of herbivory (Pincebourde & Casas, 2006a). This indirect effect is especially prominent in endophagous insects such as leaf miners and gallers. These organisms alter the structure and the properties of the leaf (Pincebourde & Casas, 2016). In general, the outcome of these modifications is an increase in the microclimatic temperature for the insect herbivore. For example, the leaf miner *Phyllonorycter blancardella* (Fabricius, 1781) (Lepidoptera: Gracillariidae) induces stomatal closure in apple leaf tissues (Pincebourde, Frak, Sinoquet, Régnard, & Casas, 2006) and generates white patches at the leaf surface (Pincebourde & Casas, 2006a). These two modifications contribute to an elevation of the temperature within the mine by up to 12°C above ambient air (Pincebourde & Casas, 2006b, 2015). These elevated temperatures can speed up the insect development, but this strategy is at risk during extreme climatic events such as heat waves (Pincebourde & Casas, 2015). During heat waves, the mosaic of favourable and risky microclimates is reshuffled (Pincebourde et al., 2007).

External feeders also induce variations in leaf surface temperatures during their feeding activity. These variations are in the order of few degrees, and are generally quite local around the leaf portion attacked by the herbivore (Nabity, Hillstrom, Lindroth, & DeLucia, 2012). These temperature

changes at the leaf surface are the consequence of alteration in stomatal conductance and evapotranspiration rates. Nevertheless, little is known on these interactive effects during warming. Indeed, insect herbivores tend to increase their feeding rate in a warmer environment (see above), suggesting that more local impacts on leaf transpiration rates are expected, thereby reinforcing the general warming effect. Overall, the plant responses to climate change should have consequences on the microclimatic conditions at the leaf surface. Many parameters impact the leaf heat budget, including its size and shape, stomatal conductance and its orientation towards the sun (Gates, 1980). Stomata have an important role in the plant responses: they regulate the overall energy and gas budget of the plant, and they react to several environmental (e.g., climatic variables) and endogenous factors (e.g., plant water status). Climate change can be expected to induce variations in these factors, with likely cascading effects on surface temperatures (Pincebourde & Woods, 2012). Finally, changing plant architecture may also partially buffer the amplitude of warming for insects at the leaf surface, but this effect seems to be quite limited given the magnitude of warming (Saudreau et al., 2013).

3.2 Biotic Interactions Matter for Insects

Species are linked by trophic links. Therefore, a series of indirect effects are expected to cascade through the entire food web, thereby increasing the difficulty to anticipate the effects, especially in complex multitrophic systems (Tylianakis et al., 2008).

3.2.1 Thermal Traits Diverge Across the Different Components of a Multitrophic System

3.2.1.1 Development Time and Growth Rate

The speed at which organisms respond to climate change is partially determined by their generation time. In general, temperature increases the development rate of plants and insects inside their tolerance range. For plants, the period of vegetation increases in length, allowing insects to feed on them for a longer period throughout the year. Some multivoltine species can realize an additional generation per year due to both the longest period of vegetation and their shorter development time. For example, in the European grapevine moth *Lobesia (Lobesia) botrana* (Denis & Schiffermüller, 1775) in South-West of France, Marchal and Feytaud (1911) observed three generations of this insect in 1910, but a century later Martin-Vertedor, Ferrero-García, and Torres-Vila (2010) noted a fourth generation at the end of fall. The increased

reproduction rate influences the population dynamics at the other trophic levels. The parasitism rate of the eastern spruce budworm, *Choristoneura fumiferana* Clemens 1865 (Lepidoptera: Tortricidae) by its parasitoids decreases when the temperature increases (Harrington, Fleming, & Woiwod, 2001). By contrast, the predation rate of the seven-spot ladybird, *Coccinella septempunctata* Linnaeus 1758 on the aphid *Acyrtosiphum pisum* (Harris, 1776) increases at high temperatures. The impact of temperature increase cannot be generalized without the understanding of the specific thermal responses.

3.2.1.2 Metabolic Rate, Longevity and Fecundity

These traits are driven by temperature in natural enemies such as parasitoids, thereby modifying the parasitism rate and then the impact of phytophagous insects on plants. An increase in temperature increases metabolism and activity (May, 1979). For example, the walking speed of the parasitoid *Aphelinus asychis* Walker 1839 (Hymenoptera: Aphelinidae) increases with temperature (Mason & Hopper, 1997). These traits are associated with an increase in the instantaneous rate of parasitism. However, the increased metabolic rate also results in a reduced longevity due to the accelerated use of energy (Huey & Stevenson, 1979; Trotta et al., 2006). Therefore, the impact at the life span level is difficult to determine. In addition, above a given temperature threshold, the negative effects of high temperature exceed the advantages. This complexity of the relationship between traits at the individual scale is found at each trophic level. An increase of temperature can increase the fecundity of the phytophagous insect and decrease that of the parasitoid, or vice versa.

3.2.1.3 Sex Allocation

Temperature can influence sex allocation in insects. This was observed for arrhenotokous hymenopteran parasitoids, in which unfertilised eggs develop into haploid males and fertilised eggs develop into diploid females. Females are able to allocate male or female eggs in one host according to internal or external factors, thus affecting the sex ratio. For example, the sex ratio of *Aphelinus varipes* (Förster, 1841) (Hymenoptera: Aphelinidae) varied from 92% female when reared at 25°C, to 70% at 20°C (Rohne, 2002). By contrast, in the parasitoid *Diaeretiella rapae* (M'Intosh, 1855) (Hymenoptera: Aphidiidae), the percentage of females was lowest at 26.7°C compared to 21°C (Bernal & Gonzalez, 1997). The effect of temperature on sex allocation is complicated by the fact that the sex ratio can be influenced by host size, with males more likely to emerge from smaller hosts. Host size is also

linked to temperature. For example, the body size of the black bean aphid, *Aphis fabae* Scopoli 1763, is larger when reared at low temperatures (Li & Mills, 2004).

3.2.1.4 Diapause

Diapause is an environmentally pre-programmed and hormonally mediated state of low metabolic activity associated with arrested development and increased resistance to environment extremes (Tauber, Tauber, & Masaki, 1986). Warmer and shorter winters act on the diapause strategy of insects. For example, the parasitoid *Aphidius avenae* Haliday 1834 was detected for the first time in its non-diapausing form on cereal fields in Brittany in the winter of 2011–12, whereas during the previous 20 years, it was observed in the diapausing phase outside cereal crops during winters and it only colonized the crops in spring (van Baaren et al., 2004; Krespi, Dedryver, & Creach, 1997; Le Lann et al., 2011). These modifications in the host-parasitoid relationship were linked to an increase in winter temperatures (Andrade, Krespi, Bonnardot, van Baaren, & Outreman, 2016). This shift in diapause strategy modified the food web, with *A. avenae* becoming a dominant species in this system and with an increase in the parasitism rate in winter. The plasticity of diapause induction may allow an efficient exploitation of available resources and, consequently, non-diapausing parasitoids should only be associated with anholocyclic aphids (i.e. aphids with incomplete life cycle, or which do not alternate parthenogenesis and sexual reproduction) that remain reproductive throughout winter. More generally, the parasitoid should remain synchronized with the host cycle (Godfray, 1994). The parasitoid either follows the diapause strategy of its host, and in this case the parasitoid does not kill its host before entering diapause, or the diapause strategy is decoupled from the host. In the context of climate change, the challenge for the parasitoid is to remain synchronized with the host strategy and to avoid the end of its diapause when the host is still diapausing.

3.2.1.5 Endosymbionts

Both parasitoids and herbivore insects may host endosymbiotic bacteria that can influence various life-history traits (for a review see chapter: Influence of Microbial Symbionts on Plant–Insect Interactions by Giron et al., 2016). For example, aphids have a variety of bacterial symbionts including an obligate association with the mutualist *Buchnera aphidicola* (Shigenobu, Watanabe, Hattori, Sakaki, & Ishikawa, 2000). They may also possess

secondary symbionts (e.g., *Wolbachia*) which are conditionally beneficial or deleterious (Degnanj & Moran, 2008). These bacteria have major effects on aphid biology, including enhanced tolerance to heat stress and changes in host plant range (Moran, Degnan, Santos, Dunbar, & Ochman, 2005; Tsuchida, Koga, & Fukatsu, 2004). Both major groups of endosymbionts, *Wolbachia* and *Buchnera*, may be negatively affected or eliminated by short exposures to high temperature (Thomas & Blanford, 2003). Moreover, the effect of secondary endosymbionts varies with temperature. Endosymbionts protect the aphid *Acyrtosiphum pisum* against heat stress at 25°C, whereas they decrease the fecundity at 20°C (Cheng, Montllor, & Purcell, 2000). The defensive immunity conferred to aphids by the endosymbiont *Candidatus Hamiltonella defensa* fails under heat stress (Bensadia, Boudreault, Guaya, Michaud, & Cloutier, 2006). In conclusion, climate change is expected to have broad-ranging indirect impacts on insect communities via direct effects on their associated endosymbionts.

3.2.1.6 Virus Transmission

Climate change is expected to modify the incidence of phytophagous-borne virus infections since temperature influences virus transmission (Thomas & Blanford, 2003). For example, barley yellow dwarf (BYD) is one of the world's most severe viral diseases of autumn-sown cereals. BYD viruses are transmitted by several aphid species. Environmental conditions govern the pattern and timing of primary infections by viruliferous alates and the speed of subsequent virus dissemination by apterae (secondary spread). Temperature influences both the population dynamics of the vector (e.g., 5°C is the developmental threshold for the aphid *Rhopalosiphum padi* (Linnaeus, 1758)) and the virus transmission process (e.g., 15°C is the take-off threshold for alatae). Warm January to August periods generate a high percentage of viruliferous aphids the following autumn, perhaps due to an increased rate of population growth and virus transmission in agroecosystems (Fabre et al., 2005).

3.2.2 Synchronization Between Trophic Levels

3.2.2.1 Phenological Synchronization

Numerous studies have reported climate change-induced phenological modifications at one particular trophic level. But few studies quantified the consequences of phenological shifts at several trophic levels. In UK, *Anthocharis cardamines* (Linnaeus, 1758) (Lepidoptera: Pieridae) exactly follows the phenology of its host plant, for which the phenology is

advanced by 2–3 weeks with warming, but this example is an exception (Parmesan, 2006). The phenological synchrony between plants and insects, and between hosts and parasitoids, can be decoupled if the species are affected by temperature differently. For example, Harrington et al. (2001) showed in the system *Picea sitchensis* Carrière (Pinaceae)—*Operophtera brumata* (Linnaeus, 1758) (Lepidoptera: Geometridae) that the onset of bud development is not modified by warming, whereas the emergence date of the insects that feed on them is advanced. Nevertheless, the development of the caterpillars collapses because buds are not yet available when they emerge.

Few studies focused on the second and third trophic levels, and they suggest that their synchrony could be affected too. Annual variation in phenological asynchrony may be an important destabilizing factor (Godfray, Hassell, & Holt, 1994). Similarly, the time of parasitoid arrival in an aphid population influences the growth rate of the parasitoid population and its impact on the host population (Hoover & Newman, 2004). If the parasitoid arrives too early (before the aphid population has entered the exponential growth phase), the parasitoid population disappears before the aphid population increases or the parasitoid eliminates the small aphid population before it reaches the exponential growth phase. By contrast, if the parasitoid arrives during the exponential growth phase of the host, large parasitoid populations will be produced. Even small climatic changes can affect the synchrony of parasitoid activity with host populations, with large effects on the population dynamics of both.

3.2.2.2 Spatial Synchronization

The geographical distribution of plants, herbivores and parasitoids may change during climate change as a result of various processes, including changes in the dispersal ability of insects and their host plants, and the destabilization of resident ecosystems (Parmesan, 2006). In the last century, the geographical distribution of species was modified by climate changes in 75% and 81% of the studied species in tropical and temperate areas, respectively (Parmesan, 1996). Phytophagous species often extend their geographic distribution northwards in temperate regions following an increase in temperature (Parmesan, 2006). For example, *Pararge aegeria* (Linnaeus, 1758) (Lepidoptera: Nymphalidae) extended its repartition towards the North since 1940 (Hill, Thomas, & Huntley, 1999). Extending the distribution becomes easier when the phytophagous insect succeeds to adapt to a new host plant. Also, a phytophagous species extending its

repartition can reach zones which are free of any natural enemies, as it is the case for the processionary pine moth, *Thaumetopoea pityocampa* (Denis & Schifferrmüller, 1775) (Battisti et al., 2005).

3.2.3 Impacts at the Guild or at the Community Levels

Communities are mixtures of specialist and generalist species. It is predicted that specialists will suffer from climate change more than generalists, because generalists exploit a large variety of host species which can be adapted to different climatic conditions (Stireman et al., 2005). The trophic rank hypothesis predicts that higher-trophic level organisms are more negatively affected by environmental changes and disturbance than species in the lower trophic levels (Holt, Lawton, Polis, & Martinez, 1999; Tscharnke & Brandl, 2004). Moreover, at each trophic level, species succeed each other along the season, or they can be active at the same time and compete with each other. Climate change can affect the phenology of species and then the strength of the competition between species.

For phytophagous insects exploiting different plants along the season, or for natural enemies exploiting different host/prey along the season, the success requires the temporal synchronization between the different species. Changes in temperature can modify the degree to which this synchronization occurs. For example, the ant *Iridomyrmex humilis* (Mayr, 1868) (Hymenoptera: Dolichoderinae) is parasitized by several parasitoids which appear successively during the season. The first species is active below 14°C, the followers are active between 14°C and 23°C and the latest species emerges above 23°C. Temperature changes will induce discontinuity or reinforce competition between these species (Folgarait, Bruzzone, & Gilbert, 2003). However, studies at this scale are rare, impairing general conclusions.



4. IMPACT OF HUMAN ACTIVITIES ON PLANT–INSECT INTERACTIONS

4.1 The Main Anthropogenic Drivers Affecting Plant–Insect Interactions

Here, we focus on the ecological and evolutionary effects of anthropogenic factors on plant–insect interactions. We suggest a distinction between two categories of human influences: acts on purpose and acts by accident.

4.1.1 Effects of Human Eco-Engineering

4.1.1.1 Influence of Agrosystems

Agriculture is mankind's great project from the Neolithic Revolution. Creating agro-ecosystems means reducing ecosystems to what is required for the primary production of biomass: an edible plant in a favourable environment. Agrosystems differ from ecosystems in their instability and the high density of plants in monospecific stands. In addition, agrosystems show rapid and contrasting changes of the milieu, at least alternating bare soil and synchronized plant growths. Agrosystems are also characterized by the weakness of physical and chemical defences of plants towards the herbivores (Chen, Gols, & Benrey, 2015).

Agriculture and forestry select pest insects that are adapted to these agricultural conditions, in particular to the abundance and short-time availability of food resources (Bianchi, Booij, & Tscharntke, 2006; Carnus et al., 2006). Insect pests usually combine high fertility and multivoltinism with great voracity and ability to access the crops. These adaptations contribute to a high population growth rate. Half of the million described species of insects are herbivorous. Among them, around 10,000 species are pests (Herrera & Pellmyr, 2002). Pests are rather rare in natural ecosystems (Pimentel et al., 1992) because herbivorous insect populations are generally regulated by the quantity and accessibility of the plants that they exploit. But 'natural pests' exist too. For example, they are represented by crickets (Orthoptera: Acrididae) in dry tropical ecosystems. Pest insects may devastate temperate and Nordic forests, for example the oak processionary, *T. processionea*. Existence of these 'natural pests' can be explained by the similarity between these ecosystems and some agrosystems: shortness of plant growth periods in the dry tropics, homogeneous forest stands over large surfaces in cold regions (Schvester, 1985).

Agriculture causes biogeographical disruptions. Thus, it is a source of sympatric or ecological speciation (Orr & Smith, 1998). Crop plants are established anywhere possible until they become cosmopolitan (wheat, rice, corn etc.). Therefore plant crops come into contact with new insects, and new trophic relationships can take place. Adaptations of insects to new plant hosts are considered as the key mechanism of sympatric speciation. The first case of speciation via host plant shift was described by Walsch around 1860 (Berlocher & Feder, 2002). The fruit fly *Rhagoletis pomonella* Walsh 1867 (Diptera: Tephritidae) shifted from the hawthorn, *Crataegus* sp. (Rosaceae), to the common apple tree, *Malus pumila* (Rosaceae). Agriculture and the transport of plants and insects amplify this type of

diversification. This is probably why examples of sympatric diversification are less observed in natural ecosystems. For example, the European species *Ostrinia nubilalis* (Hübner, 1796) (Lepidoptera: Crambidae) recently split into two sympatric sibling species which eat different wild plants (Malausa, Delacký, et al., 2007; Malausa, Leniaud, et al., 2007).

4.1.1.2 Making Landscapes From Ecosystems

Humans destroy natural habitats to build new anthropized environments, the landscapes. The main ecosystem that was destroyed in Europe was forest (Klemm, 1996, pp. 17–34). In ecology, landscapes are often analyzed as systems deviating from the original ecosystem. They are characterized by their deviation ‘distance’, which integrates the difference between landscape areas (open spaces) and relics of forests (woodlots), or a proportion of wooded areas and the degree of their connections (wooded hedgerows) compared to open spaces. This metric has led to major developments in modelling (With & Crist, 1995), in particular by making the analogy between the fragmented ecosystem and island biogeography (Fahrig, 2003; Ricketts, 2001; Young, Boyle, & Brown, 1996), and by the duality in the landscape between cultivated and uncultivated areas (Carré et al., 2009). However, authors such as Turner (2005) criticized the reference to the original ecosystem, represented by the less anthropic environments, which prevents considering the landscape itself as a new ecosystem (Manel, Schwartz, Luikart, & Taberlet, 2003). Landscapes are more heterogeneous than the original systems. They abound in contact zones between anthropic and semi-natural environments. This is very conducive to the diversification of relations between insects and plants.

4.1.1.3 Urbanization Effects

The urban environment can be considered as an extreme form of landscape, often with no precise boundary between the city and rural landscapes (McKinney, 2002). Even the most densely urbanized areas offer opportunities for spontaneous life which represent, however, small biomass. Small and interstitial habitats (borders, wasteland), and mini-landscapes (parks, cemeteries) and particular niches may host adapted or synanthropic species (commensal or parasitic). Cities are places where cultivated exotic plants abound, although native plants are surprisingly well represented (Frankie & Ehler, 1978; Kühn, Brandl, & Klotz, 2004) despite the difficulty to access soil, water and light. Plant–insect relationships are subjected to the same evolutionary influences than in other anthropized environments, but the communities and ecological

conditions differ. The herbivorous insects that are tolerated by their host plants in natural landscapes become multivoltine pests in urban areas, such as the aphid *Aphis nerii* Boyer de Fonscolombe 1841 on the shrub *Nerium oleander* L. (Apocynaceae) (Frankie & Ehler, 1978).

4.1.2 Evolutionary Responses to Accidental Anthropogenic Drivers

4.1.2.1 The Effects of Non-Intentional Anthropogenic Drivers

Human actions have secondary, not intended outcomes with effects without apparent spatial relationship with their cause. Unintentional disturbances are mainly changes in environmental conditions (pollution, dust, night lighting, urbanization etc.) and community (introductions and depopulation). This phenomenon is best illustrated by the historical example known under the generic term ‘industrial melanism of the peppered moth, *Biston betularia*’. In the 1950s, the British biologist Kettlewell worked on the assumption of an ecological factor of selection specific to industrialized regions and which should favour the black form of the butterfly rather than the white form. He discovered that the mortality of the white form was greatly increased because they were more visible to birds on trees darkened by industrial dust (Grant, Owen, & Clarke, 1996; Howlett & Majerus, 1987).

4.1.2.2 Community Disturbances (Introductions, Population Declines and Species Extinctions)

Species introductions are a worldwide problem. Human activities multiply the transportation of species (Kenis, Rabitsch, Auger-Rozenberg, & Roques, 2007). Symmetrically, we observe populations declining or disappearing, and extinction of species. In Europe, insect introductions accelerated from 4 introductions per year between 1971 and 1990 to 11 between 1991 and 2007, while higher plant introductions decreased from 27 to 18 during the same period (Hulme, Pysek, Nentwig, & Vila, 2009). Part of these taxa settle down on arrival, either through their pre-adaptations or because they are human commensals (cultivated plants and their pests, honeybees etc.). Introduced species have to contest a specific niche to indigenous species, but they take advantage of losing their main competitors in the native ecosystem (Bossdorf et al., 2005). The introduction, however, corresponds to a genetic bottleneck (Estoup et al., 2016). Some herbivore insect populations have a genetic trait that makes them invasive, and sometimes this trait is linked to a single gene (Lee, 2002). Thus, the invasive aphid *Acyrtosiphum pisum* lose the sexual part of its life cycle, thereby gaining the ability to switch to new host plants (Via, 2001).

Species extinction is a major concern in biodiversity conservation. Declines and extinction can trigger concatenated disturbances because of the interdependence of species in ecosystems. It is certainly the case for species associated in the mutualism of the entomophilous pollination (Berenbaum et al., 2006). For example, the decline of wild bees (non-*Apis*) is linked to the decline of some entomogamous flowering plants (Biesmeijer et al., 2006). In Europe, an unknown factor, likely of anthropogenic origin, is widely unfavourable to the biodiversity of pollinators and flowering plants.

4.2 Impact of Pollution on Plant–Insect Interactions

The number of pollutants is high and the plant–insect responses are highly diverse. Here, we address the major common characteristics that govern the bottom-up (host plant quality) and the top-down (natural enemies) processes that influence the fitness and population dynamics of herbivore insects. Inorganic and organic pollutants include air pollutants such as ozone, sulphur oxides (SO_x), nitrogen oxides (NO_x), carbon oxides (CO_x), fluorides and acidic precipitations, as well as soil pollutants such as metalloids and heavy metals (Butler & Trumble, 2008). Pollutants are more or less toxic to the environment according to their chemical composition, and this toxicity depends on the dose (concentration \times time) (see Calatayud et al., 2013 for review). Indeed, pollutants can have more impact on the environment when applied for a short period than when they are present for a long time, at equal dose. In plants, this peak effect is explained by plant response time relative to the pollutant residence time: plants do not have time to initiate their defence systems towards pollutants.

After penetration of the pollutant into plant tissues via the stomata or the roots, the pollutant generates a stress, such as oxidative stress for oxide pollutants and disturbance of calcium metabolism in the case of fluorides pollution (Calatayud, Garrec, & Nicole, 2013). Classically, the plant limits the absorption of pollutant and increases tolerance to it by implementing physical processes (e.g., stomatal closure, falling leaves) as well as chemical and biochemical processes (e.g., production of insoluble precipitates, enzymatic degradation by P450). The plant resistance to pollutants depends on the combination of the defence mechanisms already present in plant tissues and the defence processes that the plant can activate after the stress occurs. Resistance, however, also depends on other abiotic factors (e.g., temperature, humidity, light) and biotic factors (e.g., age, disease, genotype), which can have positive or negative impacts on plant response to air and soil pollution. In situ, there is generally an increase in insect populations

on plants in polluted areas through both bottom-up and top-down processes (Hain, 1987).

4.2.1 Bottom–Up Effects of Pollution

Pollutants have a crucial impact on the key parameters of plants that govern plant–insect relationships by changing the physiology and the biochemistry of plant tissues (Nicole, 2002). In particular, pollutants alter the parameters related to recognition by insects, nutritional quality and plant defences.

4.2.1.1 Location and Recognition of Plants

Pollutants can cause changes in the colour of plants, thereby influencing the colour of associated insects. The most famous example was reported above by the melanism mutation in British peppered moths during the industrial revolution and recently shown to be due to a transposable element (van't Hof et al., 2016). In addition, pollutants disrupt the chemical communication in plant–insect relationships. In general, the alteration of VOCs emission occurs in polluted plants, impacting orientation behaviour in herbivore insects (Blande, Holopainen, & Ninemets, 2014). Pollutants act on the plant physiology (e.g., limiting volatile emissions by stomatal closure, modifying the plant physico-chemical characteristics), or by direct degradation of VOCs in the air.

4.2.1.2 Nutritional Quality of Plants

Accumulations of toxic pollutants in plant organs such as heavy metals, arsenic and fluorine are often the cause of poisoning of plant-eating insects (Führer, 1985). In addition, pollution leads to changes in primary and secondary metabolites in plants. In particular, there is often an increase in leaf concentration of amino acids (proline), soluble protein and sugars, thereby increasing the nutritional quality of plants for insects (Kainulainen, Holopainen, & Holopainen, 2000; Warrington, 1989). Indeed, pollutants such as SO₂ and NO_x increase the concentrations of S and N in plants, with positive effects on insects. This is especially true for plants on roadsides which are major sources of NO_x (Bolsinger & Flückiger, 1987; Braun & Flückiger, 1985). But conversely, CO₂ pollution associated with NO_x leads to lower nitrogen concentrations in leaves with negative consequences for herbivore insects (Bezemer & Jones, 1998; Hättenschwiler & Schafellner, 1999). Heavy metals have in general a negative impact on the fitness of herbivores (Butler & Trumble, 2008).

4.2.1.3 Changes in Chemical and Physical Plant Defences

If secondary compounds (e.g., phenolic compounds) are part of the chemical defence systems of plants, the cuticle in turn becomes an effective barrier to insects. Pollutants such as ozone and CO₂ induce oxidative stress, and are the source of increased concentrations of phenolic compounds in plants with a negative impact on the nutritional quality of leaves for insects (Bolsinger, Lier, & Hughes, 1992; Bolsinger, Lier, Lansky, & Hughes, 1991). Meanwhile, ozone and elevated CO₂ promote the production of cuticular waxes, improving the characteristics of the physical barrier of the cuticle (Percy et al., 2002). In addition, the fitness of herbivores declines when they feed on plants contaminated by metalloids such as selenium and fluoride (Butler & Trumble, 2008).

4.2.2 Top–Down and Guild Effects of Pollution

Little is known about the impacts of pollutants on natural enemies, compared to herbivore insects. Butler and Trumble (2008) highlighted likely trends of pollution effects on insect parasitoids, predators and pathogens. The most common responses were either no effects or negative effects on natural enemies. This was reported in environments with elevated CO₂, ozone, heavy metals, metalloids and acidic precipitation. Butler and Trumble (2008) found that foliage feeders and miners often exhibit negative responses to pollutants through bottom-up process in CO₂ and heavy metal enriched environments. By contrast, phloem feeders exhibit greater fitness in environments polluted by SO₂ and NO₂. No conclusive pattern of pollution effects on bottom-up or top-down processes can be done on xylem feeders, mesophyll feeders, seed feeders and galls; and no information is available on the fitness of borers, root feeders and, more surprisingly, pollinators (Butler & Trumble, 2008).



5. CONCLUSION AND PERSPECTIVES

The complex interactions between direct and indirect effects of global change makes particularly difficult to predict its net impact on plant–insect relationships (Fig. 1). The complexity of the mechanisms at play combines with the extreme level of diversification of life-history traits in both plants and insects. For example, insects demonstrate a high diversity of feeding modes which transposes into a high variability of plant eco-physiological responses to herbivory (Welter, 1989). Another layer of variability should be expected on the effects of global change on these specific plant responses,

as reflected by the difficulty to generalize on the impacts of temperature and CO₂ on insect herbivores (Zvereva & Kozlov, 2006). Therefore, it seems illusive to extract a single general scheme depicting the net effect of global change on plant–insect relationships.

The intricate network of direct and indirect impacts of global change on plant–insect relationships is probably even more complex than it seems because several influential processes are still understudied. For example, the biochemical pathways of heat tolerance in plants are relatively well understood (Wahid, Gelani, Ashraf, & Foolad, 2007), but it remains to elucidate if these paths interconnect with the chemical machinery involved in plant defences against herbivore insects. A link can be expected because several molecules and chemicals are involved in the two processes, such as abscisic and salicylic acids, ethylene or phenolic compounds like flavonoids. In addition, pollutants may modulate these links between plant heat tolerance and plant defences. Pollutants decrease the ability of insects to tolerate heat (Slotsbo et al., 2009), but it is not clear if the same effect applies to plants.

Urban systems may provide good models to study these complex relationships because trophic webs are simplified, and also because cities may simulate the future abiotic conditions for natural habitats (Youngsteadt, Dale, Terando, Dunn, & Frank, 2014). Urban areas are often warmer and drier on average compared to natural ecosystems (Oke, 1982). The spatial heterogeneity in surface temperature in urban zones can be used as a ‘laboratory’ to study climate change impacts on the behaviour of insects (Pincebourde et al., 2016). Given the numerous stressors experienced by plants in cities, it seems appropriate to explore the complex links between plant tolerance to heat and drought, plant defences to herbivores and emission of VOC by plants in cities. However, we are not aware of such studies. Recently, it was observed that scale insects were more abundant on trees in cities as a direct effect of the urban heat island (Youngsteadt et al., 2014), suggesting that tree species may be less protected from pests in urban areas.

Nowadays, humans develop methods to increase the resilience of plant–insect communities to global changes, in particular in the agronomic context. Among them, the Conservation Biological Control (CBC, see Chapter 10 for a review) increases the efficiency of natural enemies and decreases the impacts of pests through modification of the environment (Eilenberg, Hajek, & Lomer, 2001). The success of the CBC, however, requires good knowledge of the plant–insect interactions. Several studies have shown that more diverse plant communities are functionally less susceptible

to environmental stress (Stuedel et al., 2012). This emphasizes the need to maintain biodiversity as an insurance against impacts of changing environmental conditions and sets the stage for exploring the mechanisms underlying biodiversity effects in stressed ecosystems. Indeed, biodiversity has unique effects such as complementarities and redundancies among species, dilution of plant species, or improving the stability of food webs (McCann, 2000; Naeem, 1998). Higher plant diversity, through association of plant species supplying alternative food and/or shelters at different seasons of the year, can increase the performance and fitness of natural enemies (Bompart, Jaworski, Bearez, & Desneux, 2013; Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012) thus increasing their resistance to climate stresses. More diverse vegetation can promote associational resistance of host plants. This associational resistance may result from dilution of (plant) hosts for insect herbivores and from a complementarity of (insect) hosts for phytophagous-enemies, as well as a redundancy among these phytophagous-enemies. This hypothesis will be particularly important for plants whose defences are weakened by climate stress. Alternatively, the associational resistance may emerge from a decrease in climate resistance of herbivores (e.g., delayed phenology of their host plants) and an increase in climate resistance of phytophagous-enemies (e.g., climate shelters, nectar). This hypothesis will be particularly important for phytophagous insects and phytophagous-enemies under climate stress.

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