

1 Impact of Climate Change on Macro-Organisms Used in Biological Control

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Abstract

Contemporary climate change has many effects on the behaviour, physiology, ecology and evolution of the macro-organisms involved in biological control, as well as on the pests themselves. In temperate zones, for example, global warming may increase the number of generations and improve winter survival, but responses to temperature changes, particularly in ectotherms, are highly variable from species to species, making it very difficult to draw global conclusions, whether about pests or beneficial macro-organisms. From an interspecific point of view, differential rates of reproduction and frequent phenological mismatches are also observed. The ecological impact of climate change varies with latitude: in warm tropical zones, annual thermal variations are less pronounced and ectotherms have generally evolved with little seasonal variability. As a result, in the face of global warming, it is now often postulated that tropical ectotherms are more vulnerable than their temperate counterparts, as they are often already close to their physiological optimum. This chapter attempts to discuss the validity of these assertions.

1.1 Introduction

A wide range of definitions are used for the concepts of climate change and biological control. Two of these seem particularly noteworthy: (i) climate change: 'A change of climate that is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and that is in addition to natural climate variability observed over comparable periods' (Ingram and Hamilton, 2014) (ii) biological control: 'The use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be' (Eilenberg *et al.*, 2001). On the other hand, it can paradoxically be difficult to describe what a

macro-organism used in biological control is, and it is often the precise definition of what a micro-organism is that makes it possible, as it were by difference, to define a macro-organism. For example, we can consider that micro-organisms are represented by unicellular or multicellular entities, i.e. bacteria, algae, protozoa, fungi and viruses, and that macro-organisms make up the rest of the living world (Amsellem *et al.*, 2017). As a result, the list is long and varied, e.g. nematodes that parasitize insects, beneficial insects (parasitoids, predators), predatory mites and even some species of predatory birds and bats. Parasitoids will be referred to frequently in this chapter. A size criterion can also be used, with macro-organisms larger than 500 µm (Tesson *et al.*, 2015). In this chapter, only the use of

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macro-organisms will be considered among living organisms. Macro-organisms are under the control of temperature for their activity, reproduction and development, even if certain environments they occupy (e.g. soils) partially buffer this effect of temperature (Cock *et al.*, 2013).

On another note, it would be a mistake to think that the influence of weather and climate on macro-organisms (particularly insects) used in biological control is a recent field of study. Long before the concerns associated with climate change, the relationship between insects and climate was studied in detail, as in the seminal work by Uvarov (1931). In this 232-page synthesis, Boris Uvarov discussed the various abiotic factors influencing insect life, including the combination of several factors (e.g. temperature and humidity). The final section of this review was already considering the links between weather, climate and economic entomology.

Although we now know that rising temperatures date back to the beginning of the industrial era (see for example Abram *et al.*, 2016), awareness of the consequences of climate change – mainly global warming and changes in climate variability – has been slow and gradual (cf. creation of the United Nations Environment Programme in 1972, IPCC first Assessment Report completed in 1990). Interest in biological control thus preceded in-depth study of the ecological consequences of climate change. Since then, the study of interactions between climate change and biological control, i.e. the responses of macro-organisms to global warming and the limits of these responses – has become a very active field of investigation. The importance of climate change, but also of habitat fragmentation, for the evolution of species interactions and communities functioning is therefore now well documented, and today there is a broad consensus ‘that species respond individually to climate change, not as coherent communities’ (Lovejoy and Hannah, 2005). Although rising temperatures are the most commonly perceived phenomenon, climate change encompasses several other phenomena that interact with each other, discussed first in this chapter. Moreover, climate change is expressed differently when we consider latitudinal and altitudinal gradients. This is the subject of the second part of this chapter. The aim of this

chapter is consequently to briefly describe these features with the help of review articles and multi-authored books, including some very recent ones.

1.2 Climate Change is Not Just About Higher Temperatures

For over 20 years, most textbooks documenting the ecophysiology of ectotherms – and insects in particular – have included a section or chapter devoted to the responses of macro-organisms to current environmental change (e.g. Chown and Nicolson, 2004; Angilletta, 2009; Denlinger and Lee, 2010; Storey and Tanino, 2012; Kang and Banga, 2013; Björkman and Niemelä, 2015; Lehmann *et al.*, 2020; Ma *et al.*, 2021; see also Pareek *et al.*, 2017; Yadav *et al.*, 2019; IPCC Secretariat, 2021). In addition, two recent, well-documented reviews focus on the impact of climate change on agricultural insect pests (Skendžić *et al.*, 2021a, b; Fig. 1.1). Still more recently, a number of papers, book chapters and books have been published about the influence of climate change on pest ecology and the consequences for pest management (Masood *et al.*, 2022; Srivinas Rao *et al.*, 2022; Eickermann *et al.*, 2023; Gvozdenac *et al.*, 2023; Subedi *et al.*, 2023; Ali *et al.*, 2024; Contosta *et al.*, 2024; González-Tokman and Dáttilo, 2024; Liao *et al.*, 2024; Mandal, 2024; Ramesh *et al.*, 2024; Rosace *et al.*, 2024; Şirin and Taylan, 2024; Siva *et al.*, 2024), reflecting growing concerns in this area. Moreover, until recent years, the historical development of integrated pest management (IPM) had mainly been marked by work carried out by teams from the European Community, Switzerland, UK, Canada and USA. It should be pointed out, however, that of the 14 references cited above for the 2022–2024 period, four were from India, two from Pakistan, and one each from Mexico, Serbia and Turkey. This trend is indicative of the consequences of the globalization of trade and travel (Dara, 2019), but also in raising awareness of environmentally friendly solutions to past and present pest control problems.

From all these studies emerges a complex interweaving of climatic and atmospheric factors which together constitute ‘climate

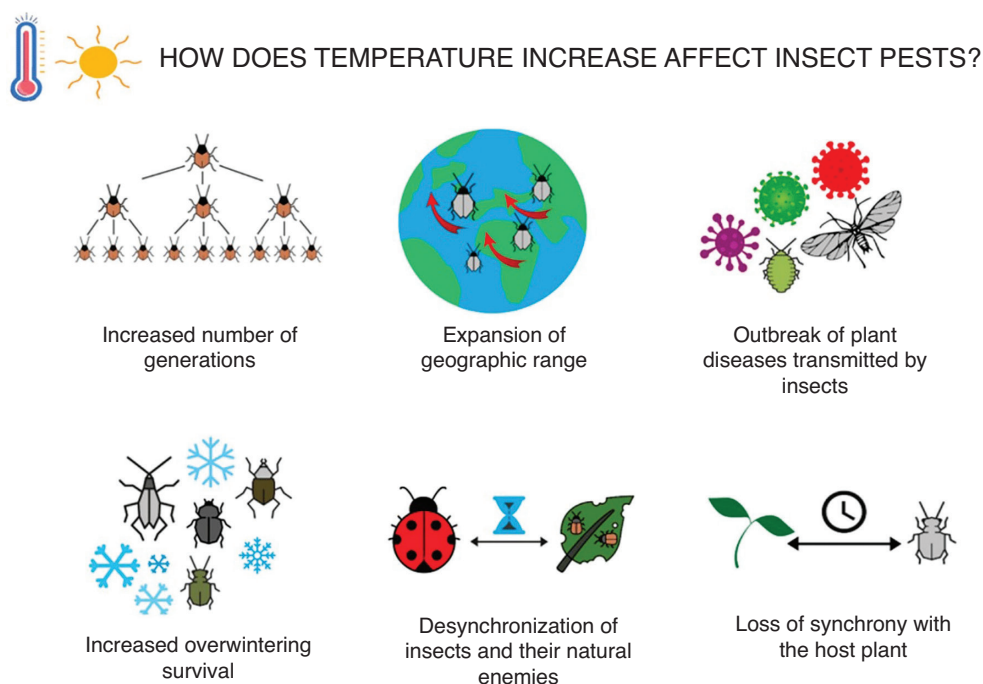


Fig. 1.1. Effects of temperature rise on agricultural insect pests. Reproduced with permission from Skendžić *et al.* (2021a) and Darija Lemić, 2025.

change'. These multiple elements can be grouped into four main components: rising temperatures (e.g. winter warming more pronounced than summers, increased thawing of ice and snow), rising atmospheric carbon dioxide levels (one consequence is the increase in leaf carbon to nitrogen ratio with cascade effects in tritrophic interactions; Dyer *et al.*, 2013), more variable precipitation patterns (changes in water availability and humidity patterns, droughts more pronounced at low latitudes), and an increase in the frequency of extreme climatic events, e.g. increased heavy precipitation periods, increased occurrence of heat waves, with heat stress consequences for host–parasitoid interactions (Wetherington *et al.*, 2017; Malinski *et al.*, 2024). It must be stressed that there is a great deal of geographical variability in the expression of sensitivity to these types of climate change. For example, the Arctic and the Alps are considered as faster warming places (cf. e.g. higher snowmelt rates, lower snow albedo values).

The impact of climate change on the potentialities of macro-organisms used for

biological control is both temporal and spatial. On a temporal level, phenological shifts are increasing, affecting, for example, species interactions (Tougeron *et al.*, 2018). These phenological mismatches have been described in detail by Forrest (2016), Buckley (2022) and Ma *et al.* (2024). Spatially, range shifts are now commonly observed, particularly with poleward movements or towards higher altitudes. It is beyond the scope of this chapter to provide exhaustive information in this latter area, as research – at the crossroads of environmental and economic imperatives – is growing rapidly. Information can be found in large reviews and books listed above (e.g. Björkman and Niemelä, 2015; Skendžić *et al.*, 2021a; González-Tokman and Dáttilo, 2024). A recent review (Ramos Aguila *et al.*, 2023) also highlights the particular importance of both phenological shifts and significant population movements to higher altitudes and the consequences of warmer winters. Here, we will focus mainly on the host–parasitoid systems, parasitoids being more and more used in biological control.

1.3 Climate Change Affects the Distribution and Seasonal Ecology of Parasitoids

A parasitoid can be defined as 'an organism which develops on or in another single ('host') organism, extracts nourishment from it, and kills it as a direct or indirect result of that development' (Eggleton and Gaston, 1990). It should be noted that this definition is not 'taxonomically restricted' to the Insect class, but while parasitoids can be nematodes, fungi, protists, bacteria or viruses (Eggleton and Gaston, 1990), the majority of those studied and recorded are insects belonging to the order Hymenoptera (Boivin *et al.*, 2012). Parasitoid wasps are an essential component of food webs in terrestrial ecosystems, with pervasive effects on community structure and diversity. Indeed, these insects have a strong influence on the abundance and dynamics of a range of host populations, exerting top-down control (Godfray and Shimada, 1999; Mills, 2009; Fei *et al.*, 2023). These features make them an effective and well-established tool in biological control programmes. However, the quality of parasitoids may be severely disrupted by climate change, particularly by increasing the amplitude and frequency of temperature variations (Hance *et al.*, 2007; Furlong and Zalucki, 2017). Indeed, each stage of the parasitoid's life cycle is critical and can be influenced by ambient temperature, whether it is host location, host stage selection, egg deposition or larval development through to adult emergence. In addition, the assessment of host quality plays a crucial role in the selection of parasitoids and sex allocation. Offspring development is limited to a finite quantity of resources contained within the host. This can profoundly affect parasitoid traits such as size, maturity, fecundity, sex ratio and longevity (Roitberg *et al.*, 2001; Pekas *et al.*, 2016), with repercussions evident in the context of biological control. This resource limitation can be directly modulated by external factors that influence the interaction between parasitoids and host populations (Fei *et al.*, 2023) but also, as we will discuss later on, by the host microbiota (Ras *et al.*, 2017).

Parasitoid wasps face a heterogeneous environment, including patchy host distribution. As they are usually short-lived, they manage their

time and energy efficiently to maximize their fitness (Charnov, 1976; van Alphen *et al.*, 2003). In a complex landscape, a variable range of host species is present, and parasitoid species tend to exhibit two distinct strategies for host exploitation: generalization vs specialization. The adage 'jack of all trades, master of none' suggests that specialist and generalist parasitoid species respond differently to environmental conditions, as host aggregation can potentially mitigate the spatial mismatch caused by warming (Straub *et al.*, 2011; Ramos Aguila *et al.*, 2023). Under increasing and fluctuating conditions, a shift in host distribution towards more suitable areas may be followed by a shift in parasitoid distribution. Recently, Li *et al.* (2023) elegantly tested this hypothesis; they used climate change simulations and knowledge of ecological niches to predict shifts in the distribution of four cereal aphid species (*Sitobion avenae*, *Rhopalosiphum padi*, *Schizaphis graminum* and *Diuraphis noxia*) and their three natural enemies (*Harmonia axyridis*, *Episyrphus balteatus* and *Aphidius gifuensis*) in China. Based on different scenarios, the range of *D. noxia* but also of *E. balteatus* and *A. gifuensis* would be reduced, whereas the range of the other three aphids would be expanded. Furthermore, under the high greenhouse gas emissions scenario for the period 2081–2100, all aphid species except *D. noxia* would move to higher latitudes and altitudes, with an increase in niche overlap between the three aphid species. This spatial expansion to higher altitudes would be less important for *A. gifuensis*. Furthermore, this specialist species shows a reduction in aphid suppressive capacity at higher temperatures, in contrast to the generalist predator *H. axyridis* (Li *et al.*, 2023). This dispersal capacity thus appears to be much greater for a generalist enemy, which can be satisfied with a wider choice of hosts and the benefits of an appropriate microenvironmental temperature.

In addition to the spatial aspect, the temporal synchrony of species during periodic seasonal events provides critical structure and stability for species interactions. Understanding the changing phenology of parasitoid species and their hosts due to climate change is crucial for biological control programmes (Boukal *et al.*, 2019). The close interaction between the parasitoid and its host is based on the optimal overlap of developmental stages, and therefore the range

of traits suitable and available for interaction. For example, parasitoids tend to select hosts with specific developmental stages to ensure ideal growth and development of their larvae (Vieira *et al.*, 2019). Changes in temperature, and thus developmental time, alter the host's window of vulnerability to the parasitoid, resulting in a temporal mismatch (Tougeron *et al.*, 2020). Phenological asynchronies between parasitoids and hosts are thus frequently observed, linked in particular to the differential physiological responses of each partner to abiotic conditions, in particular the temperature. A frequently encountered situation is that the host may complete its cycle earlier in the year, before the emergence of adult parasitoids capable of attacking it, with a consequent reduction in the effectiveness of biocontrol. In Canada, this is the case for *Choristoneura fumiferana* (Clemens, 1865) (Lepidoptera: Tortricidae) (Fleming and Candau, 1998; Kocsis and Hufnagel, 2011). However, this pattern is influenced by the variability of parasitoid development times, which may be sufficiently wide to ensure partial or complete synchronization of parasitoid emergence and host presence (see for example Régnière *et al.*, 2020; Tougeron *et al.*, 2020). For *Drosophila sulfurigaster* and *D. birchii* and their parasitoids *Asobara* sp. and *Ganaspis* sp., warming reduces the persistence of the *Drosophila*–parasitoid interaction due to a delay in parasitoid emergence. However, in a community context, the presence of an alternative host may buffer these negative effects (Pardikes *et al.*, 2022). Other studies have highlighted the effect of mild winters on the diapause strategies of parasitoids. Aphid parasitoids with relatively low cold tolerance, such as *Aphidius avenae* and *A. ervi*, must enter diapause in winter, while other species, such as *A. matricariae* or *A. rhopalosiphii*, remain present due to their cold tolerance (Le Lann *et al.*, 2011). With the increasing occurrence of mild winters, diapause is no longer selected for in *A. avenae*, while at the same time an increase in host availability is observed, leading to higher parasitoid activity. Once *A. avenae* is present, it displaces the other species in the winter guild because of the positive effect of higher temperature on this species, while other overwintering species still undergo diapause (Andrade *et al.*, 2016). Within the same season, changes were observed for over 40 years for parasitoids of the

genus *Aphidius* with a change in their overwintering strategy that may result in a modification in community structure (Tougeron *et al.*, 2018; Alford *et al.*, 2020). The effect of warming on temporal mismatch in host–parasitoid interactions is often underestimated and poorly supported because it deals with the complexity of community interactions with multiple abiotic and biotic variables. Spatial and temporal mismatch are two responses that determine population dynamics and community structure, and both can destabilize host–parasitoid interactions, reducing top-down control and leading to a relaxation of phytophagous pest pressure. These are crucial aspects to consider for biological control in a context of climate change.

1.4 Climate Change Affects Various Physiological Parameters During the Life Cycle of Natural Enemies

Before they became pests (mainly due to the intensification of agricultural practices), natural enemies were already regulating phytophagous species. Today, the emphasis is on the detailed study of trophic levels, particularly in the context of predator–prey and/or parasitoid–host interactions. While it is true that the host and parasitoid develop more rapidly under higher temperature conditions, the hosts generally have a higher thermal limit than their associated parasitoid species (Furlong and Zalucki, 2017). Extreme temperatures associated with global warming can have a range of physiological impacts that can interfere with the life cycle of parasitoids, with consequences for the effectiveness of biological control programmes. The lifetime reproductive success of parasitoids mainly depends on host availability and the availability of mature eggs, but also on other factors such as sperm quantity and quality. Parasitoid wasps are haplodiploid, meaning that sperm stored by egg-laying females is used only to produce daughters. Thus, the sex ratio of offspring depends on the availability of sperm after mating. Bressac *et al.* (2023) have shown that the male of the parasitoid wasp *Cotesia typhae* produces significantly fewer sperm when exposed to 34°C during the pupal stage, resulting in fewer female offspring. This means that high

temperatures could reduce the performance of biological control programmes by interfering with parasitoid reproduction.

Oviposition is a sensitive moment in parasitoid reproduction; its success is dependent on host defences and how the parasitoid can overcome them. Trotta *et al.* (2018) reported that heat shock reduces the success of parasitism by *Aphidius ervi* and therefore increases the chances of survival of the pea aphid *Acyrthosiphon pisum* hosts for each instar. According to the authors, aphid survival can be explained by three hypotheses, one of which is a direct effect and the other two indirect effects on the success of *A. ervi*. (i) The venom and ovarian proteins injected during oviposition lose their efficacy, leading to a reduction in stress for the host (Digilio *et al.*, 2000; Shim *et al.*, 2008); (ii) the immune system, once activated, increases the survival rate of the aphids (Martinez *et al.*, 2016); (iii) there is an adaptation to extreme temperature conditions during the nymphal instars, due to the sedentary moment of this instar compared to the adult stage. The first hypothesis requires further investigation, as it has been shown that under high temperatures, the composition of the venom changes (Cavigliasso *et al.*, 2021), but little is known about the impact of temperature on parasitoid venom functioning. In contrast, the separate application of temperature and drought as abiotic parameters seems to negatively impact the life-history traits of the cabbage aphid *Brevicoryne brassicae*, but not the parasitoid *Diaeretiella rapae*. In line with this, these two parameters induce a decrease in the growth rate of aphids without the presence of parasitoids but decrease the longevity of this one. As for the parasitoids with temperature as a parameter, emergence success is positively impacted despite a low number of offspring for the temperature whereas with drought, the number of offspring is high with no real difference in emergence chances (Romo and Tylianakis, 2013). From the various studies carried out, it is apparent that climate change will directly or indirectly affect host–parasitoid interactions. The response of the two players will depend on the species involved and its biological and ecological functions. It is also important that the application of both abiotic and biotic conditions be adequately considered to provide a clear and concise assessment. This will enable the

conditions influencing the interaction between the parasitoid and the host to be reproduced as accurately as possible. Moreover, the combination of adaptive phenotypic plasticity and evolutionary adaptations enables ectotherms to cope with predictably fluctuating temperatures. But when environmental conditions become unpredictable and/or extreme, bet-hedging – i.e. phenotypic diversity in unpredictable environments – can be an indispensable alternative (Le Lann *et al.*, 2021; Costaz *et al.*, 2023; van Baaren *et al.*, 2024).

A brief overview of the impact of warmer temperatures on ectothermic organisms, focusing mainly on insects, allows us to see that these consequences can be variable in their amplitude according to their environment, in particular along latitudinal or elevational gradients, depending on whether the species considered are more or less close to their thermal tolerance limits. A first indication to consider is the rate of change of climatic parameters, and in particular temperature parameters, that vary according to the ecosystems involved. These variables are then compared with the differential capacity of the ectothermic species studied to withstand (or not) these climatic changes. In thermal biology, a dual methodological requirement should also be promoted as far as possible: measurement of heat tolerance and assessing the impact of climate change on life-history traits.

- i. To measure heat tolerance, dynamic methods (ramping temperatures giving access to the critical thermal maximum, CT_{max}) are often to be preferred to static methods which operate at constant temperatures giving access to the survival rate (Herrando-Pérez *et al.*, 2023; see also Ørsted *et al.*, 2022 about the inclusion of both intensity and duration of thermal stress). For both high- and low-temperature tolerance measurements (critical thermal minimum, CT_{min}), it is important to precisely define the methods used, especially when taking comparative approaches (Terblanche *et al.*, 2011). In addition to this, Gunderson and Stillman (2015) emphasize that ectotherms ‘have relatively low acclimation in thermal tolerance’ and in insects, Weaving *et al.* (2022) show that CT_{max} is significantly less plastic

than C_{min} and that critical thermal limit plasticity is reduced overall. The latter authors add that, as a result, many insect species will have to rely on changes in their distribution range and behaviour to cope with the effects of climate change.

- ii. In order to assess the impact of climate change on life-history traits, it is not possible to simply take into account average values for climatic variables, as is still often the case. Living organisms are subject to fluctuating temperatures, e.g. daily temperature variations of varying intensity, depending on the season and geographical location (Colinet *et al.*, 2015). For example, Paaïjmans *et al.* (2013) suggest that fluctuating temperatures may alter sensitivity to climate warming by reducing thermal safety margins. The prevalence of significant thermal heterogeneities is also a plea for the use of microclimatic approaches, in phase with the fine localization of the species studied (Pincebourde *et al.*, 2016). In the same vein, Chevalier *et al.* (2024) warn of the limitations of combining measurements of physiological thermal limits with macroclimatic data. In addition, it is essential to stress that ‘the effects of chronic and acute thermal stressors are amplified when they act in combination’ (Pilakouta *et al.*, 2024; see also Verheyen and Stoks, 2019).

The consequences of an increase in temperature on the life-history traits of an ectothermic macro-organism are multiple and interrelated. These include acceleration of developmental time and reduction of generation time (e.g. Buckley *et al.*, 2017), the almost general reduction in body size through the phenotypic plastic temperature–size rule (Atkinson, 1994; Ohlberger, 2013), a reduction in life expectancy through accelerated ageing (e.g. Burraco *et al.*, 2020), and increase in metabolic rate (e.g. Dillon *et al.*, 2010). It should be noted that peaks in metabolic performance are observed with this optimal temperature, but also with body mass and latitude (bearing in mind that optimal temperature decreases with latitude) (DeLong *et al.*, 2018). This leads these authors to say that ‘hotter is better’ at low latitudes and that ‘colder is better’ at high latitudes. Despite

small temperature increases in tropical environments (compared to those observed in temperate environments), Dillon *et al.* (2010) indicate that tropical ectotherms are currently undergoing large increases in their metabolic rates, which may contribute to their vulnerability to climate change (e.g. increased food requirements leading to higher rates of phytophagy or predation).

However, the development of these predictive scenarios should not be focused on the thermobiological approach alone (Kellermann and van Heerwaarden, 2019). Indeed, the complementary integration of traits associated with stress, fitness and phenology is a necessity, so as to better access the plastic and genetic responses of the traits under consideration (see, for example, Kumar *et al.*, 2024). In this context, ‘incorporating adaptation into models of climate change resilience is essential for predicting how species will respond under climate change’ (Kellermann and van Heerwaarden, 2019). It is therefore essential to simultaneously consider the responses to fluctuating temperatures and abiotic stressors (Harvey *et al.*, 2020). Finally, as convincingly detailed by Kingsolver *et al.* (2011), it is also important to remember that the life cycles of macro-organisms are often complex, with life stages developing in different microhabitats with frequently contrasting abiotic conditions. These life stages can therefore differ in their ability to respond to the microclimates in which they develop, whether in terms of the survival of juvenile stages or the reproductive capacities of adult stages.

1.5 Temperate vs Tropical Species: Is Janzen’s Mountain Passes Hypothesis (1967) Still Relevant Today?

The high diversity of species in tropical zones could be *a priori* associated with a greater abundance of parasites, but it should be pointed out that despite the high species richness of tropical lepidopterans and coleopterans, the same is not necessarily true of their parasitoids, as in the case of the underrepresentation of Ichneumonidae in the tropics. An underrepresentation of potential hosts, such as aphids, in tropical zones can also

lead to a reduction in the number of parasitoid species (Godfray *et al.*, 1999).

In order to shed light on the diversity of situations observed, it is necessary to understand whether tropical environments could select species differently. In this context, Janzen's mountain passes hypothesis (1967) is an essential tool for combining past and present ideas on ecology, physiology and climate change.

Janzen's hypothesis predicts that tropical habitats with low seasonal variation in temperature would select for species with narrow thermal tolerance breadth (the difference between critical thermal maximum and minimum), which may imply a low acclimation ability and consequently a low dispersal ability along elevational – or, more generally, environmental – gradients. On the other hand, temperate habitats have greater seasonal temperature variations, species with a wider thermal tolerance breadth, a greater acclimation ability and a greater dispersal ability. For over half a century, this comparative approach between tropical and temperate environments has given rise to numerous uses and interpretations, and a number of review papers provide a better understanding of these developments (e.g. Ghalambor *et al.*, 2006; Sheldon *et al.*, 2018).

At first sight, it may seem paradoxical that ectothermic tropical species are particularly sensitive to global warming, even though they are currently subject to slight increases in temperature, but this will especially be the case for tropical species which occupy low altitude, thermally homogeneous environments (variance in spatial temperature broadly similar to variance in seasonal temperature), and which are not very well adapted for even small increases in temperature as they are already close to their optimal temperature (Deutsch *et al.*, 2008; Bonebreak and Deutsch, 2012). It should therefore be emphasized that tropical insects are closer to their lethal temperature than temperate insects, even though global warming is less pronounced in the tropics. This low thermal safety margin can be estimated using a measure of heat tolerance, in the form: [critical thermal maximum – current climatological temperature of the habitat = warming tolerance] (Deutsch *et al.*, 2008). Therefore, and even if mitigation capacities exist (acclimation, behaviour, dispersal), 'the greatest extinction risks from global

warming may be in the tropics, where biological diversity is also greatest' (Deutsch *et al.*, 2008). However, this assertion needs to be modulated if we look closely at the spatial variations in temperature that exist within the range of a given species. The existence of these thermal gradients may increase thermal tolerance. This shows that taking into account this spatial dimension (topography) is complementary to the temporal dimension (seasonality) (Bonebreak and Deutsch, 2012).

Among the geographical gradients, latitudinal and altitudinal gradients have been the subject of many studies (much more than longitudinal gradients), and the specific features of each gradient have been described by Jégo *et al.* (2023). Janzen's hypothesis combines latitudinal and altitudinal gradients (Janzen, 1967). In this era of global warming, whether we are talking about tropical or temperate environments, it is not enough to deal only with warming tolerance, and it is more informative to consider both upper and lower thermal tolerance (Sunday *et al.*, 2011, 2019). Taking into account the thermal limits of a species as a function of the temperatures to which it is exposed in the field is also an opportunity to establish a link between Janzen's hypothesis and the climate variability hypothesis (CVH) which proposes that the low magnitude of temperatures observed in the tropics is associated with a narrow window of ectotherm thermal tolerance, the opposite being proposed for temperate environments (Stevens, 1989). The CVH was later extended in the approach developed by Pither (2003), which emphasizes the importance of taking into account the most extreme values of the climate variables (climate extremes hypothesis, CEH). A detailed approach to understanding the consequences of extreme weather events has been developed by Kingsolver and Buckley (2017). These extreme climatic events (whose frequency is increasing) now play a major role in the evolution of ectotherms' thermotolerance (Sunday *et al.*, 2019).

When studying thermal tolerance width, i.e. the difference between the critical thermal maximum and minimum, it is important to consider that there is a fundamental dissymmetry between upper and lower temperature data. Indeed, Addo-Bediako *et al.* (2000) have clearly shown that the upper thermal limit

varies little with latitude, whereas lower lethal temperatures (and supercooling points, i.e. the lowest temperature to which an ectotherm may be cooled before it freezes) decrease with latitude. This heat-invariant hypothesis (low heat tolerance variability), and its counterpoint the cold variability hypothesis (high cold tolerance variability) have since been the subject of numerous studies, in latitudinal and altitudinal contexts, leading to the same conclusions (e.g. Bozinovic *et al.*, 2014; Bovo *et al.*, 2023).

Climate warming is affecting temperate regions. Interestingly, this is an opportunity to use studies already carried out in tropical regions, where temperatures are naturally higher and where species are closer to their tolerance thresholds (Cock *et al.*, 2013). In this context, it should be noted that the upper temperature limits vary much less than the lower thermal limits, resulting in a limited ability to change thermal limits during seasonal or annual warming phases (Hoffmann *et al.*, 2013). This confirms that the common status of thermal specialists for tropical taxa makes them highly vulnerable to climate change (see also Chan *et al.*, 2016), to the extent that ectotherms often have to resort to subtle behavioural adaptations and search for favourable alternative habitats in order to survive global warming (Sunday *et al.*, 2014). However, this near consensus had been discussed by Kingsolver *et al.* (2013) and convincingly challenged by Johansson *et al.* (2020) who state that 'temperate species have considerably narrower safety margins to warming than suggested by several earlier analyses' due to the frequent failure to consider length and timing of activity periods across latitudes. It must be added that even if seasonal temperature changes are reduced in the tropics, this does not mean that there are no seasonal weather patterns, and the existence of rainy and dry seasons is also subject to global warming (shorter wet seasons, longer dry seasons) (Clusella-Trullas *et al.*, 2011; Guo *et al.*, 2022).

Elevational gradients are often used as a proxy for climate change and in that context, information about species richness and food web structure depending on altitude is useful (Maunsell *et al.*, 2015). These authors show that phytophagous organisms and parasitoids may have different responses depending on altitude, which leads to host-parasitoid food

web restructuring. In addition, parasitism rates and the number of parasitoid species decrease with altitude, sometimes in a hump-shaped way for the parasitism rates (Cernecka *et al.*, 2025). This suggests a possible increase in parasitism as temperature rises, although it is not possible to predict with certainty that global warming will lead to a reduction in the density of insect pests. The role of predators and pathogens must of course also be considered (Péré *et al.*, 2013). It has also been shown that the proportion of specialized parasitoids decreases with altitude, which increases the risk of host outbreaks (Di Marco *et al.*, 2023). The same type of approach can be applied to latitudinal gradients (see, for example, Niesenbaum, 2012).

Climate change and the direct impact of human activities have resulted, in particular, in an increase in the number of invasive alien species and in their speed of expansion (McGeoch and Latombe, 2016; Sandvik, 2020). With this in mind, the question of the successful establishment of subtropical or tropical species in temperate zones arises. Are ectothermic species adapted to limited seasonal variations in temperature (these temperatures being high) capable of rapidly colonizing temperate zones where, despite warmer temperatures, the thermal differential remains significant? To our knowledge, the first clue was provided by Nedvěd and Windsor (1994), who showed that a diapausing tropical beetle *Stenotarsus rotundus* has a supercooling ability (an index of resistance to cold; Renault *et al.*, 2002) similar to that of temperate species. It is thus possible to hypothesize that this notable supercooling capacity associated with a diapause syndrome constitutes an 'anticipatory' adaptation for cold resistance in temperate environments. However, recent studies provide contrasting results. For example, Fortuna *et al.* (2023) show that a tropical parasitoid (*Cotesia typhae*) of the corn pest *Sesamia nonagrioides* does not appear to be able to withstand current winter temperatures in temperate regions. In contrast, Leon-Quinto *et al.* (2024) show that the palm borer moth *Paysandisia archon*, native to several South American countries (e.g. Argentina, Paraguay, Uruguay) and accidentally introduced into southern Europe some 30 years ago, presents a resistance to cold considered by the authors as unexpected for a tropical species, even going so

far as to be moderately tolerant to freezing. It should be noted that the species has now been reported for less than 10 years in more northern regions of Europe.

1.6 Conclusion

This brief review of the interactions between climate change and macro-organisms involved in biological control shows that the bibliographical references cover a necessarily wide range of complementary fields (behaviour, physiology, ecology, evolution), and that many of the syntheses incorporating an interdisciplinary

approach are very recent, and not just from Europe or North America. It is paramount to stress that all life-history traits of a given species are affected by climate change, either positively or negatively. It follows that in order to try to predict the consequences of the rapid intensification of global warming, the only way is to favour field work backed up by comparative experimental approaches. This requirement, which highlights the detailed study of life-history traits in pest–natural enemy models, far from being obsolete, is a convenient and efficient research path provided that geographical specificities are integrated (e.g. temperate zones vs tropical zones, latitudinal and elevational gradients).

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