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**Title: Parasitoid ecology along geographic gradients: lessons for climate change studies**

Short title: Climatic gradients in parasitoids

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**Abstract**

One method to study the impact of climate change on host-parasitoid relationships is to compare populations along geographical gradients in latitude, altitude or longitude. Indeed, temperatures, which vary along geographic gradients directly shape the life traits of parasitoids and indirectly shift their populations through trophic interactions with hosts and plants. We explored the pros and cons of using these comparisons along gradients. We highlighted that the longitudinal gradients, although understudied, are well correlated to winter warming and summer heat waves and we draw attention to the impact of the increase in extreme events, which will probably be the determining parameters of the effect of climate change on host-parasitoid relationships.

**Keywords:**

climate change; geographic gradients; climatic gradients; Direct and indirect effects; Parasitoids; extreme events

**Introduction**

Changes in climate include both an increase of average temperatures as well as an increase of the frequency of extreme events, such as droughts, heat and cold waves [1]. Both types of changes are directly challenging for ectotherms like insects, first because these organisms present generally a weak thermal plasticity and weak adaptation abilities to these rapid changes, and second because these changes affect indirectly the ectotherms via their interactions with other species [2, 3, 4, 5]. Thus, climate change can lead not only to species loss, but also to profound alterations of their physiology, behaviour and fitness traits, with subsequent shifts in abundance [6], distribution [7, 8] as well as species' assemblage and interactions with other species [4, 9, 10]. It is of tremendous importance to understand these effects for biodiversity conservation and maintaining ecosystem services such as pollination or pest regulation.

When studying the impact of climate change in nature, temporal and spatial empirical approaches can be used. Long-term data are ideal but rarely available [11]. The Space-for-time substitution approach, comparing populations of the same species/guild/community along a geographic gradient, is a useful substitute to study future climatic effects [12]. Three main types of geographic gradients are used to study insects' responses over various environmental conditions: altitudinal, latitudinal, and longitudinal ones (Fig. 1). As the most differentiating characters of each of these gradients we can note that for example, as

latitude increases, day length becomes shorter in winter and longer in summer, while temperature and precipitation decrease. For altitudinal gradients, increased elevation is associated with decreasing temperatures and partial pressure of atmospheric gases, as well as rising UV radiation input, wind speed, and precipitation in the form of rain or snow. However, these characteristics are evident especially on the windward side of a mountain. Finally, at a given longitude, the photoperiod of different localities is similar, while the temperatures can be very different, which could make it possible to dissociate the effects of temperature and photoperiod on processes which depend on them, such as the induction of diapause [12].

Among terrestrial ecosystems, parasitoids that obligatorily develop within, or on a host, leading to the death of the latter [13], are key components of agrosystems as they are, with predators, major biological controllers of pests [12, 13, 14]. , As parasitoids present tightly co-evolved interactions with their hosts, climate change may affect parasitoids and hosts separately, disrupting their interactions, especially when both partners express asymmetric responses to temperatures. Indeed, the trophic-rank hypothesis predicts that higher trophic level organisms, such as parasitoids or predators, are more strongly affected by environmental changes [15, 16], because of cascading effects in the trophic networks [3]. When interactions between species at different ranks of the food chain are altered (like parasitoids and their hosts or predators and their preys), climate change could challenge associated ecosystem functions such as biological control. In this review, we aim to demonstrate how geographic gradients can help to understand the direct and indirect effects of climate change on parasitoids. We first address the direct effects of temperature along these gradients on individual and population traits of parasitoids. Then, we address the indirect effects through their host species and the resulting consequences on their interactions and associated services along these gradients. In both sections, we discussed the limits of the use of climatic gradients for predicting climate change effects on parasitoids.

### **Direct effects of geographic gradients on parasitoids**

Geographic gradients affect insect body size, life histories, physiology, diapause and voltinism. Insect size increases along latitudinal gradients (Bergmann's rule) at both species and population levels,

individuals being larger in colder localities (higher latitudes) [17, 18]. Bergmann's rules and converse Bergmann's rules tend to be both operating in parasitoids depending on parasitoid subfamilies [19]. Indeed, in parasitoids, the Bergmann's rule could be modified by the indirect effect of the host size as for instance, smaller parasitoids tend to be egg parasitoids rather than larval or pupal parasitoids [20]. A larger body size or mass is generally correlated with higher fecundity and longevity. For example, the dry body mass, longevity and reproduction rate of the Iranian populations of the parasitoid *Leptopilina boulardi* (Figitidae), increase with latitude, which is explained by the increase of humidity, at the origin of a higher abundance of hosts [21]. In the parasitoid *Asobara tabida* (Braconidae), Northern European populations present a longer lifespan and a higher reproduction than southern ones [22]. Physiological traits, such as thermal and desiccation tolerance, also vary along geographic gradients. For ectotherms, the thermal tolerance breadth increases with latitudes: species which are both less cold and less heat resistant are living closer to the equator as an adaptation to the smaller temperature range at these low latitudes [23]. In the egg parasitoid *Trichogramma cacoeciae* (Trichogrammatidae), cold tolerance increases with the winter severity along a longitudinal gradient within the French Mediterranean region [24]. In the aphid parasitoid *Aphidius platensis* (Aphididae), cold tolerance also decreases in the colder areas along a latitudinal gradient [25]. In several insect taxa like beetles, some ant species and social wasps, the proportion of Cuticular Hydrocarbon Compounds (CHCs), involved in insect protection from desiccation, is higher for populations/species living in warmer and drier areas [26]. For parasitoids, this was only investigated in females of the globally distributed parasitic wasp *Nasonia vitripennis* (Pteromalidae). In this species, the proportion of CHCs with intermediate length increases at higher latitude sites reducing the probability of desiccation in areas with lower summer temperatures [26]. More studies will be necessary to define a general pattern. Along geographic gradients, populations vary in diapause expression and voltinism. Winter insect diapause is induced by short day length and cold temperature. Insect taxa at higher latitudes expressed the earliest onset of diapause [27]. For both the parasitoids *Nasonia vitripennis* (Pteromalidae) [28] and *Trichogramma drendrolimi* (Trichogrammatidae) [29], the proportion of diapausing offspring increased with latitude, reflecting gradients of winter severity. Earlier emergence was observed in several

parasitoid species (Family: Chalcidoidea) in response to earlier spring onset at lower latitudes in USA. In the context of global warming, populations of parasitoids from mild winter areas do not enter diapause anymore, as the temperature threshold for diapause induction is no longer reached [31]. In the parasitoid *Meteorus trachynotus* (Tortricidae) [32], voltinism (i.e. the number of generations per year) increases in populations at low, compared to these at high latitude. Studying diapause and voltinism along geographical gradients may allow to better predict the impact of climate change on these specific traits world-wide.

However, studies using geographic gradients may fail to explain phenotypic variation among populations in different cases. First, **Geographic gradients can mismatch climatic gradients.** For instance, populations of the parasitoid *Aphidius platensis* (Aphididae) did not differ in fresh body mass and reproductive traits along a 1000km latitudinal gradient in the Central valley of Chile, because climatic conditions recently became more homogeneous among localities [25]. To improve these studies, identifying climatic heterogeneity along gradients is thus necessary. Scotta et al. (2021) [24] succeeded in detecting a positive relationship between cold tolerance and winter severity by classifying three climatic zones (Mediterranean climate, Mediterranean mountain climate and continental climate) based on sampling locations in a French regional study. On a continental scale, Branca et al. (2019) [33] conducted Köppen-Geiger climate classification to identify 162 localities in Africa into five clusters to study the genetic structure of the parasitoid *Cotesia sesamiae* (Braconidae), which visualized the climatic divergence effectively. **Second, high gene flow among populations leads to trait homogeneity.** For example, the low genetic diversity of populations of *Aphidius ervi* (Aphididae) within a 700 km latitude gradient in Chile, precludes local adaptations [34]. In the host-parasitoid system including *Pleistodontes imperialis* (Agaonidae) and its *-Sycoscapter* sp. (Pteromalidae) parasitoids, distinct populations of hosts were evidenced along a latitudinal gradient of 2000 km in Australia, whereas their parasitoids formed one single population [35]. Finally, **Microclimate does matter.** The metabolic rate of the parasitoid *Leptopilina heterotoma* (Figitidae) differs among geographic populations, however the patterns could not be linked to local mean climatic conditions. The differences may be explained by microclimatic variations, e.g., orchard landscapes [36].

### Indirect effects of geographic gradients on parasitoids

At the community level, the latitudinal diversity gradient describes the general pattern of increasing species richness, abundance, and evenness with decreasing elevation [37] and latitudes [38]. This was observed in several host-parasitoid systems and gall-inducing cynipid parasitoids (Chalcidoidea) over an altitudinal gradient of 1000m in Mexico [39]. These results suggest that the diversity of parasitoids is mainly determined by the availability of their hosts [40, 41], diversity and abundance of which decrease with elevation and high latitudes [42].

These changes at the community level affect parasitism rates, which in turn decrease at increasing altitude and seems to be strongly dependent on climatic conditions. For example, at high altitude, cold and dry winters negatively affect the abundances of the pine processionary moth parasitoids. The probability of occurrence of the two most abundant parasitoid species (*Ooencyrtus pityocampae* and *Baryscapus servadeii*) declined with increasing elevation while the number of host eggs (*Thaumetopoea pityocampa*) increased, leading to a decreased parasitism rate [42].

With global change, the distribution areas of hosts and plants tend to extend from low to high latitudes [43], which gives the opportunity for parasitoids to conquer new lands, even though they have to adapt to new conditions. This can only happen if parasitoid, host and plant phenologies match. Temperature change can alter interactions within a community by changing the relative phenologies of interacting species [39, 29]. These desynchronizations can lead either to an increased or a decreased risk of pest-outbreak [5]. Nonetheless, phenological mismatch has been poorly studied along geographical gradients.

Gradient studies may not explain indirect effects on parasitoids mostly because **considering the whole trophic network is difficult**. For example, the degree of parasitoid specialization [44] or their interactions with other predatory taxa in top-down regulation may also explain the lack of significant relationships between parasitoid diversity or their impact as natural enemies [45, 46]. Hódar et al. (2021) [42] showed that increasing tree diversity at the pine processionary moth (*Thaumetopoea pityocampa*) expansion areas may favor the establishment of parasitoids. This could contribute to synchronizing host-

parasitoid interactions and minimize the risk of pine processionary moth outbreaks [42]. At the community level, one major gap in knowledge is on the effects of geographic gradients on hyperparasitoids, which apply a major influence on the parasitoid community and the parasitism rate [47].

## Discussion

Among the methods for studying the impact of climate change on host-parasitoid relationships, the use of geographic gradients, whether altitudinal, latitudinal or longitudinal, is still infrequent and concerns mostly altitudinal and latitudinal gradients (Tab 1, Fig. 2). Some studies have highlighted trait variations on altitudinal and latitudinal gradients. This concerns the vast majority of trait types, including physiological, life history and population fitness traits, with some patterns at the community level. By consequence, it allows to develop predictive studies about the impact of different aspects of climate change on parasitoid ecology (Table 2, Fig. 1, Fig. 2). Understanding the link between species traits and geographic gradients is important for understanding the evolutionary processes responsible for observed functional diversity and for predicting community responses to climate change [23]. Indeed, this allows to connect ecological and evolutionary studies. Plastic responses, which precede evolutionary ones, are often insufficient by themselves to allow individuals to survive to climate change in the long term. However, plasticity can help populations to sustain themselves over a sufficient number of generations to allow genetic adaptation. Therefore, it facilitates evolutionary adaptation by providing more time for genetic changes [2]. This integrative approach (ecological and evolutionary) will make it possible to take into account both responses (plastic and evolutionary) to climate change [23].

Another general question in the use of gradients to study the impact of climate change, is the spatial scale used. Indeed, the relevant gradients for a system may depend on research questions and on the dispersal capacity of the organisms studied (both parasitoids and their hosts). Among geographic gradients, longitudinal ones are almost never studied in insects (Fig. 2A), although they are of major interest to study the effect of climatic factors independently of other abiotic factors. For example, diapause, which is induced by both photoperiod and temperature, is largely affected by climate change, leading to an

alteration of host-parasitoid interactions and large differences in parasitism efficiency along longitudinal gradients [48].

The advantage of using geographic gradients is to include multiple climatic factors such as temperature and precipitation as well as interactions between species that can be useful to predict changes in community structure and ecosystem functioning. These parameters are incompletely taken into account in theoretical climate models. Modelling has been proven useful to predict longer-term and larger-scale processes from short-term and small-scale empirical data from climatic gradients [43]. Therefore the concomitant use of both theoretical and empirical approaches is meaningful to obtain realistic predictions regarding the impact of future climate change on parasitoid guilds and their associated community.

### **Conclusions and perspectives**

As main findings, we showed that geographic gradients are often correlated to several life-history traits of parasitoids, which allows to predict the consequence of climate change through studies of variations in these traits at a large spatial scale.. Altitudinal and latitudinal gradients can help simulating the effects of an increase of the mean temperature whereas longitudinal gradients are well correlated to winter warming and summer heat waves.

As perspectives, although geographical gradients make it possible to study variations in average temperatures, one of the major impacts of climate change on interacting species such as parasitoids and their hosts comes from the increase in extreme events [1]. The Climate Extremes Hypothesis predicts that rare extreme events are a key selective agent in the evolution of thermal tolerance [23, 49]. Moreover, studies showed that the selection pressures generated by these stressful temperatures are stronger than those generated by variable but recurring temperatures [50, 51, 52], for both plastic and evolutionary responses [3, 53]. This effect can be detected both at the molecular level [53] or at the levels of life history traits such as diapause and phenology. By extracting extreme thermal stresses relevant for particular networks of hosts and their parasitoids from meteorological data, we could map gradients of extreme

temperature events. They may differ from mean temperature geographic gradients, but could better predict the impact of climate change. Another solution to use the gradient studies in cases of large inter-annual variations could be to work using year-locality points as data point, as developed by Alfaro Tapia et al. (2022) [25]. Indeed, for the same locality, it is possible to observe strong temperature variations between years, and to study the impacts of temperatures along geographical gradients, it is necessary to take these variations into account.

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## FIGURES & TABLES

### Figure legends

**Figure 1. A conceptual diagram characterizing the variations in monthly mean temperature and in day length across different geographic gradients. (a)** Latitudinal gradient: temperature mean decreases but temperature variation increases with latitude. This leads to higher mean but smaller variation of temperature in low latitudes whereas lower mean but larger variation of temperature in high latitudes. The variation in day length (grey lines) increases with latitude. **(b)** Altitudinal gradient: temperature mean decreases with altitude while temperature variation remains relatively stable. The day length stays unchanged for a given location. **(c)** Longitudinal gradient: temperature mean varies relatively little while temperature variation increases with the distance from seacoast, according to the characteristics of continental versus marine climates. The day length remains constant across different longitudes. **(d)** A summary of the differences in temperature means and variations and in day length among the three patterns of geographic gradient.

**Figure 2.** Pie charts summarizing studies on the effect of geographic gradients on parasitoids. On the left, the types of geographical gradients, on the right the types of traits studied. **Physiology traits** include thermotolerance and metabolism; **Life history traits** include longevity, reproduction, lifespan, body size or body mass; **Population traits** include diapause and voltinism.

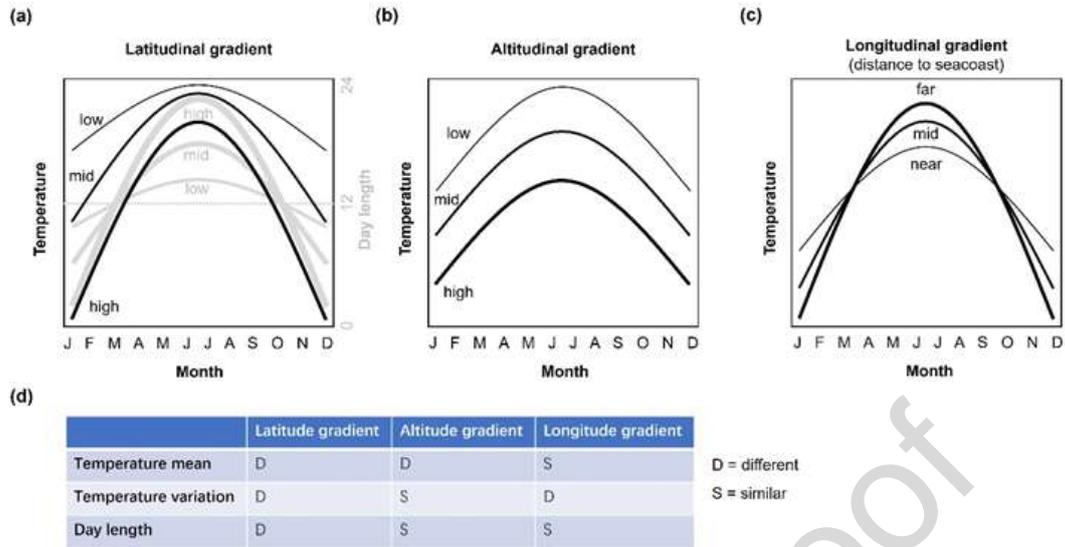


Figure 1

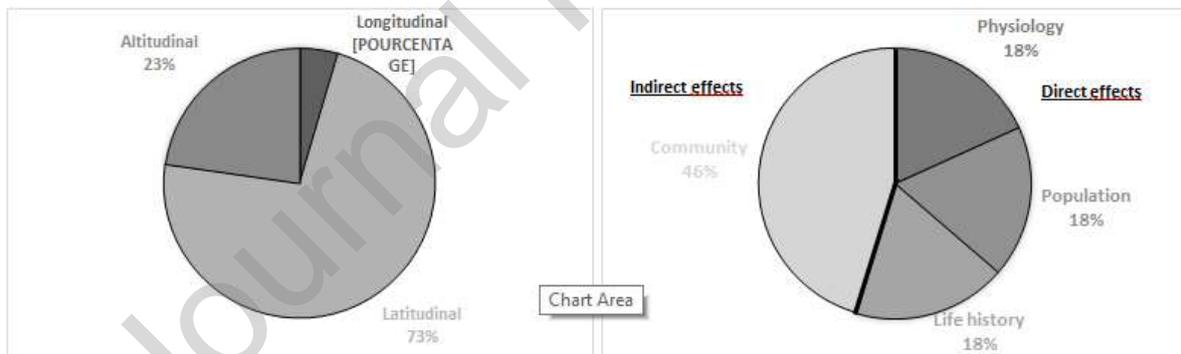


Figure 2

Table 1: References used for the Figure 2 and in the main text. Types and scales of the gradients.

References	Geographic gradients	Range	Countries	Environmental factors	Trait category	Specific traits
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Santos & Quicke, 2011	Latitudinal	0-66.7	global	Temperature	Life history	Body size
Alfaro-Tapia et al., 2022	Latitudinal	70~72°W, 34~38°S	Chile	Temperature	Life history	Body size, reproduction, body mass
Scotta et al., 2021	Latitudinal/Longitudinal	43.56~48.46°N, 2.49~7.19°E	France	Temperature	Physiology	Thermotolerance
Alfaro-Tapia et al., 2022	Latitudinal	70~72°W, 34~38°S	Chile	Temperature	Physiology	Thermotolerance
Buellesbach et al., 2021	Latitudinal	42~65°N, 6.2~23°E	Europe	Temperature	Physiology	Proportion cuticle
Ellers et al., 1998	Latitudinal	37-52°N	Europe	Temperature	Life history	Lifespan and reproduction
Moiroux et al., 2010	Latitudinal	35.5~37.1°N, 53~55.2°E	Iran	Humidity	Life history	Longevity, reproduction and dry mass
Vuarin et al., 2012	Latitudinal	43.95-46.5°N, 4.87-4.74°E	France	Not specific	Physiology	Metabolic rate
Paolucci et al., 2013	Latitudinal	42~65°N, 6.2~23°E	Europe	Photoperiod	Population	Diapause
Zhang et al., 2017	Latitudinal	32~44°N, 120~128°E	China	Temperature	Population	Diapause
Abarca & Lill, 2019	Latitudinal	28~44°N, -82~-89°E	USA	Temperature	Population	Diapause
Régnière et al., 2021	Latitudinal	46~48°N, -66~-70°E,	Canada	Temperature	Population	Voltinism
Abarca et al., 2019	Latitudinal	28.66~44.33°N, 82.29~-89.22°W	USA	Temperature	Community	Host phenology
Burington et al., 2018	Latitudinal	39.21~-4.09°N, -76.91~79,13°W	North & Central America	Temperature	Community	Parasitoid specialisation degree
Corcos et al., 2018	Altitudinal	50 – 2000m	Italy	Temperature & Habitat diversity	Community	Species diversity, richness, abundance, and evenness
Hódar et al., 2021	Altitudinal	190 – 2000m	North America	Temperature	Community	Parasitism rates
Chia-Hua et al., 2018	Latitudinal	43.48~25.32°N, 71.64~80.29°W	North America	Temperature & Precipitations	Community	Species diversity, richness, abundance, and evenness

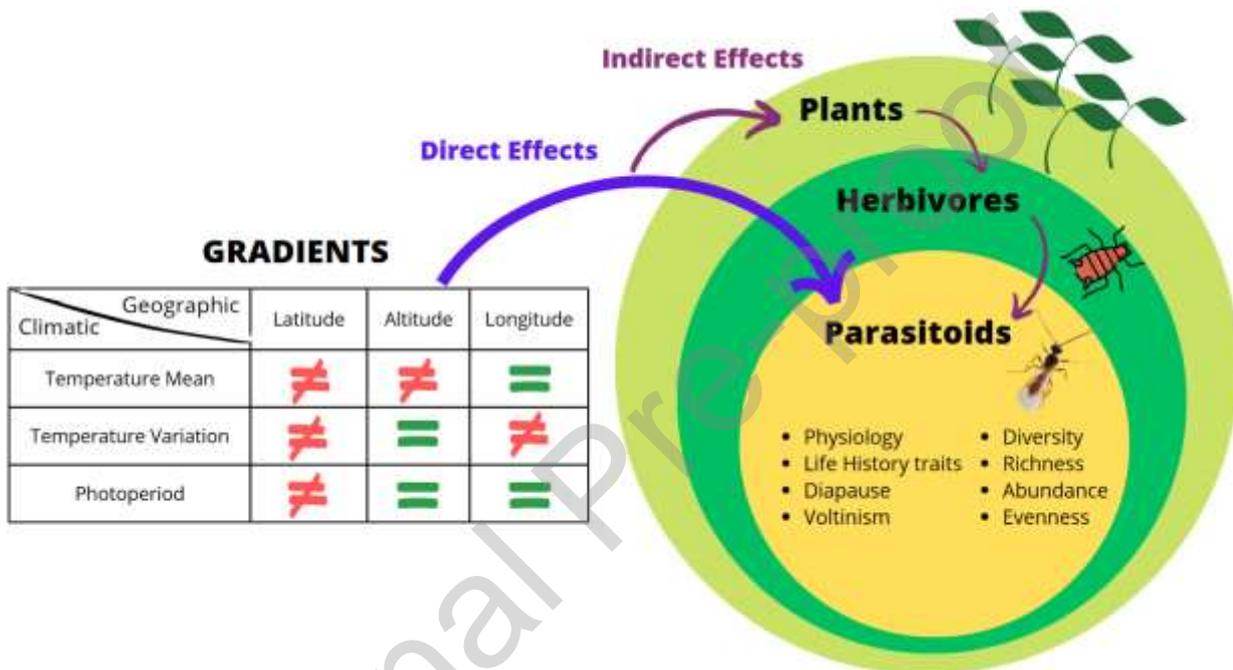
Philbin et al., 2021	Altitudinal	1600 – 2600m	North America	Habitat diversity	Community	Host abundances
Serrano-Munoz et al., 2022	Altitudinal	1000m	Mexico	Not specific	Community	Species diversity, richness, abundance, and evenness
Wermelinger et al., 2021	Altitudinal	900 – 1500m	Switzerland & Italy	Temperature	Community	Top-down regulation
Zvereva et al., 2020	Latitudinal	60~69°N	Russia	Temperature	Community	Top-down regulation
Audusseau et al., 2020	Latitudinal	500km latitudinal gradient	Sweden	Not specific	Community	Repartition area of hosts
Tougeron et al. 2022	Longitudinal	650 km (48.11~50.70° N, -1.70~4.61E)	France/Belgium	Temperature	Community	Abundances, Activity-density

**Table 2:** Main questions on parasitoid ecology (arising from Fig. 1 and Table 1) that can be addressed with the study of geographical gradients, and pros and cons of using each type of gradients (latitudinal, altitudinal and longitudinal)

Study subjects	Latitudinal	Altitudinal	Longitudinal
Study the effects of mean and variability of temperature increase	+	-	-
Focus on the effect of mean temperature increase as it is the only factor of variation	-	+	-
Impact of the photoperiod and the variability of temperatures	+	-	-
Dissociate the effects of photoperiod and temperature for diapause induction	-	-	+

Understanding the evolutionary processes responsible for observed functional diversity	+	+	+
Predicting community responses to climate change	+	+	+

## Graphical abstract



## Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

## Highlights

- Temperature affects directly life history traits of parasitoids and indirectly communities
- Longitudinal gradients are understudied but well correlated to winter warming
- Latitudinal and altitudinal gradients allow simulating mean temperature increase
- Extreme temperature events will be determinant for host-parasitoid interactions

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