

REVIEW

Dealing with predictable and unpredictable temperatures in a climate change context: the case of parasitoids and their hosts

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ABSTRACT

The Earth's climate is changing at a rapid pace. To survive in increasingly fluctuating and unpredictable environments, species can either migrate or evolve through rapid local adaptation, plasticity and/or bet-hedging. For small ectotherm insects, like parasitoids and their hosts, phenotypic plasticity and bet-hedging could be critical strategies for population and species persistence in response to immediate, intense and unpredictable temperature changes. Here, we focus on studies evaluating phenotypic responses to variable predictable thermal conditions (for which phenotypic plasticity is favoured) and unpredictable thermal environments (for which bet-hedging is favoured), both within and between host and parasitoid generations. We then address the effects of fluctuating temperatures on host–parasitoid interactions, potential cascading effects on the food web, as well as biological control services. We conclude our review by proposing a road map for designing experiments to assess if plasticity and bet-hedging can be adaptive strategies, and to disentangle how fluctuating temperatures can affect the evolution of these two strategies in parasitoids and their hosts.

KEY WORDS: Bet-hedging, Fitness, Fluctuating, Global warming, Insects, Plasticity

Introduction


Globally, climatic conditions are currently changing at an unprecedented pace, both in terms of an overall increase in mean temperature, and in the occurrence of more catastrophic and unpredictable events, such as frost or heatwaves (Bathiany et al., 2018; Easterling et al., 2000; IPCC, 2014; Lenton et al., 2017; Vasseur et al., 2014). Some species can avoid detrimental thermal changes through range shifts or migration (Parmesan and Yohe, 2003), but a major concern is that many species will not be able to migrate and will therefore become (locally) extinct. Extreme temperatures can indeed lead to sterility and death if unfavourable temperatures are not avoided (Zwoinska et al., 2020). Novel temperature changes can thus impose strong selection for pre-existing adaptive genetic variants, leading to local adaptation. Although some examples of rapid local adaptation exist, such fast responses to novel environmental changes remain rarely documented (Kristensen et al., 2020; Parmesan, 2006) and may occur too slowly in a rapidly changing climate (Barrett and Schluter, 2008; Gienapp et al., 2013; De Meester et al., 2018 and references therein). This is simply because mutations appear randomly, and allele frequency changes take time even when there is sufficient variation

and strong selection. Variability and unpredictability of the environment may further continually shift potential fitness optima.

Animal responses to a rise in mean temperature have received considerable attention (Parmesan and Yohe, 2003), but comparatively little is known about the evolutionary responses to cope with fluctuating thermal environments, particularly regarding the predictability of temperature changes. Phenotypic plasticity and bet-hedging are considered critical strategies by which individuals can persist when faced with more immediate, intense and unpredictable temperature changes (Simons, 2011; van Baaren and Candolin, 2018). Phenotypic plasticity is the capacity of a single genotype to generate two or more phenotypes depending on the environment (Pigliucci, 2005). Plasticity can occur within a generation (within-generation plasticity, hereafter WGP), but also over successive generations (transgenerational and intergenerational plasticity, hereafter TGP and IGP) and can be adaptive or not (Ghalambor et al., 2007, 2015). TGP refers to indirect effects of an environmental factor on an organism that persists for two or three generations (depending on whether the phenotype is transmitted by a male or a female, respectively) (Perez and Lehner, 2019). For many animals, TGP is often measured from the grand-offspring generation onwards for females, as an environmental stimulus can directly affect already-formed oocytes within the female's body (Perez and Lehner, 2019). Effects that are observed earlier than the grand-offspring generation are considered parental effects or IGP. In contrast, for bet-hedging, variable phenotypes are generated irrespective of the environment (Starrfelt and Kokko, 2012). Bet-hedging theory suggests that under fluctuating thermal conditions with low predictability, genotypes with a reduced arithmetic mean fitness may be at an evolutionary advantage if this is associated with a reduced temporal variation in fitness, meaning an increase in geometric mean fitness (Philippi and Seger, 1989). In other words, it may be better to have at least some success each generation than having high success in some generations and complete failure in others. Three types of bet-hedging strategies have been described: conservative bet hedging, i.e. a 'play it safe' strategy; diversified bet-hedging, i.e. a 'don't put all your eggs in one basket' strategy; and the adaptive coin-flipping strategy, i.e. where a strategy is chosen at random from a fixed distribution (Olofsson et al., 2009). In conservative bet-hedging, a 'generalist' phenotype with an intermediate fitness is produced, for which variance is reduced over generations when exposed to variable climatic conditions. This means that the generalist strategy provides greater reproductive success in most thermal environments, but has less success than the specialist in its optimal thermal environment. In contrast, diversified bet-hedging is achieved by increasing the phenotypic variance among individual offspring (within a generation) to ensure that at least some of them will be successful (Haaland et al., 2019; Philippi and Seger, 1989; Starrfelt and Kokko, 2012). Bet-hedging differs from phenotypic plasticity by being an adaptation to unpredictability or to change itself, whereas plasticity can be adaptive in predictable thermal environments (Simons, 2011; Tufto, 2015; van Baaren and Candolin, 2018). Adaptive coin-flipping, a

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stochastic decision to produce one phenotype from a single genotype (flipping a coin) from a range of possible phenotypes can lead to diversified bet-hedging (Hopper, 1999; Menu and Desouhant, 2002; Menu et al., 2000; Seger and Brockman, 1987). Several strategies can thus be adaptive and are not mutually exclusive depending on the predictability of the environment.

Abiotic changes in temperature are a logical focus for studies on climate change, but species persistence also depends on changes in biotic factors. Altered interactions between species can have major effects on one or both interacting partners. This is particularly true for species that share a long co-evolutionary history, and for which thermal changes in one or both species can disrupt the interaction (Blanford et al., 2003; Ellers et al., 2012). Climate change can lead to spatial and temporal mismatches, for example between mutualistic partners, such as plants and their pollinators, at the detriment of pollination (Hegland et al., 2009; Memmott et al., 2007), and between antagonistic partners, such as predators and prey (Grigaltchik et al., 2012) or parasites and hosts (Blanford et al., 2003; Jeffs and Lewis, 2013; Senior et al., 2020). Direct and indirect effects of temperature changes on biotic interactions could thus severely affect population dynamics, community structure and food webs, as well as ecosystem functioning and services (Parmesan, 2006; Schröter et al., 2005).

For ectotherm insects, body temperature matches the ambient temperature; hence thermal fluctuations and unpredictability of extreme climatic events pose a significant challenge to their survival. Here, we focus on responses to variable temperatures that are either predictable or unpredictable in parasitoids, their hosts (mainly other insects), and the consequences for both interacting partners. Several host species have featured prominently in the climate change literature, such as fruit flies and aphids (Hoffmann et al., 2003; Hullé et al., 2010; Xue et al., 2019). Parasitoids feed on the outside or inside of their host, which is often completely consumed and killed by the time the parasitoid completes its development (Godfray, 1994). Parasitoids are considered important natural enemies of insect pests, as they play a critical role in terrestrial communities by regulating lower trophic levels (Jervis, 2005). The intricate relationship and dependence of parasitoids on a host also means that negative effects of climate change experienced by hosts can cascade up the food chain, because parasitoid development naturally lags behind. Compared with their diploid hosts, parasitic wasps (hymenopteran parasitoids) are further at a disadvantage in the race to adapt to changing conditions, because haplodiploids (unfertilised eggs are males; fertilised eggs are females) have lower standing genetic variation and mutation rates (Biale et al., 2020; Smith and Shaw, 1980).

This review addresses how hosts and parasitoids each deal with predictable (section I) and unpredictable variation in temperature (section II), as well as the effects on their interaction and consequences for population dynamics, community structure, food web and biological control services (section III) within the context of non-genetic short-term responses (i.e. plasticity and bet-hedging). We further provide a roadmap for future studies ('Perspectives' section).

I. Host and parasitoid responses to predictable thermal variation

Within generations

WGP includes both behavioural and physiological variation. Unfavourable temperatures can be avoided on a microscale, where thermotolerance can be achieved by choosing specific microhabitats, i.e. behavioural thermoregulation. For example, Burdick et al. (2015) showed that aphids modified their feeding behaviour by settling mostly under leaves to protect themselves against UV radiation. For

parasitoids, oviposition can affect the behaviour of the host away from unfavourable temperatures to the benefit of parasitoid development. This was indeed shown in aphid parasitoids, where parasitised hosts more often leave their current host plant in search for more favourable conditions (Alford et al., 2016). In host fruit flies, *Drosophila subobscura* and *D. melanogaster*, extreme low temperatures can be avoided when individuals overwinter inside compost heaps acting as refugia (Schou et al., 2015; Sørensen et al., 2015). When there is variation in temperature, juvenile *Drosophila* hosts also have thermal preferences for the location where they develop. Early during development, larvae avoid temperatures lower than 23°C (Rosenzweig et al., 2008), while wandering larvae (searching for a location to initiate metamorphosis) prefer temperatures closer to 18°C (Kwon et al., 2008; Liu et al., 2003). Furthermore, pupation location is affected by temperature in several *Drosophila* species (Josso et al., 2011; Pandey and Singh, 1993). Interestingly, parasitism of *D. melanogaster* and *D. simulans* by the parasitoid *Asobara tabida* affected the location of pupation, which was closer to the feeding substrate (Josso et al., 2011). If and how manipulation of the pupation behaviour of *Drosophila* is of benefit to the parasitoid remains to be tested, but parasitism by *Aphidius ervi* (Lagos et al., 2001), *Aphidius nigripes* (Brodeur and McNeil, 1989) and *Eucelatoria bryani* (a dipteran parasitoid; Reitz and Nettles, 1994) could lead to host behavioural thermoregulation.

Phenotypic variation resulting from WGP depends on the environmental conditions an individual experiences (Scheiner, 2013, 2014), either during development (developmental plasticity) or as an adult (reversible plasticity). In *D. melanogaster*, larval exposure to predictable temperature fluctuations of ~4°C around a mean of 19–23°C did not have any effect, but fluctuations of ~8°C negatively affected cold tolerance, while positively affecting heat tolerance (Salachan and Sørensen, 2017). The negative effects on cold tolerance were not seen when adults were exposed to a similar fluctuating temperature regime, suggesting that the effects of acclimation during development are stronger compared with the adult stage (Kristensen et al., 2008). Moreover, heat tolerance responses resulting from the developmental treatment could be completely reversed following adult exposure. In the parasitoid *Telenomus podisi*, exposure during development to a predictable fluctuating temperature regime (30°C during the day and 20°C during the night) significantly increased fitness (compared with a constant temperature) by reducing development time and increasing female longevity and fecundity (Castellanos et al., 2019). Increased thermotolerance resulting from exposure to fluctuating developmental temperatures may increase fitness in both hosts and parasitoids. Nevertheless, responses are species-specific and strongly depend on the thermal regimes. How this affects host–parasitoid interactions largely remains to be studied (see section III).

Between generations

Plastic responses to predictable fluctuating temperatures can also extend to the next generation through parental effects (i.e. IGP) and disappear or persist (or only appear) in subsequent generations (i.e. TGP). In *D. melanogaster*, for example, thermal variability (28±4°C) during development increased heat tolerance not only in the parental generation, but also in offspring (Cavieres et al., 2019). Such positive parental effects to predictable fluctuating temperatures have also been found in parasitoids, such as an increase in body size and lipid reserves of the offspring when the parental generation was exposed to low temperatures (Tougeron et al., 2020a). Parental effects on insect hosts can also affect their parasitoid. For instance, Iltis et al. (2020) exposed the host moth

Lobesia botrana to a recurring fluctuating temperature regime, either mimicking current thermal conditions (~20°C) in the region under study or the predicted thermal conditions in 2081–2100 (~26°C). Emergence of its parasitoid *Trichogramma cacoeciae* was negatively affected when host mothers and host eggs developed under the 26°C fluctuating regime, even when developing parasitoids were themselves experiencing the milder 20°C regime (Iltis et al., 2020). Stressful temperature events can thus modify the way host offspring interact with parasitoids and this might also be true for other host–parasitoid systems. How parental effects in parasitoids subsequently affect their hosts has so far been overlooked and remains to be investigated.

Adaptive TGP in response to cold has been demonstrated in *D. melanogaster* through male line-mediated transgenerational epigenetic inheritance (Karunakar et al., 2019). Here, exposure of fathers to cold triggered metabolic changes in the grand-offspring generation that had increased triglyceride (i.e. fat) levels, which is a common response to survive cold conditions (Karunakar et al., 2019). Adaptive TGP in insects is also expected for the induction of diapause in fluctuating, but predictable environments (Hopper, 1999). Winter diapause is a metabolic arrest of development to anticipate future harsh environmental conditions, mainly in response to short day length and low temperatures. As winters are warming up and temperature changes are becoming more variable also between generations, TGP of diapause probably plays an important role in the ability of insects to cope with climate change (Donelson et al., 2016; Tougeron et al., 2020b). Parasitoids need to accurately detect and use signals indicative of environmental changes, such as upcoming cold or hot temperatures, but also reductions in host densities (Tougeron et al., 2020a). In some aphid parasitoids, for example, the percentage of individuals entering facultative diapause decreased with a mean increase in temperature, as well as increased aphid density during winter, and parasitoid species that were diapausing decades ago are now active during the winter (Andrade et al., 2016; Tougeron et al., 2017). A similar pattern is also found during summer, for which an increase in mean temperatures was associated with an increase in competition between parasitoids (but not to a decrease in host density), inducing higher diapausing levels (Tougeron et al., 2018a). Nevertheless, whether parental effects (IGP) disappear or persist in subsequent generations has not clearly been demonstrated in parasitoids (Castellanos et al., 2019; Tougeron et al., 2020a).

Whether TGP is adaptive or not in ectotherm insects, including hosts and parasitoids, depends on the predictability of the environment. If the environment experienced by grandmothers resembles that of their grand-offspring, even partially, then TGP could be adaptive. If not and grandmothers cannot anticipate future environments (Uller et al., 2013), TGP may not be adaptive (Donelson et al., 2018; Marshall and Uller, 2007; Sgrò et al., 2016). Indeed, TGP can impose fitness costs on the offspring, particularly in highly unpredictable environments (Donelson et al., 2018; Sgrò et al., 2016). In these cases, bet-hedging strategies could be an alternative to allow persistence under a changing climate.

II. Host and parasitoid responses to unpredictable variation

Within generations

Extreme climatic events, including heat or cold shock, represent an unexpected and unpredictable change in temperature that can act on species survival. In host species such as *D. melanogaster*, heat shocks of different durations decrease adult survival (Jackson et al., 2015; Krebs and Loeschcke, 1994). Similar effects were found for the parasitoid *Aphidius avenae* (Roux et al., 2010) and for different

Trichogramma parasitoid species (Chihirane et al., 1993; Reznik and Vaghina, 2006; Wang et al., 2014). Heat and cold shock can also negatively affect mating and fertility in both hosts and parasitoids, such as *D. melanogaster* hosts (Krebs and Loeschcke, 1994), and the parasitoids *Dinarmus basalis* (Lacoume et al., 2007) and *Trichogramma* species (Chihirane et al., 1993; Reznik and Vaghina, 2006; Wang et al., 2014). How host and parasitoid populations are affected by thermal shocks depends on their thermal limits and geographical origin. Surprisingly, tropical populations, living in warmer but more buffered environments, seem to cope better with high temperature events than temperate ones, living in colder but more variable environments (Rohmer et al., 2004). To cope with heat or cold shocks, many species, including parasitoids and their hosts, upregulate heat shock proteins (HSPs) that mitigate the negative consequences of stress through plasticity at the physiological level (Dahlgaard et al., 1998; Feder and Hofmann, 1999; Sørensen et al., 2003). The unpredictability and intensity of heat and cold shock can thus lead to high mortality (and therefore strong selection), but potential negative effects may be mitigated by plasticity in the physiological stress response.

When heat or cold shocks are followed by another stressful temperature exposure, ectotherms can also become acclimated, meaning that they are better equipped to deal with future temperature changes. For example, when both pupae and adults of *Trichogramma carverae* parasitoids were exposed to a heat shock, survival at even higher temperatures increased (Scott et al., 1997; Thomson et al., 2001) in both males and females (Scott et al., 1997). Moreover, acclimation increased adult fitness under hot field conditions in *T. carverae* (Thomson et al., 2001). Acclimation in unpredictable fluctuating environments was also found to increase thermal tolerance in other parasitoids (Bahar et al., 2013; Cònsoli and Parra, 1995; Delava et al., 2016; Torres et al., 2002). For the moth *Chilo partellus* and its parasitoid *Cotesia flavipes*, acclimation of both species was considered (Mutamiswa et al., 2018). Exposure to both high and low temperatures improved critical thermal limits, heat knockdown time, supercooling point and chill coma recovery time in *C. partellus* larvae and *C. flavipes* adults. Overall, the host *C. partellus* was more plastic compared with *C. flavipes*. Differences in plastic responses between hosts and parasitoids, and particularly lower plasticity in parasitoids, can challenge the ability of parasitoids to cope sufficiently with novel and unexpected temperature changes.

Between generations

Rapid, unexpected and stressful temperature changes can have lasting effects on the descendants of exposed individuals. In *Drosophila*, for example, over-expression of a small heat shock protein (Hsp23) in female ovaries increased thermal tolerance of progeny (Lockwood et al., 2017). Moreover, the negative effects of heat exposure during an early embryonic stage could be mitigated when offspring produced by an exposed mother were provisioned with Hsp23. In the aphid *Rhopalosiphum padi*, the intensity of heat stress experienced by mothers leads to contrasting effects in the progeny: a mild exposure leads to an increase in offspring fecundity, whereas heat stress leads to prolonged development time of the offspring (Peng et al., 2020). Although not often studied in parasitoids, similar effects were found as observed in hosts. In the aphid parasitoid *A. ervi*, for example, exposure of parents to a prolonged mild heat stress led to a higher egg load at emergence in progeny (Ismael et al., 2013). These positive effects on some traits can, nevertheless, come at a cost for the expression of other traits due to energy allocation trade-offs towards main functions, such as between longevity, reproduction or dispersal

(Stearns, 1989). In *A. ervi*, for example, the abovementioned increase in fecundity of progeny comes at the expense of a longer development time and lower survival (Ismaeil et al., 2013). Moreover, increased early fecundity may not always reflect a higher realised lifetime fecundity and thus a higher fitness; hence these parental effects may still be non-adaptive. Finally, positive effects of parental exposure on progeny may further be sex dependent. Indeed, Roux et al. (2010) found that short exposure to elevated temperatures in adult males of the aphid parasitoid *A. avenae* led to shorter development times of progeny, whereas this effect was not observed when mothers were exposed.

When exposed to unpredictable environments over several generations, insects may adopt adaptive coin-flipping, which are stochastic decisions that can lead to diversified bet-hedging strategies (Hopper, 1999; Menu and Desouhant, 2002; Menu et al., 2000; Seger and Brockman, 1987). For aphids, the winter can be spent as diapausing eggs, which are cold resistant, or as parthenogenic active adults that continue to reproduce during the whole winter, which comes at the risk of dying during extreme cold events (Halkett et al., 2004). As the climate changed and thermal fluctuations increased in incidence and severity, the population of aphids started spreading the production of sexual forms over a larger time interval. Indeed, when the weather is unpredictable it is advantageous to invest in parthenogenesis for as long as possible, but to simultaneously produce some sexual individuals that will in turn produce diapausing eggs when thermal conditions become harsher (Halkett et al., 2004). Aphid parasitoids cannot develop in diapausing aphid eggs and thus completely depend on the presence of aphid larval and adult stages to remain active and reproduce. For these parasitoids, both increased unpredictability of thermal conditions and host availability could select for different overwintering phenotypes within a population, such as undergoing diapause at a juvenile stage within the host, entering quiescence as an adult, or being an active adult and reproduce (Tougeron et al., 2020a). To adopt an adaptive 'coin-flipping' strategy, the proportion of parasitoids entering diapause should match the probability of a parasitoid undergoing harsh winters and experiencing host shortage (Hopper, 1999; Rajon et al., 2014). Within populations of aphid parasitoids exposed to winter diapause conditions, some mothers did not produce diapausing offspring, others produced only diapausing offspring, and many mothers produced a mix of both (Tougeron et al., 2019). This could be regarded as conservative and diversified bet-hedging strategies, respectively. In these examples, the proportion of each offspring phenotype may be adjusted to the probability of encountering a given environment when biotic or abiotic cues are partially predictable (Hopper, 1999; Marshall and Uller, 2007; Menu et al., 2000). When a parasitoid female cannot precisely assess which offspring phenotype would be favoured in the future environment, she may produce both diapausing and non-diapausing offspring to optimise her fitness (Tougeron et al., 2020a). Environmental predictability is then determining the establishment of such mixed strategies (Burgess and Marshall, 2014), and also for traits correlated with diapause, such as dispersal and sex (Gerber and Kokko, 2018).

Bet-hedging strategies in summer diapause or aestivation are expected to be observed within (He et al., 2010) or between (Tsukada, 1999) parasitoid populations throughout seasons with variable host availability. The apple leaf-curling midge parasitoid *Platygaster demades* regulates the frequency and duration of aestivating phenotypes from late spring to mid-autumn and adjusts the rate of non-aestivating phenotypes from early to late autumn, producing univoltine, bivoltine, trivoltine and quadrivoltine phenotypes throughout the season. The regulation of aestivation frequency and

duration matched expected periods of host shortage, thereby avoiding negative fitness consequences and asynchronisation with hosts (He et al., 2010). As pointed out by Simons (2011), most studies on insects have so far only identified candidate bet-hedging traits, sometimes in response to unpredictable environmental factors and potentially with variation in candidate bet-hedging genotypes. However, only few studies have demonstrated bet-hedging strategies to unpredictable conditions with fitness consequences over several environments and multiple generations (Joschinski and Bonte, 2020; Simons, 2011; Tougeron et al., 2020a). Whether candidate bet-hedging traits may lead to a higher fitness thus remains to be tested in both hosts and parasitoids.

III. Consequences on species interactions, population dynamics, community structure, food web and ecosystem functioning

How responses and strategies by hosts and parasitoids to predictable and unpredictable thermal conditions can influence host–parasitoid species interactions, population dynamics, community structure and the food web, as well as the regulation of host pests by parasitoids, is a major concern. Responses of these interacting species to predictable temperatures have been mainly studied by comparing differences in thermotolerance and perception of signals inducing diapause, while responses to unpredictable temperatures have mainly focused on prolonged diapause (i.e. diapause for 1 year or more, but rarely more than 3 years) on a temporal scale, and on over-distribution of progeny on a spatial scale.

Host–parasitoid mismatches in thermal biology

Mismatches in thermal physiology between hosts and parasitoids lead to increased vulnerability of parasitoids to climate variation compared with their hosts, because each reacts differently to both predictable and unpredictable thermal conditions. In a meta-analysis, the optimal temperature for parasitoid development was significantly lower than that of hosts in predictable thermal conditions (Furlong and Zalucki, 2017). Modelling then suggested that this difference in optimal temperatures may result in parasitoid exclusion or biogeographical mismatch after a mean temperature increase. Moreover, given the limited plasticity of insect responses to high temperatures and the proximity of the optimal temperature to critical thermal maxima, host–parasitoid interactions could also be negatively affected by unpredictable climatic events, such as heatwaves. Indeed, Le Lann et al. (2014) showed that parasitoids displayed a stronger thermal response in resting metabolic rate compared with hosts in response to a sudden increase in temperature. These changes in resting metabolic rate were linked to a decrease in parasitoid attack rates and an increase in aphid defensive behaviour, resulting in lower parasitism success. This could in turn increase the probability of pest outbreaks. Several studies have indeed confirmed that parasitoids have lower thermotolerance capacities than their hosts, which should result in lower effectiveness of parasitoids as biocontrol agents (Biale et al., 2020; Machekano et al., 2018; Mutamiswa et al., 2018).

In ectotherms, extreme climatic events rather than gradual increases in mean temperatures, are more likely to drive genetic and phenotypic changes (Logan and Cox, 2020). Nevertheless, parasitoids and hosts may still differ in their sensitivity to extreme and mean temperatures. This was investigated by measuring thermotolerance capacities of aphid parasitoids (Tougeron et al., 2016) and their hosts (Alford et al., 2018), collected in cereal fields within simple and complex landscapes. In this environment, landscape complexity significantly affected microclimate, as complex landscapes (i.e. with high hedgerow density, small field sizes and presence of grassland areas) were on average

cooler, but with smaller temperature variation than simple landscapes (i.e. with low hedgerow density, large field sizes and presence of few semi-natural elements). Hosts and parasitoids had different thermotolerances according to the landscape type. Parasitoids originating from complex landscapes were less cold tolerant than those from simple landscapes (Tougeron et al., 2016), whereas the reverse was found for aphids (Alford et al., 2018). This leads to the hypothesis that parasitoids are more sensitive to extreme temperatures, such as unpredictable cold stress, whereas hosts are more sensitive to changes in predictable mean temperatures.

Plasticity: responses to predictable climatic conditions

Using the loss of diapause in aphid parasitoids as detailed in section I as an example, we will here examine the incidence of this response to both abiotic (increase in predictable temperature) and biotic (increase of resources during winter following an increase in temperature) conditions within the framework of plasticity at the community and food web levels. In Brittany (France), the typical winter communities of aphids and parasitoids in cereal fields have been described for the last 30 years. During winter, two main aphid species, *Sitobion avenae* and *R. padi*, were observed to reproduce parthenogenetically 30 years ago in France's warmest areas (Dedryver et al., 2001), and a third aphid species *Metopolophium dirhodum* being present in cereal fields only in the spring. Two parasitoid species were also present, *Aphidius matricariae* and *Aphidius rhopalosiphi* (Krespi et al., 1994). A decade ago, the number of active species increased with the first appearance of the spring aphid *M. dirhodum* and the parasitoid *A. avenae* during the winter of 2011 (Andrade et al., 2016). In the following years, the number of parasitoid species present during winter continued to increase, and at present the food web consists of three aphid species, six parasitoid species and a few hyperparasitoid species. With a higher availability of host aphids during winter, the biotic and abiotic thresholds inducing diapause are no longer present for the parasitoid species, and diapause becomes a very rare strategy in natural populations. The production of non-diapausing offspring, a new optimal phenotype for the novel environmental conditions that results from parental effects (loss of the response to photoperiod) is an example of TGP that plays a major role in species adaptation to climate change, with consequences at the population and community levels for both guilds. The food web is completely modified in terms of complexity and relative abundance of all species, with a high variability between years (Tougeron et al., 2018b). In addition to these studies linking changes in individual strategies to changes in populations and communities, other studies have examined the specific impact of fluctuating temperatures on the resilience or stability of host–parasitoid systems. For example, Bannerman and Roitberg (2014) showed that an exposure to more frequent warm days can be at the origin of host–parasitoid extinction. Most models and experimental studies do not, however, examine the mechanisms behind the change in host–parasitoid interactions. There is thus a need to combine studies at the individual level with community responses to biotic and abiotic factors to disentangle the role of plasticity at the food web level.

Responses to unpredictable conditions: temporal and spatial bet-hedging

In host–parasitoid interactions, a temporal scale (prolonged diapause) and a spatial scale (over-dispersion of progeny) strategy of bet-hedging were studied, including impacts at the community level.

An example of diversified bet-hedging can be found in some insect species inhabiting unpredictable environments for which part of the

population displays prolonged diapause, i.e. for more than 1 year (Corley et al., 2004; Danks, 1987; Tauber et al., 1986). Theoretical studies by Menu et al. (2000) and Mahdjoub and Menu (2008) showed that despite a dispersal cost, mixed diapause strategies with low prolonged diapause frequency can have a higher invasion speed than a simple diapause strategy (emergence after 1 year) when environmental stochasticity is sufficiently high. Diversified bet-hedging in prolonged diapause can evolve in response to selection imposed by environmental stochasticity (including biotic stochasticity such as the presence or absence of hosts for parasitoids) and increasing species persistence. The conclusion from theoretical studies that prolonged diapause is a response to temporal variation in resource condition is supported by the observation that species with such a diapause strategy often inhabit unpredictable environments or feed on unpredictable resources, e.g. Brockerhoff and Kenis (1997) and Ringel et al. (1998). A consequence of prolonged diapause is that a given genotype is maintained over considerable time periods, which allows part of the progeny to grow and reproduce in good environmental conditions that do not occur each subsequent year. In the context of climate change, if winters are cold it is more advantageous to enter diapause, whereas if winters are warm it is more advantageous to remain active. When the environment becomes more and more unpredictable, with warmer winters including numerous short cold events, diversified bet-hedging (having offspring with different strategies: prolonged diapause, simple diapause or no diapause according to the environments) is advantageous.

The developmental synchrony between parasitoids and hosts affects populations of both communities, with consequences at the food web level, and is therefore an important attribute of biocontrol success. The proportion of diapausing parasitoids depends on the proportion of diapausing hosts and its predictability. An imperfect matching resulting from prolonged diapause can produce temporal refuges for a part of the host population. Diapause of parasitoids can be linked to host diapause or be independent. When parasitoids do not kill their hosts during early development, they develop in conformation with their host's physiology ('conformers') and host and parasitoid populations remain synchronised. In such a situation, parasitoids enter prolonged diapause if hosts do, because parasitoids are sensitive to host hormones and more generally to host physiology. When parasitoids kill their host at an early developmental stage, diapause is completely independent from that of their host, also preventing host (prolonged) diapause. These parasitoids are referred to as 'regulators' (Corley et al., 2004). Ringel et al. (1998) proposed a model showing that prolonged diapause strongly increases the stability of the interaction in host–parasitoid systems, because part of the host population that remains in diapause is inaccessible to foraging parasitoids. In this model, regulator parasitoids achieve higher suppression levels than conformers when the proportion of hosts in prolonged diapause is high. However, Corley et al. (2004) showed that the conditions required by the model of Ringel are rarely encountered in nature and that prolonged diapause of hosts has only a weak potential to stabilise host–parasitoid relationships, because this refuge is reached by only a small part of the host population. A more recent study assessed the impact of winter warming in a host population (the pine processionary moth) that displays prolonged diapause at a highly variable incidence within their geographical range (Salman et al., 2019 preprint). At both lower and upper ends of the thermal range in winter, prolonged diapause tended to be higher than at intermediate temperatures. Climate change leads to a decrease in the proportion of individuals entering prolonged diapause in colder regions, whereas the proportion increases in warmer regions, with

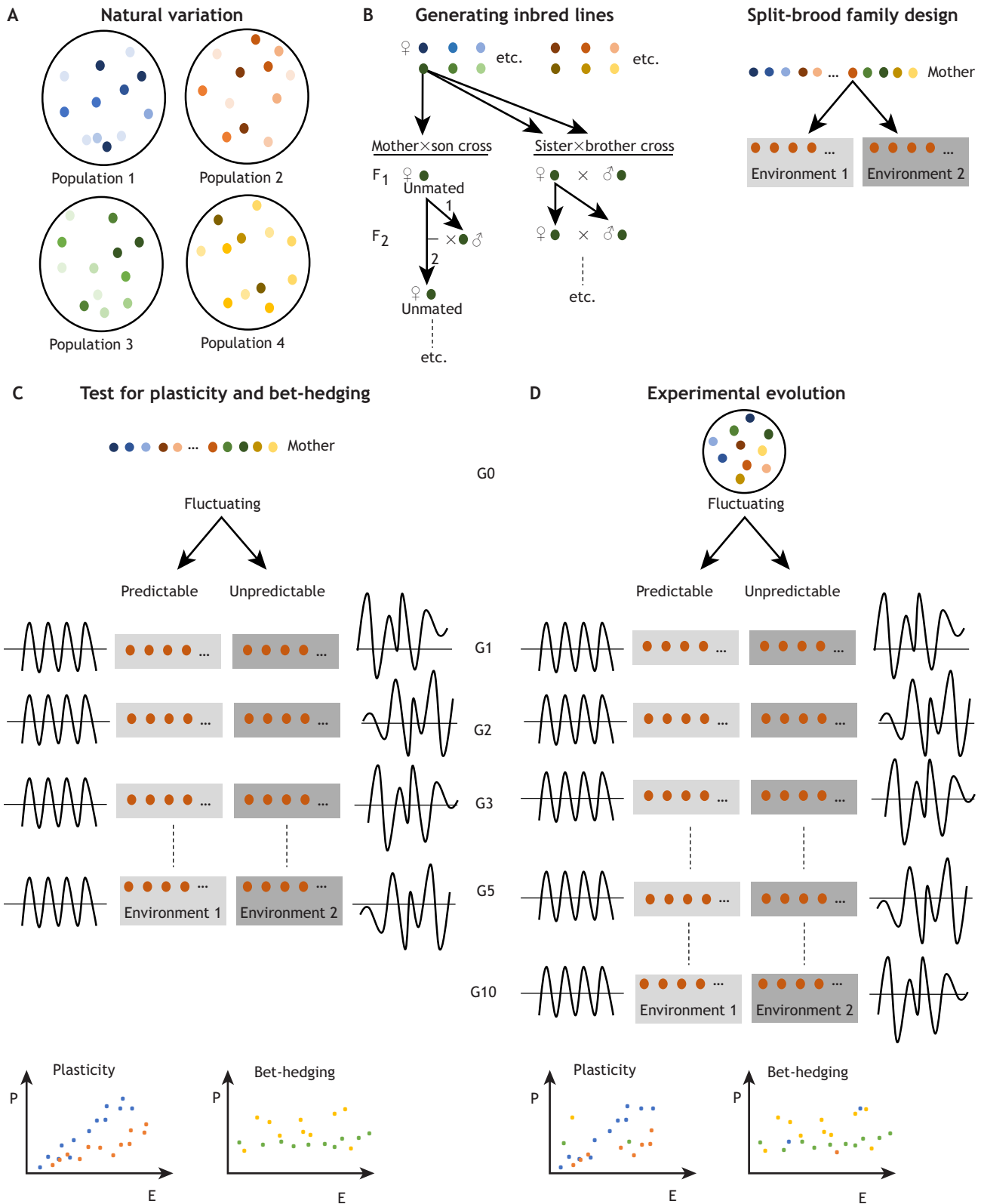


Fig. 1. Experiments to test for plasticity and bet-hedging. Collecting natural populations with phenotypic variation (A), generating inbred lines and performing a split-brood design (B), and testing for plasticity and bet-hedging using inbred lines exposed to predictable and unpredictable fluctuating environments up to the 5th generation G5. Plasticity is expected under predictable thermal regimes, while bet-hedging is expected under unpredictable thermal regimes (C). Experimental evolution with similar thermal regimes using populations with standing genetic variation originating from inbred lines, i.e. with known genotypic combinations. Plastic genotypes may outcompete others under predictable environments, while bet-hedging genotypes may outcompete others under unpredictable environments (D). P, phenotype; E, environment.

consequences for host population dynamics. As numerous parasitoids and predators of the pine processionary moth are univoltine and cannot continue synchronisation with individuals entering prolonged diapause, we can expect that these pest populations will be better able to escape their natural enemies in the warmer places of their range area, but this remains to be studied.

On a spatial scale, an efficient bet-hedging strategy was shown in the parasitoid *Anaphes victus* in Canada. In this species, the winter strategy of individual females is to over-disperse their progeny by ovipositing eggs in more different locations, while parasitising fewer host weevil eggs per location. This allows a female to avoid losing all her progeny if the host eggs are exposed to cold events. Indeed, during winter a large number of weevil eggs are covered by snow, which offers good protection against cold air, but is unpredictable, because it depends on snowfall and snowbanks that shift as wind blows across fields and bushes (Boivin, 1994; Hance et al., 2007). Winter warming will decrease snow cover, and even if mean winter temperatures increase, developing parasitoids will be exposed to cold stress more often, with consequences for population dynamics the following spring, and a probable decrease of the biocontrol service, although this was not explicitly measured. In this example, the benefit of an efficient spatial bet-hedging strategy can be cancelled out by winter warming. No study has, however, showed new bet-hedging strategies in responses to the increase of fluctuating environments as a consequence of climate change.

In conclusion, aside from these studies of prolonged diapause and over-dispersion of the progeny, no studies were performed on bet-hedging strategies in host–parasitoid systems in the context of climate change and with consequences at the population and community levels. As quantitative predictions of theoretical models on the effects of fluctuating environments differ from those of optimisation models using maximisation of arithmetic mean fitness, other traits should be studied in more detail to understand their modification in the context of increased unpredictability.

IV. Perspectives

The examples described in sections I and II show that predictable and unpredictable variation in temperature can trigger markedly different phenotypic responses in single species. Phenotypic plasticity is expected when variation is at least partially predictable, whereas bet-hedging will be favoured in unpredictable environments. Both hosts and parasitoids can, however, still respond very differently to changes in the mean and variance in temperature due to trade-offs, evolutionary history and genetic background. A host's response to fluctuating temperatures can in turn affect that of its parasitoid; hence interacting species should be studied together. We propose future studies on the effect of predictable and unpredictable fluctuating environments to focus on natural host and parasitoid populations that differ in thermal responses (Fig. 1A; e.g. low versus high latitude or altitude, populations at range margins), using genetically similar individuals (e.g. clones, inbred lines, split-brood family designs) to test for plasticity (Fig. 1B), bet-hedging (Fig. 1C), and longer-term evolutionary responses (Fig. 1D). This could be achieved by measuring a suite of distinct traits (physiological, behavioural and morphological) that may also be correlated such as sex, dispersal and diapause (Gerber and Kokko, 2018) and including fitness-related traits (e.g. survival and reproduction). The novelty lies in the use of naturally co-evolved host and parasitoid strains, and studying the expression of multiple traits of single genotypes, which allows for a more accurate prediction of how hosts and parasitoids will respond to rapid climatic change.

We propose several study systems. *Drosophila* species and their natural guild of parasitoids, because they are easily collected from the

field and maintained in the laboratory, and a large knowledge base already exists for several *Drosophila* species (sections I and II). Aphids and their parasitoids provide another interesting system for measuring the resulting consequences of both host availability and thermal constraints on parasitoid plasticity and bet-hedging strategies. Indeed, the loss of sexuality in insects, including aphids, seems to be an adaptation to the colonisation of more stable predictable environments, whereas sexual populations may live in more variable climatic conditions. Sexual lineages tend to be more plastic and show a greater capacity to resist extreme temperatures or rapid changes in temperatures (Amat et al., 2017). Sexual strains may therefore need to produce more diverse progeny, a condition for plasticity and bet-hedging evolution (Amat et al., 2017). For parasitoids, host choice (Eoche-Bosy et al., 2016; Kraaijeveld et al., 1995) and availability (Moiroux et al., 2013) may in turn trigger different plastic and bet-hedging responses, in particular in the context of diapause (Tougeron et al., 2020a). However, in all these examples the link with food web modification remains to be characterised, because a change in host or parasitoid behaviour will impact the interaction.

We can further identify several untested hypotheses that can be addressed with our proposed framework (Fig. 1). To date, transgenerational effects of temperature on offspring behavioural traits have not yet been measured in parasitoids or in insects in general (Abram et al., 2017). Behavioural plasticity can evolve when insects are faced with rapid changes in temperatures. Thermal preferences especially for climatic micro-habitats within one generation (section I) may be selected on a longer term. Furthermore, responses to mean temperature, acute exposure to extreme temperatures and fluctuations act through largely independent mechanisms (Sørensen et al., 2016). Therefore, adaptations to more or less predictable fluctuating environments may be under distinct genetic control, and how this would lead to differential evolutionary responses still needs to be investigated. This would require identifying genotypes expressing bet-hedging or (transgenerational) plasticity and to assess which ones outcompete the others over several generations. This has never been addressed empirically so far in insects, as was done for bacteria (Beaumont et al., 2009). Moreover, we need to consider that, in natural conditions, there is a continuum of entirely predictable and entirely unpredictable thermal conditions. A unifying framework was therefore proposed by Joschinski and Bonte (2020), based on traits with binary outcomes like diapause incidence, to connect transgenerational plasticity to bet-hedging and their role in adaptation in the context of climate change. Finally, a growing number of studies have shown that the interplay between rapid evolution and ecology can affect community and food web dynamics, but we still need to explore how pervasive this conclusion is in host–parasitoid systems.

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Competing interests

The authors declare no competing or financial interests.

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