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1 **Survive a Warming Climate: Insect Responses to Extreme High**
2 **Temperatures**

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16

17 Running title: Insect Responses to Heat Extremes

18

19 **Abstract:**

20 Global change includes a substantial increase in the frequency and intensity of
21 extreme high temperatures (EHTs) which influence insects at almost all levels. The
22 number of studies showing the ecological importance of EHTs has risen in recent
23 years but the knowledge is rather dispersed in the contemporary literature. Here we
24 reviewed the biological and ecological effects of EHTs actually experienced in the
25 field, i.e. when coupled to fluctuating thermal regimes. First, we characterized EHTs
26 in the field. Then, we summarized the impacts of EHTs on insects at various levels
27 and the processes allowing insects to buffer EHTs. Finally, we argue that the
28 mechanisms leading to positive or negative impacts of EHTs on insects can only be
29 resolved from integrative approaches considering natural thermal regimes. Thermal
30 extremes, perhaps more than the gradual increase in mean temperature, drive insect
31 responses to climate change, with crucial impact on pest management and biodiversity
32 conservation.

33

34 **Keywords:**

35 climate change, extreme climate, life history trait, demographics, heat tolerance,
36 thermoregulation

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41 **1. INTRODUCTION**

42 Temperature varies across temporal and spatial scales in terrestrial and aquatic
43 ecosystems (65, 117). Most insect species experience thermal fluctuations that can
44 involve sublethal or lethal extreme high temperatures (EHTs) which affect
45 physiological processes (39) and ecological systems (34). Frequent EHTs may even
46 lead to adaptive evolution in insects (65). For decades, however, most studies
47 concerning thermal effects on insects concentrated on the response to mean
48 temperature or to fluctuations within the tolerable range while ignoring variations in
49 the characteristics of EHTs (89, 105). Recently, researchers realized the biological and
50 ecological importance of fluctuating temperature regimes but little attention is paid to
51 the impacts of ecologically-relevant EHTs (17).

52 Global climate change includes a substantial increase in the occurrence of EHTs
53 (1, 60), and this increase will continue in the near future (96). By contrast, the
54 occurrence of cold extremes (cold spells, cold nights) is largely decreasing (1, 34).
55 Thus, in a warming world, insects will be challenged mostly by elevated body
56 temperatures (65). Neglecting daily temperature extremes generates inaccurate
57 predictions when modeling the impacts of climate warming on populations (89). The
58 key role of EHTs in the response of insects to warming is now attracting more
59 attention and there is an urgent need to synthesize the disparate works. Here, we
60 provide an overview of how natural EHTs impact insect performance at individual,
61 population and community levels, by considering that EHTs are filtered by
62 microhabitats and buffered by insects through behavioral thermoregulation,

63 phenotypic plasticity (e.g., acclimation), ontogeny variation, adaptive evolution and
64 the resilience of their network (Figure 1). Our synthesis complements previous works
65 that focused on the effects of low temperatures (125), or increase in mean temperature
66 (119) and fluctuation regimes (26), to finally provide a comprehensive understanding
67 of the impact of climate change on insects.

68 **2. HOW DO WE CHARACTERIZE THERMAL EXTREMES?**

69 **2.1. Definition and description of extreme high temperatures**

70 Until recently, no unified definition of EHTs existed in an environmental perspective.
71 Meteorologists define EHTs as the temperatures above the 90th, 95th or 99th
72 percentile of temperature distributions (1, 60), and similar indices are used by
73 ecologists (17). The definition of EHTs can also be based on their societal impacts.
74 The historical heat wave that hit Europe in 2003 is often used as a reference (9).
75 Finally, another definition comes from biology, with environmental temperature
76 exceeding upper physiological thresholds of focal organisms (96). Overall, a hybrid
77 definition for EHTs corresponds to an “episode where climate or climate-driven
78 conditions trigger a negative threshold-like (non-linear) biological response” (6).

79 The variables used to characterize EHTs are highly variable among studies,
80 resulting in difficulties to compare directly their results. Most studies on EHTs are
81 opportunistic and usually lacking replication (126). Controlled field experiments often
82 simulate a single level of a given climate extreme imposed at a small spatial scale
83 (126). The lack of a clear description of characteristics of EHTs limits our
84 understanding of how such irregular EHTs affect biological systems (46, 87, 92, 122).

85 Thus, resolving the main components of EHTs becomes more meaningful than a
86 general definition for ecological research (Figure 2). Based on field temperature data
87 including EHTs (87), we identified several important characteristics: daily maximum
88 and minimum temperatures which define the daily amplitude during the EHT events;
89 the frequency of EHT events over long temporal scale (typically the number of hot
90 days during a given period); the time elapsed between each subsequent EHT event,
91 defining the temporal variance of extreme events. By manipulating values of each
92 variable and their combinations, experimental designs in laboratory, mesocosms or in
93 the field can quantify the impacts of EHTs with varying intensity, frequency, duration
94 and temporal variance on fitness-related life history traits and demography (Figure 2).

95 In the field, insects experience temperature cycles with a single or several
96 successive hot days alternating with a few mild days (87, 148). Diurnal cycles also
97 alternate several hot hours around mid-day with mild hours (89, 147). Thus, the
98 effects of EHTs depend largely on their characteristics which are complex to describe
99 and to simulate in the lab or mesocosms due to the stochastic nature of EHTs.
100 Intensity, duration and frequency are often used to link ecological performance and
101 EHTs (46, 92, 122), despite the high uncertainty in these metrics. Simple statistical
102 characteristics of EHTs were designed to explore the impact of different temperatures
103 during daytime (89) and nighttime (147), different frequencies of hot days (86, 145)
104 and different amplitude of fluctuation (140). During hot events, insects can be injured
105 by EHTs approaching their physiological thresholds but the mild temperatures
106 between hot events allow insects to repair (5, 87). The temporal sequence of hot and

107 mild phases is therefore an important characteristic of EHTs (87, 148). The impact of
108 EHTs should be a subtle balance between heat injury and recovery (5, 87, 148).

109 **2.2. Thermal extreme vs. mean temperature**

110 Thermal performance curves (TPCs) are often used to describe the response of
111 biological performance to temperature based on constant temperature treatments (124).
112 TPCs are asymmetrical and nonlinear, thereby generating Jensen's inequality (120)
113 which is used to describe the biological effects of environmental variability (31).
114 TPCs, combined with Jensen's inequality, are frequently used to compute insect
115 performance under fluctuating/changing temperatures, feeding predictions of climate
116 change impacts (15, 72, 105, 124, 134). Based on Jensen's inequality, the effects of
117 temperature variation would be positive, small and dramatically negative at low,
118 intermediate and high temperatures, respectively (31, 76). The left-skewed TPCs
119 show that the thermal optimum (T_{opt}) is close to the critical thermal maximum (CT_{max}),
120 meaning that even a small variation in mean temperature above T_{opt} can push insects
121 over CT_{max} , leading to dramatic decline in performance and fitness (105).

122 By causing an increase in thermal variance and in the strength of the Jensen's
123 inequality, EHTs negatively impact insect fitness even if mean temperature remains
124 near the optimal range (87, 89, 105). Indeed, the impact of increasing variance on key
125 traits related to fitness can be larger than an increase in mean temperature (89, 105,
126 140). Greater variance caused by EHTs can lead to decreased maximum performance,
127 truncated thermal performance breadth and narrow thermal safety margin (105, 134).
128 However, ambient temperature fluctuates usually with reasonable amplitude up to

129 sublethal daily maxima. Near-optimal temperature may occur during some parts of the
130 day (e.g., morning, night) and thus provide an opportunity for insects to recover from
131 heat injuries occurring around midday (87, 148). A better performance is therefore
132 expected under variable regimes than under constant high temperatures. For example,
133 temperature variation can improve rather than depress the development of aphids
134 when the mean temperature is higher than the T_{opt} for development, thereby
135 challenging the “Kaufmann effect” (147). Importantly, using TPCs derived from
136 constant temperatures to predict insect fitness in field conditions contains the
137 unrealistic assumption that performance is independent of thermal history, rates of
138 temperature change and exposure times (124). More work on the thermal responses to
139 the EHT characteristics will certainly help to design novel approaches to draw TPCs
140 that could incorporate the influence of EHTs on insect performance and fitness.

141 **2.3. The seasonal and diurnal patterns of EHTs**

142 The amplitude of warming, including more frequent and intense extremes, is higher in
143 spring, autumn and winter than in summer (1, 60). However, the biological impacts of
144 EHTs in these seasons are relatively overlooked. EHTs in spring affect the
145 phenological synchronization between plants and herbivore insects (77, 115) and
146 parasitoids (37). EHTs in autumn may affect diapause induction, subsequent
147 overwintering survival and spring population growth (132). EHTs in winter may
148 influence survival during diapause and post-diapause development (11, 127).
149 Individuals of univoltine species can experience EHTs across different seasons (118).
150 Yet we have little information on seasonal stage-specific responses and their

151 consequences at the population level. Moreover, the amplitude of nighttime warming
152 is higher than daytime warming (1, 60). Nighttime warming leads to contrasting
153 effects on thermal performance and fitness, in contradiction with the predictions based
154 on constant temperatures (147) or daytime warming (8, 89). To date, however, only
155 few studies explored the specific effects of diurnal vs. nocturnal patterns of EHTs on
156 insects (5, 8, 89, 147).

157 **3. HOW DO INSECTS RESPOND TO THERMAL EXTREMES?**

158 **3.1. Physiological, biochemical and symbiont responses**

159 **3.1.1. Mechanisms underlying heat damage**

160 Heat damage in insects involves a series of disorders at the molecular, biochemical
161 and physiological levels (14, 25). Heat-induced changes in the fluidity of
162 phospholipidic membranes and cellular homeostasis initiate heat damage (14). The
163 OCLTT hypothesis (oxygen and capacity limitation of thermal tolerance) proposes
164 that performance is constrained by the capacity for oxygen delivery relative to oxygen
165 demand. The delivery of oxygen is the limiting factor during EHTs (35, 114). This
166 hypothesis was confirmed in several aquatic species (135). However, it is not
167 generally applicable to terrestrial insects since they are unlikely to become oxygen
168 limited (14, 79), except if they live in close microenvironment such as plant galls
169 (109). Finally, EHTs can disrupt the cellular ion balance (hyperkalemia), thereby
170 impairing neurophysiological functions (103) and damaging mitochondria (14).

171 **3.1.2. Physiological and molecular responses**

172 Insects can produce and accumulate particular molecules to prevent protein
173 denaturation or cell inactivation during EHTs. Polyols, e.g. mannitol in *Aphis gossypii*
174 and sorbitol in *Bemisia argentifolii*, are accumulated to cope with daytime EHTs (54).
175 Mannitol and sorbitol quantities were higher at noon than during early morning.
176 Heat-shock proteins (Hsps) (39, 85) and cuticle proteins (102) are induced and/or
177 accumulated to deal with EHTs. Apple maggots express Hsp increasingly from
178 midday to peak in late afternoon, paralleling the dynamics of air and fruit temperature
179 in summer (85). Locusts are more heat-tolerant at low- than at high-latitude as a result
180 of their expression pattern of Hsp70 and Hsp90 (22). The potato aphid increases
181 concentration of several exoskeletal proteins during heat stress (102).

182 **3.1.3. Symbiont-mediated responses**

183 Bacterial endosymbionts provide essential nutrients to their insect host. EHTs depress
184 the diversity, abundance and activity of endosymbionts, decreasing heat tolerance and
185 fitness of the host insect (38, 70). For example, EHTs decrease the quantity of
186 symbiotic bacteria, lowering heat tolerance in ants (38) and aphid species (142), and
187 altering fitness-related traits in stinkbugs (70). Nevertheless, endosymbiosis may
188 assist insect hosts to adapt to natural EHTs. In aphids, clones with heat tolerant
189 symbionts develop faster than clones without under EHTs (52). Mutants of the
190 symbiont *Buchnera aphidicola* with lower expression of heat-shock gene *ibpA*
191 decrease heat tolerance of pea aphids (142). In addition, facultative symbionts, e.g.
192 *Serratia symbiotica* and *Acetobacter* can protect *B. aphidicola* from short-term heat
193 shock, improving aphid fecundity and offspring survival under EHTs (100).

194 **3.1.4. Morphological responses**

195 EHTs can induce changes in body size of insects. High developmental temperature
196 generally produces small individuals due to enhanced metabolism and fast
197 development (4, 20, 131). This temperature-size rule arises due to phenotypic
198 plasticity or selection for smaller body sizes (4, 41), although smaller individuals are
199 more vulnerable to dehydration and overheating (44). However, small body size may
200 facilitate heat damage in insect gut or gut symbionts, depriving nutrients and water
201 (70). However, we know little about the growth trajectories under repeated EHTs and
202 the underlying physiological mechanisms. For example, frequent heat exposure
203 produces large individuals sometimes(123, 140). The selective advantage of smaller
204 size might become disadvantageous under repeated EHTs (44).

205 **3.2. Fitness-related life history traits and demography**

206 **3.2.1. Stage-specific responses**

207 All stages of insects may experience EHTs. Meanwhile, different stages or instars
208 often have different thermal sensitivities (13, 74, 146). Therefore, EHTs may produce
209 stage-specific thermal responses. Generally, the thermal response of development,
210 survival, reproduction and longevity varies with life stage (144) and adults are often
211 more vulnerable to EHTs. For example, EHTs reduced more reproduction when they
212 occurred closer to adulthood (141, 143). Both early and reproductive stages of
213 *Sitobion avenae* (146) and *Plutella xylostella* (143) are the most sensitive to EHTs
214 compared to mature larvae. Thus, the stage at which the insects are exposed to EHTs
215 is an important component setting the impact of EHTs. Three potential mechanisms

216 may be involved in ontogenetic variations of thermal tolerance. 1) “Microclimate
217 selection” hypothesis states that different stages live in and thus adapt to different
218 thermal environments (74, 108, 139). 2) “Body size” hypothesis (75) explains why
219 larger larvae are more heat tolerant than the smaller early life stages (86, 144, 146)
220 which have faster increase of body temperature (3) and water loss (45), but it fails to
221 explain the decreased tolerance at adult stage. 3) “Bogert effect” hypothesis suggests
222 that the immobile stages (egg and pupa) should be more heat tolerant than mobile
223 adult and larval stages due to their lower ability for behavioral thermoregulation (58),
224 but this hypothesis has been rejected frequently (75).

225 **3.2.2. Trait-dependent responses**

226 Different life history traits differ in their thermal sensitivity (69). Among the main life
227 history traits, reproduction has the narrowest thermal range, followed by development,
228 while survival has the widest. Reproductive potential is expected to be the most
229 vulnerable fitness-related life history traits to EHTs (136, 143). For example, a single
230 hot event of few hours does not affect survival but decreases reproduction in the
231 moths *Plutella xylostella* (145) and *Grapholitha molesta* (80). The optimal
232 temperature for reproduction is lower than for development (89, 147), while the
233 optimal temperature for immature survival is often a relatively wide range. When
234 temperature increases continuously and surpasses the optimum, development would
235 be restricted and soon mortality occurs (46, 63, 89), indicating slightly higher
236 temperature thresholds for survival than for development. Thus, the critical upper
237 thermal limits are: reproduction < development < survival (89, 147).

238 **3.2.3. Immediate, cross-stage and transgenerational responses**

239 The impact of EHTs occurs at various temporal scales across insect life cycles,
240 leading to immediate impacts at the exposed stage (24, 86, 116, 140), permanent
241 damage at later stages through carry-over effects (24, 75, 141, 144, 146), and
242 transgenerational effects via parental effects (145). The immediate impacts incur all
243 the molecular, physiological, and morphological mechanisms developed above and
244 are reflected in heat death or delayed development during the events. EHTs in early
245 life stages can influence performance of later stages or next generation depending on
246 the intensity of EHTs, although this is still a matter of debate. Lifecycle modularity
247 hypothesis and adaptive decoupling hypothesis (116) state that early life stress has no
248 effects on adult performance, probably because the stressful temperatures are not
249 extreme enough. However, there is evidence that extreme temperatures occurring in
250 egg, larval or pupal stages can decrease survival (144) and fecundity (24, 75, 141, 146)
251 of adults through carry-over effects, or even result in decreased offspring survival via
252 transgenerational effects (145). Nevertheless, we still know little about the
253 mechanisms underlying carry-over and transgenerational effects of extremes.

254 **3.3. Population dynamics**

255 **3.3.1. Phenology and voltinism**

256 Frequent EHTs increase overall mean temperature, advancing spring and postponing
257 autumn in the calendar, and causing shorter winters and longer growing seasons (99).
258 For non-diapausing insects, frequent EHTs may advance phenology in spring and
259 postpone phenology in autumn, increasing thereby the number of annual generations

260 (2, 99). However, for insects with obligate diapause, the combination of longer
261 summers and shorter/warmer winters delays adult emergence due to insufficient
262 winter chilling for diapause termination and to the reduced ability to regulate the
263 onset and termination of diapause (20). For insects with facultative diapause, winter
264 warming leads to earlier diapause termination (127). Nevertheless, EHTs do not
265 always significantly increase the overall mean temperature and their effects on
266 phenology and voltinism remain largely unknown for most insects. Few consecutive
267 hot days occurring in autumn or spring would potentially disturb diapause induction
268 or post-diapause development, thereby altering the phenology of insects.

269 **3.3.2. Abundance**

270 Repeated EHTs generally depress insect survival, fecundity and abundance (20, 87, 89,
271 101, 122, 147). For example, the increase in daily maximum temperature dramatically
272 reduces arthropod biomass in a rainforest (82). However, the effects of EHTs on
273 insect abundance are complex due to the variations in the characteristics of EHTs,
274 local baseline climates and habitat uses, species-specific thermal sensitivity of insects
275 and the biotic interactions with other species. For instance, frequent EHTs depress
276 abundance of heat sensitive species *Sitobion avenae* and *Schizaphis graminum*
277 whereas they have null or even positive impacts on the heat tolerant species
278 *Ropalosiphum padi* (92). Frequent EHTs reduce the abundance of *S. avenae* at the
279 southern margin but not in the north (92). EHTs may also favor soil insects by
280 enhancing their reproduction and abundance (81). Extremely warm winters occurring
281 at high latitudes can increase insect abundance (48). However, EHTs in the Arctic

282 winter also accelerate snowmelt, decreasing indirectly insect abundance (11).

283 **3.4. Biotic interactions and community structure**

284 **3.4.1. Changes in community composition and structure**

285 Differences in thermal tolerance of insects at the same trophic level can alter the
286 relative dominance and interspecific competition among species (11, 21, 46, 92),
287 leading to EHT-driven changes in the composition of communities (130). For example,
288 more frequent EHTs alter the structure of cereal aphid communities across large
289 temporal and geographical scales (92). In this case, EHTs alter the dominant pest
290 species in winter wheat crops (92). EHT during summer affects interspecific
291 competition in Mediterranean ant communities by changing the circadian rhythm of
292 foraging in subdominant ants but not for dominant species (21). Insects are usually at
293 the intermediate or lower trophic levels in communities and ecosystems. The
294 EHT-induced changes in the composition and structure of insect communities could
295 potentially influence top-down and bottom-up processes in plant-insect
296 herbivore-predator systems.

297 **3.4.2. Cascading effects across multitrophic systems**

298 Increasing frequency and intensity of EHTs enhances vulnerability of species at
299 higher trophic levels (23, 101), although this rule cannot be generalized (42, 122).
300 Thus, EHTs are likely to reduce predator diversity and disrupt ecosystem services
301 such as natural biological control (7). Nevertheless, biodiverse multi-trophic
302 assemblages are more resilient to EHTs (46, 61, 122). For simplified food-chains

303 including only two trophic levels such as plant-insect herbivore (46), prey-predator
304 (101, 122) or parasitoid-hyperparasitoid systems (23), the species at higher trophic
305 levels are more susceptible to EHTs. However, the overall effects of EHTs on
306 tri-trophic systems such as plant-insect herbivore-predator/parasitoid are much less
307 dramatic and often similar to patterns under normal climates (46, 122). Studies on the
308 relationship between EHTs and the responses of each trophic level are helpful to
309 clarify the resilience of ecological communities to changes in climate extremes.

310 **3.5. Geographical distributions**

311 Heat tolerance is weakly linked to latitude in insects, but tolerant species often are in
312 warm microhabitats while heat vulnerable species remain mostly in cooler
313 microhabitats (42, 110). Thermal safety margin, defined as the difference between the
314 CT_{max} of insects and the ambient maximum temperature of the hottest month (66,
315 134), is frequently used to predict insect distribution following EHTs. Thermal
316 extremes exceeding CT_{max} restrict the thermal performance range and influence the
317 distribution across latitudes and altitudes and in heterogeneous landscapes (72, 104,
318 134), shaping thereby the distribution of insects worldwide (66, 94). EHTs can shift
319 distributions through local extinction induced by mass mortality due to fitness decline,
320 to mismatch in the phenology of insects and host plants (20, 97) or to interaction with
321 landscape fragmentation (106). However, EHTs in winter or nighttime may release the
322 constraint of low temperatures, leading to positive effects such as increased winter
323 survival and dispersal abilities in insects (9, 10), resulting in range expansion.
324 Prolonged heat waves lead to an increase in number of nights above the flight

325 threshold temperature, promoting the take-off behavior in *Thaumetopoea pityocampa*
326 and causing a rapid distribution shift to higher altitudes in the Alps (9). Some species
327 with higher adaptive potential in heat tolerance can expand their range to lower
328 latitudes (56).

329 **4. HOW DO INSECTS BUFFER AGAINST THERMAL** 330 **EXTREMES?**

331 **4.1. Microhabitats as filters of thermal extremes**

332 **4.1.1. Mosaic of microclimates**

333 Forecasting biological impacts of EHTs requires general understanding how
334 microhabitats filter environmental fluctuations and whether the heterogeneity will
335 allow insects to escape heat extremes (65, 113, 129). Living and non-living objects in
336 the environment produce a complex mosaic of microclimates which depends on the
337 nature of the objects and how the microhabitat transfers atmospheric variations (138).
338 Little is known, however, on the dynamics of these microclimatic mosaics during
339 thermal extremes (111). In the apple tentiform leaf miner, the location within the tree
340 canopy mosaic of optimal, sub-optimal and lethal micro-environments can be totally
341 reversed during EHTs (112). The temperature gradient at micro-scale matters much
342 for arthropods to escape EHTs. For example, in the flat-rock spider in Australia, few
343 centimeters below hot rocks are enough to change the temperature by 9°C (107).
344 Similarly, the temperature heterogeneity on surface of leaves can be 6 to 12°C (121).
345 Spider mites can fully exploit this heterogeneity by moving over few centimeters but

346 this possibility is restricted during EHTs (19). Aphids are more constrained for their
347 feeding behavior and cannot really exploit this heterogeneity (18). EHTs are expected
348 to alter these fine-scale temperature gradients (19), depending on the baseline
349 buffering property of the microhabitat (138).

350 **4.1.2. Buffering ability of microhabitats**

351 EHTs are transmitted through microhabitat before they reach insects. Different
352 microhabitats filter atmospheric conditions differently. For example, differences
353 of $>5^{\circ}\text{C}$ in the maximal microclimate temperature were measured when comparing
354 different habitats e.g. grassland, heathland and deciduous woodland (128). The
355 understory of forests is probably the strongest buffer of EHTs (28), which is almost
356 independent of the dominant tree species and of latitude (29). Insects would benefit
357 from moving to these microhabitats during EHTs although a direct effect remains to
358 be demonstrated. Nevertheless, some insect species are specialized to microhabitats at
359 the top canopy and the potential for vertical zonation of herbivore insects across forest
360 canopies is important (78). The temperature of leaves hit by solar radiation is higher
361 than ambient air temperature in temperate and boreal latitudes (113), thus the leaf
362 surface magnifies the amplitude of thermal extremes (138). The thermal limit of small
363 herbivore arthropods living at the leaf surface is related to leaf temperature during
364 EHTs (110). Therefore, these herbivores are already vulnerable to contemporary
365 thermal extremes. Similarly, endophagous insects such as leaf miners and
366 gall-inducing organisms are living in their structures (mines, galls) where temperature
367 increases more than ambient air during thermal extremes (108, 109). By contrast,

368 aquatic systems buffer atmospheric temperature variations due to the thermal inertia
369 of water bodies and geophysical processes (138). In general, we lack data on the
370 temperature of most microhabitats to provide an exhaustive ranking from the best to
371 the worse buffer of EHTs.

372 **4.2. Thermoregulation**

373 Behavioral thermoregulation across the mosaic of microclimates plays an important
374 role in avoiding EHTs (95). Thermoregulatory behavior can directly increase survival
375 during EHTs (12, 65, 138). Nevertheless, the availability of suitable microclimates is
376 needed for thermoregulation (138), determining the efficacy of insect buffering
377 against climate warming (19, 65). However, it is predicted that warming will reduce
378 seasonal and diurnal temperature ranges (60), causing decreases in temperature
379 heterogeneity across temporal and spatial scales (65) including microhabitats (19).
380 Thus, behavioral thermoregulation alone may not be sufficient to buffer ongoing
381 climate warming (19).

382 Behavioral thermoregulation can also bring costs and lead to ecological
383 consequences.. More frequent EHTs increase occurrence of thermoregulatory
384 behaviors (90, 137) and maintenance energy costs (65), and in turn decrease foraging
385 activity, energy efficiency and reproduction (65, 87). For example, aphids leave their
386 host plants by dropping off or walking downward to seek cooler microhabitats to
387 escape EHTs (86, 90, 91, 102). Therefore, they may have to endure food and water
388 deprivation and spend time and energy to find another suitable feeding site, thereby
389 reducing reproduction opportunities (88). Moreover, behavioral thermoregulation may

390 also alter the microhabitat use of insects (7, 88). Differences in behavioral regulations
391 and microhabitat use between species can change interspecific interaction and food
392 web structure (7). Furthermore, thermoregulatory behavior may limit evolutionary
393 adaptation by reducing or even eliminating the selection pressure of EHTs (58).

394 **4.3. Ontogenetic variations and tradeoff between different traits**

395 Insects evolved complex life cycles with multiple developmental stages differing in
396 thermal sensitivity (13). However, the role of ontogenetic variation of thermal
397 sensitivity in buffering EHTs has received little attention. Different stages/age cohorts
398 can overlap in field populations, resulting in the coexistence of multiple life
399 stages/age cohorts during growth season. When the mixed-stage population
400 experiences EHTs, the most sensitive stages would be injured or die whereas the most
401 tolerant may survive and develop to adult stage for reproduction during the following
402 mild phases, thereby contributing to population recovery. Comparing to pupal and
403 adult stage, medium and late larval stage can particularly resist heat stress in both
404 immediate survival and subsequent reproduction (145) Larval stages may acquire
405 sufficient nutrients and water to both resist EHTs and provide enough time to recover
406 from heat injury, reducing thereby the carry-over effects of EHTs on adult
407 reproduction.

408 The intrinsic rate of increase, a metric for fitness, integrates survival, development
409 time and reproduction (87, 89). Different responses to EHTs and even trade-off
410 between these traits may also help buffer impacts of EHTs. Temperatures above the
411 optimum for reproduction reduce fecundity (eg, number of offspring) but can also

412 accelerate maturation and reproduction processes (143, 147). Then, when temperature
413 surpasses the optimum for development, insects tend to invest more energy in heat
414 tolerance to improve survival, generating costs that reduce reproduction output (146)
415 and delay development at least temporally (116, 140). Thus, variations in thermal
416 sensitivity of different traits may contribute to buffer heat stress in insects.

417 **4.4. Phenotypic plasticity**

418 Phenotypic plasticity is a non-genetic strategy to cope with environmental variation
419 including thermal extremes (49, 57, 133). Most of the insect responses detailed above
420 relate to phenotypic plasticity. Four types of plasticity in heat tolerance were
421 identified based on the time scale and temperature intensity. “Rapid hardening/heat
422 shock” corresponds to a short and harsh exposure to high temperature for a few
423 minutes or hours (68, 133). The other types of thermal plasticity are all generated by
424 exposure to moderately high temperatures for several hours to days for “acclimation”
425 (laboratory) or “acclimatization” (field) (62, 68), days to weeks for “development
426 acclimation/plasticity” (67, 68, 133) and weeks to months for “transgenerational
427 acclimation” (62). In general, previous exposure to elevated temperatures increases
428 heat tolerance both within and across generations.

429 Nevertheless, the potential to buffer against EHTs through plasticity may be
430 limited. Quantitatively, there is limited scope for plasticity to increase heat tolerance
431 significantly in many arthropod taxa (49, 57, 67, 133). For instance, the increases in
432 CT_{max} of some *Drosophila* species and the moth *Manduca sexta* are limited to only
433 0.6~1.0 °C (67, 133) and 1~2 °C (73), respectively, via hardening and developmental

434 acclimation processes. In addition, increased heat tolerance brings a series of
435 concurrent costs in other plastic traits that are related to fitness (36, 83, 133). These
436 costs can generate considerable transgenerational consequences such as declined
437 offspring size and survival (93).

438 **4.5. Evolutionary adaptation**

439 Frequent EHTs could induce evolution of thermal tolerance to buffer against high
440 temperature impacts (16, 57). Thermal evolution occurs in small insects during
441 artificial selections (40, 51). Long-term thermal selection is commonly found in local
442 adaption, e.g. drosophila and ants at different latitudes (32, 104), or beetles and
443 butterflies at different altitudes (43, 55). Urban heat island also triggers thermal
444 adaptation. Urban workers of ants evolved a CT_{max} 1°C higher than the rural
445 populations (32). Local adaptation often results from a subtle interaction between
446 generation time, heritability, covariance between phenotypes, phylogenetic inertia and
447 the strength of selection (66).

448 However, rapid evolution of thermal traits hardly occurs under natural selection in
449 insects. Higher feeding rates evolved only after decades in nature under more frequent
450 EHTs in *Colias eurytheme* (55). EHTs imbedded in fluctuating patterns may constrain
451 the evolution of thermal traits due to lower heritability under ramping temperature
452 than artificial static temperature (98), slowing down the speed at which insects can
453 track climate warming (51). Thermal selection can also modify fitness-related life
454 history traits (59, 71). Thermal tolerance often incurs fitness costs due to antagonistic
455 genetic interactions between traits (84). Thermal tolerance could also be shaped by

456 phylogenetic inertia rather than thermal selection in nature (66). To some extent,
457 thermal evolution can be a way to buffer EHTs, but its mechanisms are still evasive.

458 **5. KNOWLEDGE GAP AND FUTURE PERSPECTIVES**

459 **5.1. Ecological relevance of experimental designs**

460 The biological impacts of complex EHTs are difficult to investigate
461 experimentally because of their stochastic nature. Open top chambers, infrared
462 irradiation and electronic heating systems are widely used to simulate climate
463 warming including EHTs in the field (50). However, results from these studies are
464 difficult to apply broadly because the mechanisms are not fully understood. The
465 different statistical moments of EHTs (intensity, duration, and frequency) may have
466 biological impacts differing in their direction and amplitude, and their interactive
467 effects could generate counter-intuitive responses in insects. Simulated regimes of
468 EHTs are highly diverse in the literature, including constant temperature for given
469 periods or fluctuations with fixed cycles. Currently, these regimes do not include
470 alternative patterns of EHTs and mild periods which allow stress recovery (87, 147).
471 Here we call for experimental designs with enhanced ecological relevance in future
472 studies by incorporating the complete statistics of EHTs despite the inherent logistic
473 complexity of factoring several variables. In addition, the simulated temperature
474 regimes should be based on microclimatic rather than macroclimatic patterns to
475 improve the ecological relevance. Such level of complexity is mandatory to help us to
476 draw the landscape of insect performances under EHTs in natural thermal conditions.

477 **5.2. Enlarging our vision of extremes**

478 EHTs are by climatological definition relatively infrequent but intense (eg, heat
479 waves). The biological perspective is more conservative in the sense that the thermal
480 events challenging the physiology of insects are likely frequent. Environmental
481 conditions may become suddenly challenging for organisms when several normal
482 events co-occur leading to environmental extremes (30). This shift in perspective was
483 only rarely applied to insects but the methodology and the concepts exist (33). Insects
484 are constrained by several factors in their microhabitats. Dryness aggravates the
485 physiological stress during hot periods. Wind decreases body temperature in the short
486 term, but it incurs higher water loss. The same set of environmental conditions may be
487 extreme for individuals deprived of appropriate endosymbionts but near optimal for
488 those that host these microorganisms. Entomological sciences need to embrace more
489 original and innovative characterizations of extreme events, to be combined with the
490 standard climatological view.

491 **5.3. Rise of integrative approaches**

492 The ultimate goal of global change biologists is to anticipate the future trend of
493 biodiversity. This goal can only be achieved by comprehensive understanding of the
494 mechanisms for organism-environment interactions, and predicting population
495 dynamics and community structure across time/generations. It seems crucial to link
496 physiological mechanisms of thermal stress and the demographic variables.
497 Physiological and genomic approaches have been successfully integrated in studies to
498 link physiological impacts of environmental changes and field patterns of thermal

499 stress. Intertidal ecologists probably led this vision for decades (53), but
500 entomologists now are aligned (47). The next challenge is to integrate the ‘field
501 ecophysiology’ of thermal stress, especially during EHTs, and the population
502 dynamics. Given the importance of individual processes (e.g., carry-over effects,
503 hardening of thermal tolerance, and more generally phenotypic plasticity), approaches
504 including individual-based models (27) are promising candidates to interconnect these
505 processes and link individual and population scales. In addition, microclimate models
506 are needed (64, 111, 112) to simulate the heterogeneous environmental arena within
507 which individuals and species are interacting. Nevertheless, all these processes need
508 to be fine-scaled to incorporate cross-seasonal impacts of EHTs at given moment in
509 the life cycle of insects. Intense collaborations between physiologists, ecologists,
510 climatologists and modelers are key for successful developments.

511 **6. CONCLUDING REMARKS**

512 Thermal extremes are complex events that combine different statistical moments.
513 This complexity adds up the difficulty of getting a comprehensive understanding of
514 their impacts on biological processes. While thermal extremes are defined as rare
515 events by climatologists, ecologists realized that thermal extremes are much more
516 frequent once they are defined relative to the thermal biology of organisms.
517 Nevertheless, the impacts of ongoing climate change on these “biologically-relevant
518 thermal extremes” remain to be identified. In this context, the most studied biological
519 models are *Drosophila* species (39, 51, 66) and other species with conservation
520 importance (61, 82). The thermal ecology of most species with economic importance

521 for agriculture, horticulture and forestry remains largely unknown. Extreme absence
522 of knowledge is an important frontier limiting our ability to anticipate the ecological
523 consequences of extreme heat events.

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SUMMARY POINTS

1. Thermal extremes are complex, multicomposite events. Despite a lack of unified definition of thermal extremes due to this complexity, we can describe natural temperature extremes with several variables related to both the environment and the species thermal biology, defining together the intensity, frequency and temporal variance of extreme high temperature events.
2. Classic thermal performance curves (TPCs) derived from constant temperature experiments cannot be used to estimate the biological impacts of thermal extremes. More sophisticated TPCs are needed to include the influence of the all statistical moments of thermal extremes.
3. Extreme high temperatures often, but not always affect insects at various levels, ranging from molecular and physiological responses, at individual to population scales, to community structure and functioning.
4. Thermal extremes can affect instantaneously survival. They can also produce long-lasting impacts on life history traits and demographics of insects. The magnitude of these effects depends mainly on thermal history, traits and life-cycle stage. Collectively, all these effects translate into population dynamics.
5. Insects may buffer partly or completely the thermal extremes via behavioral thermoregulation, phenotypic plasticity, ontogeny variations, trade-off between different traits and evolutionary adaptation. However, most of these buffering strategies probably have limited potential quantitatively, and they may incur costs for other fitness-related traits.

FUTURE ISSUES

1. Innovative, ecologically-relevant experimental designs are crucially needed to better understand the effects of realistic natural thermal extremes on insect populations, communities and ecosystems.
2. Beyond the instantaneous impacts of thermal extremes, the carry-over effects of heat stress and the stage-specific responses of insects deserve more comprehensive studies to better detail the consequences of thermal extremes.
3. We lack studies on the relative effects of the various strategies to buffer against thermal extremes, including physiological and behavioral thermoregulation, ontogenetic variation, phenotypic plasticity and adaptive evolution in insects. These buffering strategies may incur trade-offs with fitness-related traits, generating complex interactive effects that need to be identified to feed prediction models.
4. The mechanisms underlying heat injury and thermal recovery of insects at the molecular, physiological and ecological levels should be revealed to better comprehend the combined effects of alternating thermal extremes and mild periods.
5. The impacts of extreme high temperatures occurring in fall, winter and spring as well as at night on insect diapause, phenology, interspecific interactions and communities remain relatively understudied.
6. Microclimate models should be used more extensively to generate realistic thermal environments within which insects experience thermal extremes under field conditions in their microhabitats.
7. The thermal biology in context of thermal extremes of insect species of economic importance such as agricultural, horticultural and forestry pests, and their potential biological control agents, should be given priority to improve pest management and beneficial conservation worldwide.

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946 **RELATED RESOURCES**

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985 **Figure captions**

986 **Figure 1.** Diagram illustrating how natural thermal extremes are filtered (often
987 intensity is lowered) by microhabitats and buffered by insects through behavioral
988 thermoregulation, phenotypic plasticity, ontogeny variations and adaptive evolution to
989 ultimately increase survival to heat. Even after filtering and buffering, thermal
990 extremes still impact insect performance at the individual, population and community
991 levels within and across generations.

992

993 **Figure 2.** Characterizing Extreme High Temperatures (EHTs) in the field. (a) A
994 temporal series of microclimatic temperature for a theoretical insect illustrates the
995 different metrics used to describe the occurrence of EHTs (in *red*) and mild periods (in
996 *blue*): their intensity (maximal and minimal temperatures of hot days (HT_{\max} and
997 HT_{\min}) and mild days (MT_{\max} and MT_{\min}), respectively); frequency (the number of
998 consecutive hot days and the frequency at which hot periods occur); temporal
999 variance (the timing of occurrence of hot and mild phases); the biological threshold
1000 (temperature inducing thermal stress in a given organism, or CT_{\max}). The dichotomy
1001 between hot and mild events hides a large range of possibilities when designing
1002 experiments to simulate natural thermal extremes. (b–c) In particular, the maximum
1003 and minimum temperatures of mild and hot days vary within their own range. (d)
1004 These complex thermal extremes with a daily sub-unit are embedded in naturally
1005 fluctuating temperature regimes that can be described by their temporal variance of
1006 EHT occurrence and their frequency (eg, the number of consecutive hot or mild days).

1007 Here, the temporal arrangement of hot and mild days varies across two axis defined
1008 by number of hot days during a period of 10 days (frequency) and the variance in the
1009 number of mild days between each hot day (temporal variance). Note that in panel *d*,
1010 the global mean and variance of temperature remain the same across all
1011 configurations at a given frequency of hot days.

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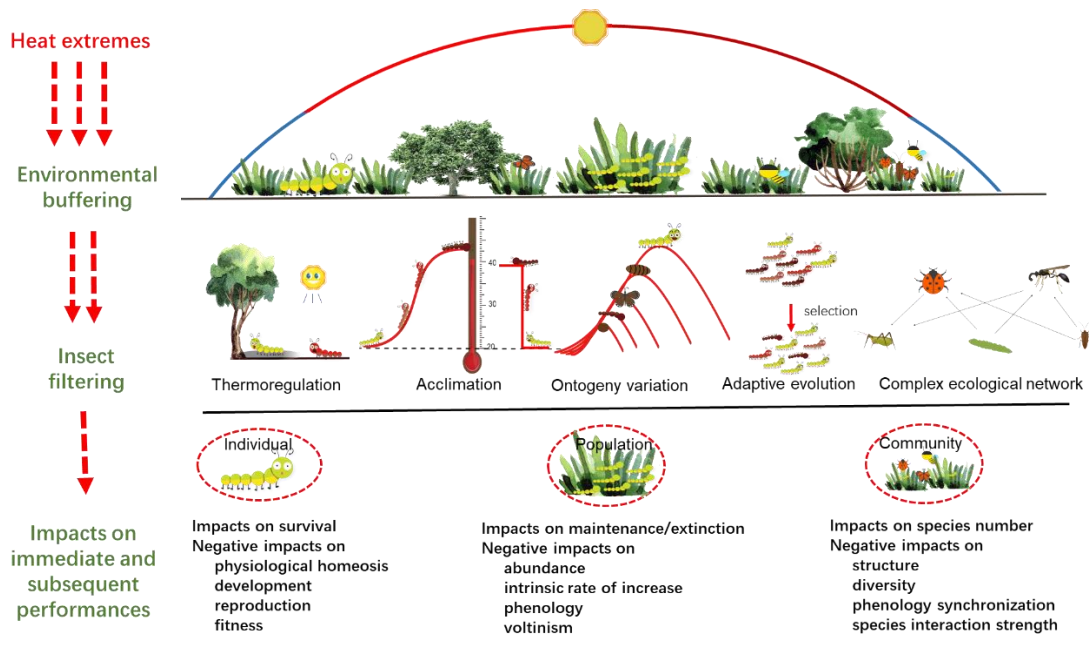
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Figure 1

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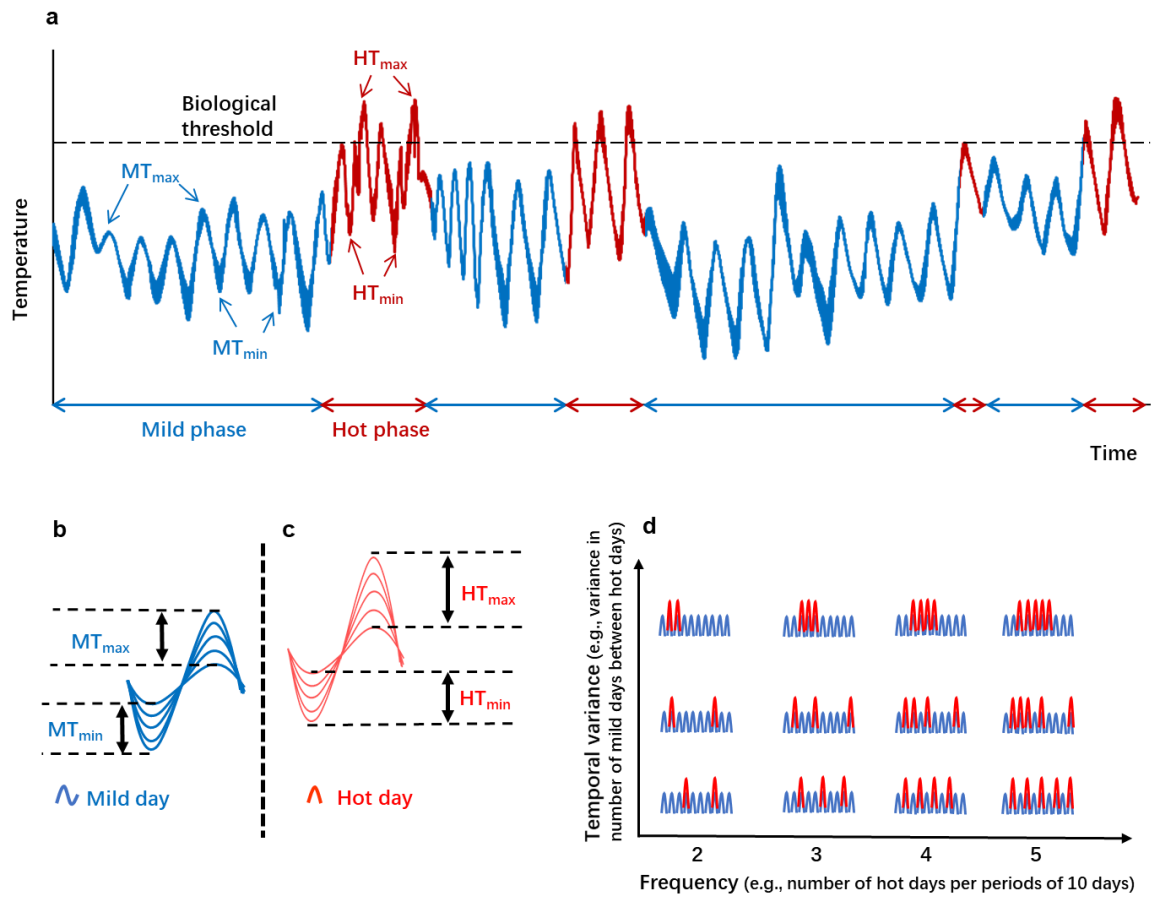
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Figure 2