



**HAL**  
open science

## Evolutionary adaptation to climate change

Allan Edelsparre, Mark Fitzpatrick, Marjo Saastamoinen, Céline Teplitsky

► **To cite this version:**

Allan Edelsparre, Mark Fitzpatrick, Marjo Saastamoinen, Céline Teplitsky. Evolutionary adaptation to climate change. *Evolution Letters*, 2024, 8 (1), pp.1-7. 10.1093/evlett/grad070 . hal-04765370

**HAL Id: hal-04765370**

**<https://hal.science/hal-04765370v1>**

Submitted on 14 Nov 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# 1 Evolutionary adaptation to climate change

2

3 Allan H. Edelsparre<sup>1</sup>, Mark J. Fitzpatrick<sup>2</sup>, Marjo Saastamoinen<sup>3,4</sup> & Céline Teplitsky<sup>5</sup>

4

5 <sup>1</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada, <sup>2</sup>

6 Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada,

7 <sup>3</sup>Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland, <sup>4</sup>Institute

8 of Life Sciences, University of Helsinki, Helsinki, Finland, <sup>5</sup>CEFE, Univ Montpellier, CNRS, EPHE,

9 IRD, Montpellier, France

10

11 Corresponding author: Department of Ecology and Evolutionary Biology, University of Toronto, 25

12 Willcocks Street, Toronto, Ontario, Canada. M5S 3B2. Email: a.edelsparre@utoronto.ca

13

## 14 Abstract

15 When the notion of climate change emerged over 200 years ago, few speculated as to the impact of  
16 rising atmospheric temperatures on biological life. Tens of decades later, research clearly demonstrates  
17 that the impact of climate change on life on Earth is enormous, ongoing and with foreseen effects  
18 lasting well into the next century. Responses to climate change have been widely documented.

19 However, the breadth of phenotypic traits involved with evolutionary adaptation to climate change  
20 remains unclear. In addition, it is difficult to identify the genetic and/or epigenetic bases of phenotypes  
21 adaptive to climate change, in part because it often is not clear whether this change is plastic, genetic,  
22 or some combination of the two. Adaptive responses to climate driven selection also interact with other  
23 processes driving genetic changes in general, including demography as well as selection driven by  
24 other factors. In this Special Issue, we explore the factors that will impact the overall outcome of  
25 climate change adaptation. Our contributions explain that traits involved in climate change adaptation  
26 include classic phenomena, such as range shifts and environmentally dependent sex determination, but  
27 also often overlooked phenomena such as social and sexual conflicts and the expression of stress  
28 hormones. We learn how climate driven selection can be mediated via both natural and sexual  
29 selection, effectively influencing key fitness related traits such as offspring growth and fertility as well  
30 as evolutionary potential. Finally, we explore the limits and opportunities for predicting adaptive  
31 responses to climate change. This contribution forms the basis of ten actions that we believe will

32 improve predictions of when and how organisms may adapt genetically to climate change. We  
33 anticipate that this Special Issue will inform novel investigations into how the effects of climate change  
34 unfold from phenotypes to genotypes, particularly as methodologies increasingly allow researchers to  
35 study selection in field experiments.

36 Keywords: adaptation, epigenetics, climate change, evolutionary genomics, prediction

## 37 Lay Summary

38 What are the major factors driving evolutionary adaptation to climate change? How can we harness this  
39 understanding to better predict how populations can adapt to a rapidly changing climate? The urgency  
40 of answering these questions is critical as more than a million species are currently directly facing the  
41 risk of extinction due to climate driven environmental change. This puts research exploring processes  
42 and mechanisms that affect evolutionary rescue at the core of mounting a global response to the current  
43 climate crisis. Here, we highlight key contributions that collectively demonstrate the breadth of  
44 evolutionary responses that organisms exhibit in response to climate change, including classic  
45 responses (e.g. range shifts, plasticity, and evolutionary responses), but also less conspicuous  
46 phenomena such as social and sexual conflicts. Some contributions go right to the heart of  
47 understanding the genetic and epigenetic bases of the observed responses, ultimately linking the  
48 environmental effects to the genotype-phenotype map. Other contributions investigate the interplay  
49 between different types of selection with climate driven selection in facilitating or hindering  
50 evolutionary adaptation, a major uncertainty that has been the focus of evolutionary research for a long  
51 time. These are pressing issues that require a deep understanding of processes which determine our  
52 ability to predict evolutionary outcomes of ongoing climate change. The final contribution of the  
53 Special Issue therefore explores the limits and opportunities for predicting adaptive responses to  
54 climate change. It builds on all the contributions of the Special Issue, and the viewpoints of many of  
55 their authors, to provide a road map for how we might be able to improve predictions with our current  
56 knowledge and what might be possible to predict in the future. We anticipate that this Special Issue will  
57 ignite investigations of how the effects of climate change unfold from phenotypes to genotypes and the  
58 selective forces that produce evolutionary rescue in response to climate change.

59

60

## 61 Introduction

62

63 When the notion of global warming first emerged over 200 years ago (Arrhenius 1896) few thought  
64 that human activity was capable of altering the global climate. Consequently, the urge to understand  
65 how changes in global temperatures could affect Earth's ecosystems and biodiversity was limited. Fast  
66 forward to present day and we have arrived at a reality where nearly all ecological processes, including  
67 ecosystem function and services, are affected by a globally changing climate induced by human  
68 activities (Sheffers et al. 2016). Thus, the accelerating effects of climate change on biodiversity remain  
69 the nexus of our current climate crisis as more than a million species now directly face the risk of  
70 extinction (Diaz et al. 2019; IPBES 2019), although extinctions only represent the tip of the iceberg  
71 (Fraixedas et al. 2022).

72

73 Historically, the successful tackling of environmental crises caused by human societies have been  
74 fostered by a deep understanding of the biological processes involved. For example, major  
75 environmental crises caused by man-made chemicals, such as ozone depleting substances and DDT,  
76 were unravelled and tackled by understanding how the chemicals entered and interfered with entire  
77 food chains, ultimately causing cancer and genetic damage to organisms. The current climate crisis  
78 differs from historical ones in that ecosystem change is on a global scale wherein the effects on global  
79 biodiversity are both highly unpredictable and continually advancing (Marquet et al. 2019). Even if we  
80 successfully decreased the warming of the atmosphere, we find ourselves with limited alternatives but  
81 to allow the climate warming scenario forecasted for the 21st century to unfold (IPCC, 2022; Nadeau et  
82 al. 2017; Marquet et al. 2019). These alterations in climatic conditions will lead many species to adapt  
83 or face extinction. Thus, climate change has become an unfortunate global experiment with  
84 evolutionary adaptation at its core, and the study of evolutionary rescue plays a major role in predicting  
85 which species manage to persist, consequently influencing the future of all ecosystems.

86

87 There are two key questions. First, how will species adapt to climate change. Second, which critical  
88 factors best predict which species (or populations) can adapt and be rescued by evolution in the face of  
89 a rapidly changing climate? An important part to answering these questions lies rooted within the  
90 relevant traits that are directly or indirectly influenced by climate change (Urban et al. 2024, this issue).  
91 Many reports have already demonstrated that climate change has influenced the distribution patterns of

92 many species and altered phenomena such as migration, the timing of events such as reproduction  
93 (Inouye 2022; Walter et al. 2002), or diapause (Bradshaw and Holzapfel 2001). However, it remains  
94 unknown why such responses are evident in some, but not all, species influenced by climate change. In  
95 cases where responses to climate change are evident, studies rarely demonstrate whether such changes  
96 are caused by plastic responses, genetic changes, or some combination of the two (Bonnet et al. 2019;  
97 Merilä and Hendry 2014; Ramakers et al. 2018). In fact, studies rarely investigate whether selection in  
98 the wild is driven by climate change (Bonnet et al. 2019). In addition, adaptive responses to climate  
99 change-driven selection may interact with other ecological and evolutionary processes that drive  
100 genetic changes in general (e.g. dispersal, demography, species interactions, and sexual selection).  
101 These factors represent major limitations to our understanding of ‘whether’ and ‘how’ species will  
102 adapt to climate change. Moreover, without uncovering how such interactions unfold it will be difficult  
103 to predict evolutionary outcomes promoted by climate change (e.g. Pujol et al. 2018; Pelletier et al.  
104 2009). Accordingly, a section of this Special Issue is dedicated to studies that investigate traits that  
105 respond directly to selection, including the role of traits in mediating evolutionary adaptive responses  
106 to climate change and the plastic/genetic bases of these responses. A second section is dedicated to  
107 studies that investigate the impact of climate change on selection and evolutionary potential. The  
108 contributions in this section shed light on the complex relationship between climate driven evolutionary  
109 change and change driven by ecological processes in general. In a concluding article, we merge  
110 perspectives of many of the contributors of this Special Issue to develop a road map for predicting  
111 adaptive responses to climate change. We do this by exploring what we may be able to currently  
112 predict, opportunities that are likely to advance future predictions, and factors that we likely will not be  
113 able to predict (or may not even need to predict). In the current article, we highlight some transversal  
114 themes that emerged from the Special Issue (Figure 1).

## 115 Predicting phenotypic responses to climate change

116

117 Predicting adaptive responses is a long-standing challenge. Historically, predicting adaptive evolution  
118 has been the aim of quantitative genetics (Roff 2007), and is notoriously challenging in the wild (Kruuk  
119 et al. 2008; Pujol et al. 2018). Therefore, comparisons between predicted and estimated responses to  
120 selection in the wild in the context of climate change are scarce (but see for example Gienapp et al.  
121 2006; Moiron et al. 2024, this issue). Data sets from long-term monitoring are ideal for bridging such  
122 gaps. Using a long-term pedigree dataset, Moiron et al. (2024, this issue) show that arrival dates in

123 migrating common terns (*Sterna hirundo*) are shifting earlier in the season. Theoretical models predict  
124 earlier arrival, and accordingly, they do find ongoing evolution in the population. However, according  
125 to Moiron et al. (2024, this issue), both empirical and predicted genetic trends fall short compared with  
126 actual arrival dates trends, suggesting that a part of the response involves plasticity. Genomic  
127 approaches offer the possibility of exploring adaptation beyond single traits, for example over a wide  
128 range of unmeasured traits. Using Gene Ontology, Stonehouse et al. (2024, this issue), identify  
129 genomic regions in 20 populations of great tits (*Parus major*) across the entire European range that  
130 have responded to past and present climates. In an elegant study demonstrating that climate adaptation  
131 is genetically complex, the authors identify over 40 climate-associated genes, and infer their biological  
132 roles. Similar approaches could help predicting the ability of populations to adapt and thus assess their  
133 vulnerability to climate change (Bay et al. 2018).

134  
135 Predicting evolutionary responses to climate change requires predicting patterns of evolutionary  
136 potential and selection under new or novel conditions. How genetic variance fluctuates across  
137 environments (G\*E), populations, and traits is still poorly understood (Salt et al. 2018). Because  
138 selection and gene flow among populations can shape evolutionary potential, space-for-time  
139 substitution experiments can offer some insights on the expected changes in additive genetic variance.  
140 For example, in wild birds, evolutionary potential for morphological traits has been suggested to be  
141 highest when local habitat conditions are close to the niche optimum but not too close (intermediate  
142 habitat favourability, Martínez-Padilla et al. 2017). Similarly, Chantepie et al. (2024, this issue) show  
143 that in great tits, the genetic (co)variances of life history (e.g. phenology, reproduction etc.), but not  
144 morphological traits, are shaped by the climatic conditions. This directly supports the conclusions from  
145 the genomic study by Stonehouse et al. (2024, this issue). However, Nadeau and Urban (2024, this  
146 issue) present a cautionary tale regarding predicting evolutionary potential based on the selection  
147 history of wild populations of *Daphnia magna*. Despite clear expectations of how spatial and temporal  
148 variation in temperature should shape genetic variation of fitness and critical thermal maximum, no  
149 such pattern was detected. Our predictions of evolutionary potential are still often based on verbal  
150 models because numeric predictions are extremely complex to devise. Basing predictions of  
151 evolutionary potential on empirical estimations of selection and gene flow (Arnold et al. 2008,  
152 Chantepie and Chevin 2020) would be a challenging but necessary next step.

153  
154 Local and global climate are known to be a major drivers of selection pressures (Siepielski et al. 2017).  
155 Consequently, climate change is expected to alter selection pressures, including intensifying ongoing

156 ones, such as stronger selection for earlier breeding under extreme climatic events (Marrot et al. 2017)  
157 or altering them radically, for example leading to winter diapause counter selection (Tougeron et al.  
158 2020). Other environmental features may also strongly affect selection patterns. In support of this,  
159 Sauve et al. (2024, this issue) show the intensity of selection on growth in black-legged kittiwakes  
160 (*Rissa tridactyla*) is fluctuating according to air temperature. Thanks to a long-term feeding experiment  
161 in a wild population, they also demonstrate how variable resource dynamics can alter and even locally  
162 buffer selection. The importance of environmental conditions is further supported in a study by Nomato  
163 et al. (2024, this issue) investigating the effects of competition within plant communities. They utilize a  
164 transplant experiment along an altitudinal gradient and estimate shifts in directional selection on alpine  
165 plant morphology and phenology in response to climate and to competition. Their results highlight that  
166 by depressing fitness, competitive interactions may limit the potential for selection. This study thus  
167 demonstrates that future studies should aim to also understand the more indirect effects of climate  
168 change, such as changing biotic interactions, on the potential for evolutionary rescue of natural  
169 populations. Doing so will be key to teasing apart the contribution of different sources of  
170 environmental heterogeneity in shaping selection and ultimately evolutionary responses.

171

172 An equally important aspect of predicting evolutionary responses to climate change requires improving  
173 our understanding of the evolution of plasticity itself since environmental cues can be altered by  
174 climate change (Bonamour et al. 2019, Bradshaw et al. 2001), and the expression of plasticity in  
175 extreme situations might reach its limits. These questions are often discussed in the context of plasticity  
176 in continuous traits (e.g. Chevin and Hoffmann 2017), but less discussed for discrete traits that can be  
177 of major importance (e.g. environment-dependent sex determination, colour morph etc.) (Reid and  
178 Acker 2022). Crowther et al. (2024, this issue) investigate how plasticity in discrete traits impact  
179 evolutionary responses to environmental change. Environmental sex determination is common in many  
180 taxa (e.g. reptiles and teleost fishes) where the temperature experienced during embryonic or larval  
181 development determines the sex of the offspring. Interestingly, sex determination can be plastic in  
182 different ways (visualized via the slope of a non-linear latent sex ratio reaction norm and a linear  
183 reaction norm of the temperature threshold producing either sex). The authors demonstrate how both  
184 types of plasticity differently affect the evolution of the threshold in response to climate change. For  
185 example, while a steep latent plasticity promotes the evolution of the threshold, linear plasticity of this  
186 threshold actually hampers its evolution. Hence, the type of ancestral plasticity will be crucial in  
187 determining the role of plasticity in facilitating or hindering evolution.

188

189 The role of plasticity in constraining or promoting evolved responses following environmental change  
190 is important for understanding how traits in general are going to adapt to climate change (Ghalambor et  
191 al. 2007, Noble et al. 2019). In an elegant experiment, Swaegers et al. (2024, this issue) show that  
192 populations of the damselfly (*Ischnura elegans*) in a southward expansion from France into Spain have  
193 evolved increased heat tolerance compared with French core populations of the same species. By  
194 manipulating heat tolerance in the southward expanding populations via the use of a hypermethylating  
195 agent, the authors are able to significantly increase their heat tolerance beyond those typically  
196 measured in an older Spanish expansion zone. Thus, recent migrants are more plastic relative to older  
197 migrants. Experiments such as those conducted by Swaegers et al. (2024, this issue) demonstrate that  
198 epigenetic and therefore plastic responses can be critical during the early stages of range shifts, but that  
199 genetic adaptations likely prevail over time.

## 200 Harnessing the power of evolutionary history

201  
202 The notion of using evolutionary history to inform future predictions is based on the premise that  
203 history often repeats itself. Evolutionary history can influence our predictions in various ways. The  
204 previous section emphasized how selection pressures may shape evolutionary potential, but more  
205 complex scenarios can arise. In addition to Swaegers et al. (2024, this issue), two other studies from  
206 this Special Issue emphasize how species and population-specific history can affect responses to  
207 ongoing climate change, either through changes in distribution range or *in situ* adaptive responses.  
208 Predicting whether species will shift their distribution range or adapt locally is an important question as  
209 the requirements and limitations of each are different (e.g. need for habitat corridors vs genetic  
210 variance). Moreover, the consequences of range shifts are evolutionarily important because they may  
211 affect the evolutionary trajectory of entire systems when the shifting species encounters novel habitats  
212 and novel competitors/communities (Súarez et al. 2022). In order to generate better predictions of how  
213 such evolutionary trajectories may unfold in response to climate change, we need candidate predictors  
214 that influence the extent and probability of range shifts. Hällfors et al. (2024, this issue) ask whether  
215 adaptation to climate niche in the past, a proxy for tolerance to changing environmental conditions, can  
216 predict a poleward range shift of 283 species of moths, butterflies and birds in Finland. Based on  
217 nationwide long-term monitoring data over two decades, they find that birds and moths with narrower  
218 climatic niches display stronger northward shifts. Surprisingly, they find an opposite pattern in  
219 butterflies in relation to moisture niche. This finding is critical because such large-scale patterns make



220 it possible to detect general trends and also provide insight into potential proximate causes (adaptation  
221 to thermal and moisture regimes) driving climate change adaptation.

222

223 Another way through which evolutionary history can inform future predictions is through studies of  
224 sexual selection. In particular, the role of sexual selection in evolutionary rescue has been subject to  
225 strong debate wherein sexual selection can reduce the effective population size and lead to sexual  
226 conflicts impeding natural selection. Sexual selection may also accelerate adaptation to novel  
227 environments by increasing the breeding success of better adapted individuals (e.g. Arnqvist and Rowe  
228 2005). Fuelled by these ideas, several reviews have synthesized the effect of the interplay between  
229 natural and sexual selection on the rate of adaptation, especially in the context of changing  
230 temperatures (e.g. Pilakouta and Ålund 2022; Candolin and Heuschele 2008). Baur et al. (2024, this  
231 issue) offer a fresh perspective by asking how the history of sexual selection affects thermal sensitivity,  
232 since the expression of sexually selected traits may reduce stress tolerance. Using long-term  
233 experimental evolution, the authors assess how different levels of sexual and natural selection affect  
234 male fertility under acute heat stress in the seed beetle (*Callosobruchus maculatus*). The performance  
235 of males with a history of polyandry are most affected by stressful thermal conditions as are their  
236 female counterparts. In particular, the experiment demonstrated that heat stress and sexual selection  
237 together may exacerbate species vulnerability to climate change. These results highlight the need to  
238 integrate the effects of sexual selection not only as an ongoing process, but also in terms of how it can  
239 affect organismal trade-offs, particularly between postcopulatory traits (e.g. sperm competition) and  
240 fertility.

## 241 No organism is an island... The importance of interactions, between 242 mating partners and beyond

243

244 Interactions between organisms have strong potential to affect responses to climate change. For  
245 example, competition may affect the intensity of selective pressures (Nomoto et al.2024; Sauve et al.  
246 2024, both this issue) or shape adaptive potential (Baur et al. 2024, this issue). Kulmuni et al. (2024,  
247 this issue) suggest that hybrid mating interactions among closely related species will be of importance  
248 as well. Because the generation of new adaptive mutations is a slow process and standing genetic  
249 variation may not be sufficient for small or isolated populations, hybridization can 'fast track' the  
250 generation of adaptive genetic variance. Even though hybrids are generally associated with having

251 lower fitness, which can play an important role in maintaining barriers between species, there are  
252 accumulating empirical reports highlighting the adaptive potential of hybridization (e.g. Martin-Roy et  
253 al. 2021). Kulmuni et al. (2024, this issue) propose that strongly changing environments may increase  
254 the occurrence of hybrid vigour. Using both modelling and simulations, they show that hybrids of both  
255 haploid and diploid populations adapt faster to a rapidly changing environment relative to parental  
256 populations in virtually all models. As reflected here, current studies involve mostly dyadic  
257 interactions, such as mating partners, but there is a significant need to integrate a network of social  
258 interactions that includes, for example, helpers or competitors (from the same or a different species).  
259

260 Recently, much emphasis has been placed on understanding how social relationships can affect  
261 evolutionary trajectories (and ultimately population persistence) both through selection (e.g. Fisher et  
262 al. 2017) and their effects on evolutionary potential (e.g. Baud et al. 2022). In this Special Issue, two  
263 contributions evaluate the role of interactions between mating partners in population persistence.  
264 Focusing on laying date, a textbook example of adaptive phenological response to climate change,  
265 Murray et al. (2024, this issue) investigate whether the male partner can affect the rate of evolutionary  
266 response of laying date and hence the maximum sustainable rate of environmental change (cf/sensu  
267 Chevin et al. 2010). If females are expressing a plastic response to male phenotype, then the evolution  
268 of male phenotype can have a strong impact on population persistence, facilitating or hindering  
269 population adaptation depending on the genetic correlations between sexes. Gómez-Llano and  
270 colleagues (2024, this issue) ask whether male harm could influence adaptation and evolutionary rescue  
271 to a changing environment. Using a meta-analysis approach, the authors demonstrate that male harm in  
272 general exerts negative effects on female fitness, the extent of which depends on the type of harm (e.g.  
273 male harassment vs traumatic insemination). The authors develop a theoretical model around these  
274 findings and further find that population decline can be reduced when sexual conflict influences local  
275 adaptation, but at the expense of genetic adaptation. The authors describe this trade off as a double-  
276 edged sword where male harm can buffer demographic costs (e.g. less adapted males exert weaker  
277 harm on females) of climate change, but in turn delay genetic adaptation and consequently evolutionary  
278 rescue. An interesting twist to this story, however, is that variation in mating systems and the kind of  
279 harm that males exert on females can mitigate this trade off, suggesting that eco-evolutionary processes  
280 that promote such variation will be critical to facilitate evolutionary rescue in systems where male harm  
281 is prominent. Consequently, both Gómez-Llano et al. (2024, this issue) and Baur et al. (2024, this  
282 issue) highlight the complex effects of social interactions on evolutionary trajectories.

## 283 Conclusion

284 In general, predictions are still hampered by a lack of integration among population dynamics,  
285 individual responses, and evolutionary responses (Johnston et al. 2019). This is highlighted by the  
286 contribution of Crino et al. (2024, this issue) presenting a conceptual framework centered on  
287 glucocorticoids, a major stress hormone in vertebrates mediating, among other things, responses to  
288 thermal stress. Physiological and behavioural responses to glucocorticoids have short term adaptive  
289 effects but their effects on fitness become more complex under chronic stress. The longer-term effects  
290 can also include both adaptive and maladaptive transgenerational consequences (Crino et al. 2024, this  
291 issue). Understanding the interplay between the pleiotropic effects of glucocorticoids as well as  
292 between the different time scales will provide keys to understand fitness variations and predict  
293 selection patterns as well as evolutionary trajectories.

294

295 The diversity of evolutionary responses to climate change documented in this Special Issue clearly  
296 demonstrates that the solution to understanding ‘when’ and ‘how’ we can predict adaptive responses is  
297 as complex as the scope of the problem. To gain a perspective of the problem and its solutions, the  
298 concluding paper by Urban et al. (2024, this issue), builds on the views of many contributors to this  
299 Special Issue to highlight key challenges to advancing research on factors that promote evolutionary  
300 rescue (e.g. the capacity of systems to adapt to a rapidly changing environment). In particular, we need  
301 to investigate multiple traits simultaneously to gain insights into the potential changes in trait-space, to  
302 better understand when plasticity reaches its limits or hinders adaptive evolution, including plasticity  
303 evolution (Iler et al. 2013).

304

305 Urban et al. (2024, this issue) also highlight the diversity of methods needed to address questions  
306 related to climate change adaptation. This is also evident in the diversity of methods used in the  
307 contributions of the Special Issue in general. In the future, experimental evolution, resurrection, and  
308 transplant experiments will play an enormously important role in unpacking adaptive capacity and the  
309 molecular bases of adaptive responses, particularly in conjunction with novel genomic tools. Similarly,  
310 long-term monitoring programmes of individuals or communities will be critical to shed light on how  
311 they are responding to climate change in general and how selection promotes evolutionary rescue.  
312 Using data from long-term monitoring programs to test against new data will play a key role in  
313 forecasting long term evolutionary change.

314

315 Merging the challenges mentioned above with the perspectives of many of the contributors to this  
316 Special Issue, Urban et al. (2024, this issue) outline a road map for future research by providing key  
317 actions that will enable predictions of evolutionary change in response to climate change. We hope that  
318 outlining these actions will lead to important research that seeks to fill important gaps that currently  
319 hamper our ability to inform future predictions. We therefore anticipate these actions will ignite  
320 investigations of how the effects of climate change unfold from phenotypes to genotypes and the  
321 selective forces that produce evolutionary rescue in general.

322

## 323 Acknowledgments

324

325 We would like to thank both prospective and contributing authors to this Special Issue. We thank the  
326 many reviewers that kindly donated their time and efforts to evaluate each contribution. Their efforts  
327 ultimately improved the quality of the Special Issue. We would also like to thank Loeske Kruuk, who  
328 provided valuable feedback during the earlier stages of developing the outline for the Special Issue.  
329 Irene Conenna is acknowledged for her help with figure illustrations and the cover. C.T. would like to  
330 thank the BNP-Paribas foundation (« Climate and Biodiversity initiative », project Mommy Knows  
331 Best) and M.S. would like to thank Jane and Aatos Erkkö Foundation. A.H.E. acknowledges that much  
332 of his research is largely possible because of the historical and ongoing indigenous stewardship of  
333 biodiversity in Canada. A.H.E. commits to deepen his knowledge and understanding of the local  
334 Indigenous communities and actively work towards reconciliation.

335

## 336 Author contributions

337

338 C.T. led the initiative for the Special Issue. C.T., M.S., M.J.F. and A.H.E. conceived of the framework.  
339 A.H.E. wrote the first draft, and C.T., M.J.F. and M.S. contributed to and wrote the manuscript.

340

## 341 Conflict of interest

342

343 The authors declare no conflict of interest. C.T., M.S. and A.H.E. are Associate Editors of the Special  
344 Issue. Editorial processing of the manuscript was done independently of these editors.

345

## 346 References

- 347 Arnold, S. J. J., R. Bürger, P. A. Hohenlohe, B. C. Ajie and A. G. Jones. (2008). Understanding the  
348 Evolution and Stability of the G-Matrix. *Evolution*. 62: 2451–2461.
- 349
- 350 Arrhenius, S. (1896). On the influence of carbonic acid in the air upon the temperature of the ground.  
351 *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*. 41: 251. 237-  
352 276.
- 353 Arnqvist, G. and L. Rowe. (2005). *Sexual Conflict*. Princeton University Press.
- 354 Bay, R. A., R. J. Harrigan, V. L. Underwood, H. L. Gibbs, T. B. Smith and K. Ruegg. (2018). Genomic  
355 signals of selection predict climate-driven population declines in a migratory bird. *Science*. 359: 83–86.
- 356 Baud, A., S. McPeck, N. Chen, and K. A. Hughes. (2022). Indirect Genetic Effects: A Cross-  
357 disciplinary Perspective on Empirical Studies. *Journal of Heredity*. 113: 1-15.
- 358 Baur, J., M. Zwoinska, M. Koppik, R. R. Snook and D. Berger. (2024). Heat stress reveals a fertility  
359 debt owing to postcopulatory sexual selection. *Evolution Letters*. 8(1).  
360 <https://doi.org/10.1093/evlett/grad007>. Advance access publication 16 March 2023.
- 361 Bonamour, S., Chevin, L., Charmantier, A. & Teplitsky, C. (2019). Phenotypic plasticity in response to  
362 climate change: the importance of cue variation. *Philosophical Transactions of the Royal Society B:*  
363 *Biological Sciences*. 374: 1768.
- 364 Bonnet, T., M. B. Morrissey, A. Morris, S. Morris, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B.  
365 Kruuk. (2019). The role of selection and evolution in changing parturition date in a red deer population.  
366 *PloS Biology*. 17: e3000493.
- 367 Bradshaw, W. E. and C. M. Holzapfel. (2001). Genetic shift in photoperiodic response correlated with  
368 global warming. *Proceedings of the National Academy of Sciences of the United States of America*. 98:  
369 14509-14511.
- 370 Candolin U. and J. Heuschele. (2008). Is sexual selection beneficial during adaptation to environmental  
371 change? *Trends in Ecology and Evolution*. 23: 446–452.

372 Chantepie, S. and L. M. Chevin. (2020). How does the strength of selection influence genetic  
373 correlations? *Evolution Letters*. 4: 468–478.

374 Chevin, L. and Hoffmann, A.A. (2017) Evolution of phenotypic plasticity in extreme environments.  
375 *Philosophical Transactions of the Royal Society B: Biological Sciences*. 372: 20160138.

376 Chevin, L., R. Lande, and G. M. Mace. (2010). Adaptation, plasticity, and extinction in a changing  
377 environment: towards a predictive theory. *PLoS Biology*. 8: e1000357.

378 Crino, O. L., R. Bonduriansky, L. B. Martin and D. W. A. Noble. (2024). A conceptual framework for  
379 understanding stress-induced physiological and transgenerational effects on population responses to  
380 climate change. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/qrad037>. Advance access  
381 publication 29 September 2023.

382 Crowther, C., B. Stephen & L. Schwanz. (2024). Plasticity and the adaptive evolution of switchlike  
383 reaction norms under environmental change. *Evolution Letters*. 8(1).  
384 <https://doi.org/10.1093/evlett/qrad035>. Advance access publication 31 August 2023.

385 Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agar, A. Arneeth, P. Balvanera, K. A. Brauman, S. H.  
386 M. Butchart, K. M. A. Chan, et al. (2019). Pervasive human-driven decline of life on Earth points to the  
387 need for transformative change. *Science*. 366: eaax3100.

388 Fisher, D. N., S. Boutin, B. Dantzer, M. M. Humphries, J. E. Lane, and A. G. McAdam. (2017).  
389 Multilevel and sex-specific selection on competitive traits in North American red squirrels. *Evolution*  
390 71: 1841-1854.

391 Fraixedas, S., T. Roslin, L. H. Antão and A.-L. Laine. (2022). Nationally reported metrics can't  
392 adequately guide transformative change in biodiversity policy. *Proceedings of the National Academy*  
393 *of Sciences of the United States of America*. 119: e2117299119.

394 Ghalambor, C.K., J. K. McKay, S. P. Carroll & D. N. Reznick. (2007). Adaptive vs non-adaptive  
395 phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional*  
396 *Ecology*. 21: 394-407.

398 Gienapp, P., Postma, E. & Visser, M.E. (2006) Why breeding time has not responded to selection for  
399 earlier breeding in a songbird population. *Evolution*. 60: 2381–2388.

400 Gómez-Llano, M., G. S. Faria, R. García-Roa, D. W. A. Noble and P. Carazo. (2024). Male harm  
401 suppress female fitness, affecting the dynamics of adaptation and evolutionary rescue. *Evolution*  
402 *Letters*. 8(1). <https://doi.org/10.1093/evlett/qrac002>. Advance access 31 January 2023.

403 Hällfors, M., R. K. Heikkinen, M. Kuussaari, A. Lehikoinen, M. Luoto, J. Pöyry, R. Virkkala, M.  
404 Saastamoinen and H. Kujala. (2024). Recent rangeshifts of moths, butterflies, and birds are driven by  
405 the breadth of their climate niche. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/qrad004>.  
406 Advance access publication 12 March 2023.

407 IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the  
408 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. Brondizio, J.  
409 Settele, S. Díaz, and H. T. Ngo (editors). IPBES secretariat, Bonn, Germany. 1148 pages.  
410 <https://doi.org/10.5281/zenodo.3831673>)

411 Iler, A. M., T. T. Høye, D. W. Inouye and N. M. Schmidt. (2013). Nonlinear flowering responses to  
412 climate: are species approaching their limits of phenological change? *Philosophical Transactions of the*  
413 *Royal Society of London. B*. 368: 20120489.

414 Inouye, D. W. (2022). Climate change and phenology. *Wiley Interdisciplinary Reviews Climate*  
415 *Change*. 13: 1-17.

416 IPCC. (2022). Climate Change 2022: Impacts, Adaptation, and Vulnerability. UNEP.

417 Johnston, A.S.A., Boyd, R.J., Watson, J.W., Paul, A., Evans, L.C., Gardner, E.L., et al. (2019)  
418 Predicting population responses to environmental change from individual-level mechanisms: towards a  
419 standardized mechanistic approach. *Proceedings of the Royal Society B*. 286: 20191916.

420 Kruuk, L.E.B., Slate, J. & Wilson, A.J. (2008) New answers for old questions: the evolutionary  
421 quantitative genetics of wild animal populations. *Annual Review of Ecology, Evolution, and*  
422 *Systematics*. 39: 525–548.

423 Kulmuni, J., B. Wiley and S. Otto. (2024). On the fast track: hybrids adapt more rapidly than parental  
424 populations in a novel environment. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/qrad002>.  
425 Advance access publication 1 March 2023.

426 Marquet, P.A., S. Naeem, J. B. C. Jackson, and K. Hodges. (2019). Navigating transformation of  
427 biodiversity and climate. *Science Advances*. 5: a0969.

428 Marrot, P., D. Garant and A. Charmantier. (2017). Multiple extreme climatic events strengthen  
429 selection for earlier breeding in a wild passerine. *Philosophical Transactions of the Royal Society B:*  
430 *Biological Sciences*. 372: 20160372.

431 Martin-Roy, R., E. Nygård, P. Nouhaud, J. Kulmuni. (2021). Differences in thermal tolerance  
432 betweenparental species could fuel thermal adaptation in hybrid wood ants. *American Naturalist*. 198:  
433 278-294.

434 Martínez-Padilla, J., A. Estrada, R. Early, and F. Garcia-Gonzalez. (2017). Evolvability meets  
435 biogeography: Evolutionary potential decreases at high and low environmental favourability.  
436 *Proceedings of the Royal Society B: Biological Sciences*. 284: 20170516.

437 Merilä, J. & Hendry, A.P. (2014) Climate change, adaptation, and phenotypic plasticity: The problem  
438 and the evidence. *Evolutionary Applications*. 7: 1–14.

439 Moiron, M., C. Teplitsky, B. Haest, A. Charmantier and S. Bouwhuis. (2024). Micro-evolutionary  
440 response of spring migration timing in a wild seabird. *Evolution Letters*. 8(1).  
441 <https://doi.org/10.1093/evlett/qrad014>. Advance access publication 3 May 2023.

442 Murray, M., J. Wright and Y. G. Araya-Ajoy. (2024). Evolutionary rescue from climate change: male  
443 indirect genetic effects on lay-dates and their consequences for population persistence. *Evolution*  
444 *Letters*. 8(1). <https://doi.org/10.1093/evlett/qrad022>. Advance access publication 13 July 2023.

445 Nadeau, C. P. And M. C. Urban. (2024). Macroecological predictors of evolutionary and plastic  
446 potential do not apply at microgeographic scales for a freshwater *cladoceran* under climate change.  
447 *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/qrad042>. Advance access publication 12 October  
448 2023.

449 Nadeau, C. P., M. C. Urban, and J. R. Bridle. (2017). Climates Past, Present, and Yet-to-Come Shape  
450 Climate Change Vulnerabilities. *Trends in Ecology and Evolution*. 32: 786-800.



451 Noble, N. W. A., R. Radersma, and T. Uller. (2019). Plastic responses to novel environments are biased  
452 towards phenotype dimensions with high additive genetic variation. *Proceedings of the National*  
453 *Academy of Sciences of the United States of America*. 116: 13452-13461.

454 Nomoto, H., F. Simone & J. Alexander J. (2024). Competitors alter selection on alpine plants exposed  
455 to experimental climate change. *Evolution Letters*. 8(1). **ADD DOI**.

456 Pelletier, F., D. Garant, and A. P. Hendry. (2009). Eco-evolutionary dynamics. *Philosophical*  
457 *Transactions of the Royal Society B*. 364: 1483-1489.

458 Pilakouta, N., and M. Ålund. (2021). Sexual selection and environmental change: what do we know  
459 and what comes next? *Current Zoology*. 67: 293-298.

460 Pujol, B., S. Blanchet, A. Charmantier, E. Danchin, B. Facon, P. Marrott, F. Roux, I. Scotti, C.  
461 Teplitsky, C. E. Thomson and I. Winney. (2018). The Missing Response to Selection in the Wild.  
462 *Trends in Ecology and Evolution*. 33: 337-346.

463 Ramakers, J.J.C., Gienapp, P. & Visser, M.E. (2019). Phenological mismatch drives selection on  
464 elevation, but not on slope, of breeding time plasticity in a wild songbird. *Evolution*. 73: 175–187. Roff,  
465 D. A. 2007. Centennial Celebration for Quantitative Genetics. *Evolution*. 61: 1017–1032.

466 Reid, J. M. and P. Acker. (2022). Properties of phenotypic plasticity in discrete threshold traits.  
467 *Evolution*. 76: 190-206.

468 Saltz, J.B., A. M. Bell, J. Flint, R. Gomulkiewicz, K. A. Hughes and J. Keagy. (2018). Why does the  
469 magnitude of genotype-by-environment interaction vary? *Ecology and Evolution*. 8: 6342-6353.

470 Scheffers, B.R., L. De Meester, T. C. L. Bridge, A. A. Hoffmann, J. M. Pandolfi, R. T. Corlett, S.H. M.  
471 Butchart, P. Pearce-Kelly, K. M. Kovacs, D. Dudgeon, et al. (2016). The broad footprint of climate  
472 change from genes to biomes to people. *Science*. 354: aaf7671.

473 Siepielski, A.M., M. B. Morrissey, M. Buoro, S. M. Carlson, C. M. Caruso, S. M. Clegg et al. (2017).  
474 Precipitation drives global variation in natural selection. *Science*. 355: 959–962.

475 Stonehouse, J. C., L. G. Spurgin, V. N. Laine, M. Bosse, M. A. M. Groenen, K. van Oers, B. C.  
476 Sheldon and M. E. Visser. (2024). The genomics of adaptation to climate in European great tit (*Parus*

477 major) populations. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/grad043>. Advance access  
478 publication 12 October 2023.

479 Swaegers, J., S. De Cupere, N. Gaens, L. T. Lancaster, J. A. Carbonell, R. A. Sánchez Guillén and R.  
480 Stokes. (2024). Plasticity and associated epigenetic mechanisms play a role in thermal evolution during  
481 range expansion. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/qrac007>. Advance access  
482 publication 31 January 2023.

483 Suárez D., P. Arribas, E. Jiménez-García and B. C. Emerson. (2022). Dispersal ability and its  
484 consequences for population genetic differentiation and diversification. *Proceedings of the Royal*  
485 *Society B*. 289: 20220489.

486 Tougeron, K., J. Brodeur, C. Le Lann and J. van Baaren. (2020) How climate change affects the  
487 seasonal ecology of insect parasitoids. *Ecological Entomology*. 45: 167–181.

488 Urban, M. C., J. Swaegers, R. Stokes, R. R. Snook, S. P. Otto, D. W. A. Noble, M. Moiron, M. H.  
489 Hällfors, M. Gómez-Llano, S. Fior, J. Cote, A. Charmantier, E. Bestion, D. Berger, J. Baur, J. M.  
490 Alexander, M. Saastamoinen, A. H. Edelsparre and C. Teplitsky. (2024). When and how can we predict  
491 adaptive responses to climate change. *Evolution Letters*. 8(1). <https://doi.org/10.1093/evlett/grad038>.  
492 Advance access publication 29 November 2023.

493 Walther, G-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J-M. Fromentin, O.  
494 Hoegh-Guldberg, and F. Bairlein. (2002). Ecological responses to recent climate change. *Nature*. 416:  
495 389-395.

496

497







498

499

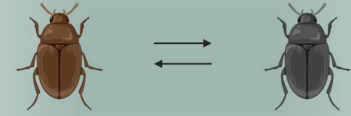
500

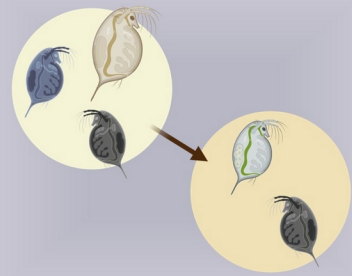















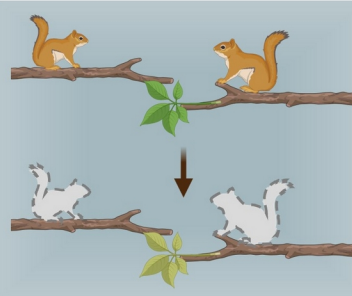





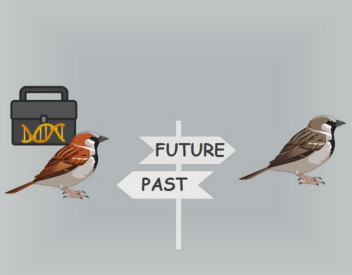



501



## EMERGING THEMES FROM THE SPECIAL ISSUE ON CLIMATE CHANGE ADAPTATION

-  Conceptual
-  Experimental data
-  Theoretical modelling
-  Genetic analysis
-  Meta-analysis
-  Long-term monitoring in the wild

### Interactions among organisms



<b>Predicting <math>V_a</math> and selection</b>		<p>Chantepeie et al.  </p> <p>Crowther et al.  </p> <p>Moiron et al.  </p> <p>Nadeau &amp; Urban  </p> <p>Stonehouse et al. </p>	<p>Kulmuni et al. </p> <p>Nomoto et al.  </p> <p>Sauve et al.   </p>
<b>Population persistence</b>		<p>Crino et al. </p>	<p>Gomez-Llano et al.  </p> <p>Murray et al.  </p>
<b>Evolutionary history</b>		<p>Hällfors et al. </p> <p>Swaegers et al. </p>	<p>Baur et al. </p>

Urban et al.  

506 **Figure 1. Schematic illustration of the key themes that emerged from the 14 contributions in the**  
507 **Special Issue: Evolutionary Adaptation to Climate Change, such as predicting  $V_a$  (e.g. additive**  
508 **genetic variance), population persistence, and evolutionary history.** Interactions among organisms  
509 include both within and among species interactions. Several contributions could fit in more than two of  
510 these themes, but here we highlight only the main aspects. Experiments ranged from short term  
511 reaction norm experiments to experimental evolution studies. Genetic analyses cover both genomic and  
512 quantitative genetic studies, and long-term monitoring in the wild refer to species occurrence and  
513 individual monitoring data.