

1 **Do the benefits of hybridization outweigh the costs under conditions**
2 **of global change?**

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10

11 **Abstract**

12

13 Global change is predicted to facilitate hybridization but whether the hybrid populations persist
14 and shape biodiversity remains unknown. At the grey zone, before speciation is completed,
15 hybridization is likely leading to simultaneous costs and benefits for hybrid fitness. Whether the
16 benefits outweigh the costs depends on the environment, as hybrid fitness, and potential
17 incompatibilities, can be context dependent. However, hybrid fitness is rarely investigated in
18 environmental conditions that simulate global change. Further knowledge gaps exist in
19 understanding whether adaptive plasticity of hybrids and novel behaviours they may display can
20 facilitate or hinder their persistence under conditions of global change. Previous work has
21 discussed the impact of global change on the erosion of species barriers and persistence of
22 parental lineages, but here we draw attention to the role of hybrids themselves and selective
23 pressures acting on them. We predict that benefits of hybridization can outweigh the costs in
24 scenarios where hybrid incompatibilities can be purged and the environment is sufficiently
25 different from the parental environments. This can give hybrid populations an advantage due to
26 their increased genetic diversity and plasticity to outcompete the parental species or establish in
27 environments where the parental species cannot. Persistence of hybrid lineages over ecological
28 and evolutionary time scales may help to preserve parental genetic diversity, especially in
29 scenarios where parental species would go extinct.

30

31 **Keywords:** adaptation; admixture; climate change; fitness; global change; hybridization;
32 persistence of biodiversity

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34 **Hybridization can lead to positive and negative fitness outcomes simultaneously**

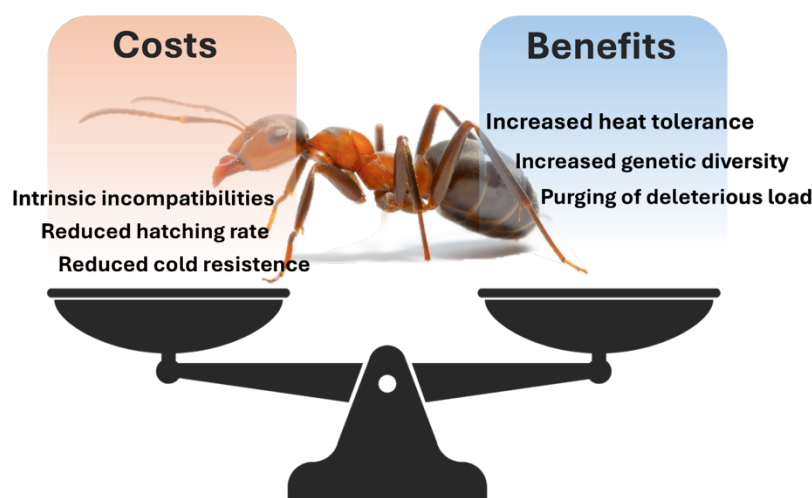
35 Hybridization is the interbreeding between species or genetically divergent populations
36 producing offspring of mixed ancestry (Barton and Hewitt, 1985). This rather broad definition of
37 hybridization is useful, since the process of speciation is continuous (Stankowski and Ravinet,
38 2021), and the definition encompasses interbreeding between diverging taxa at various stages
39 of this process. For a long time, studies (especially on animals) have emphasized the
40 deleterious consequences of hybridization (i.e. hybrid breakdown) (Arnold, 1997) as it can lead
41 to hybrid sterility and inviability or individuals who are maladapted to parental environments.
42 However, hybridization can also facilitate adaptation by transferring locally adaptive alleles from
43 one species into another (i.e. adaptive introgression). For example, high altitude adaptation in
44 humans is enabled by genes which we received from Denisovans (Huerta-Sánchez *et al.*, 2014)
45 and *Heliconius* butterflies have borrowed protective wing pattern genes from closely related
46 species (Dasmahapatra *et al.*, 2012). Hybridization can also generate novel gene combinations
47 as well as genotypic and phenotypic variation on which selection can act, fueling adaptation and
48 adaptive radiations, as documented in Cichlid fish (Meier *et al.*, 2017). Several studies have
49 investigated either the fitness benefits or costs of hybridization. However, at the grey zone of
50 speciation, where speciation has not yet completed, hybridization is likely to generate both
51 fitness costs and benefits simultaneously. This is because hybridization combines genetic
52 material from two diverged lineages, resulting in novel allelic combinations that are either
53 neutral, deleterious (i.e., incompatible), or beneficial. However, major gaps exist in our
54 understanding of the conditions for which benefits of hybrid genotypes outweigh the costs, and
55 how hybrid fitness across time and space links to long-term population persistence.

56

57 **Costs and benefits of hybridization are context dependent**

58 Outcomes of hybridization in terms of hybrid fitness and persistence are usually investigated in
59 the environment of the parental taxa. This is because speciation biologists have been interested
60 in identifying what keeps two related taxa separate, and this question has been most relevant in
61 the environments of the parental taxa. Yet, several case studies highlight how hybrid fitness and
62 fixation of parental ancestry in hybrid populations depend on the environment (de Boer, 1982;
63 Martin-Roy *et al.* 2021; Thompson *et al.*, 2022). Allelic combinations from diverged taxa that
64 were deleterious in one environment can be neutral or beneficial in another (Ono, Gerstein and
65 Otto, 2017; Thompson *et al.*, 2022, 2024). For example, hybrids between benthic and limnetic
66 stickleback fish suffer from functional mismatch between phenotypic traits that reduces the
67 growth of some hybrids beyond that expected from an intermediate phenotype, suggesting a

68 role for epistasis (Arnegard *et al.*, 2014). However, in a benign lab environment, stickleback
69 hybrids do not experience the same fitness cost. Insights on the extent of environment
70 dependent hybrid fitness could be gained from species that hybridize outside their native range
71 (i.e. in a novel environment), like some invasive species (Muhlfeld *et al.*, 2014; Mesgarana *et*
72 *al.*, 2016), or the breeding of divergent varieties for climate resilient crops (discussed in
73 Khazaei, Dodd and Ortiz, 2026).



87 **Figure 1.** In the mound-building wood ants hybridization between *Formica aquilonia* and *F. polyctena* in
88 Finland generates simultaneous costs and benefits for the hybrid populations. As parental *F. polyctena* is
89 absent or very rare in Finland, the ecologically meaningful comparison is between hybrids and locally
90 dominant *F. aquilonia*. Compared to *F. aquilonia* the hybrids have increased heat tolerance and genetic
91 diversity (Satokangas *et al.*, 2023). They also show a signature of purging deleterious load that has
92 accumulated in parental species (Nouhaud *et al.*, 2022). On the other hand, the hybrids suffer from
93 intrinsic incompatibilities, reduced hatching rate, and reduced cold resistance in contrast to *F. aquilonia*.

94
95 Despite growing interest, fitness of hybrids in different or varying environments and the extent to
96 which hybrid fitness is environment dependent remain poorly studied. Investigating hybrid
97 fitness beyond parental environments is highly relevant in the context of current global change:
98 populations around the globe will be facing novel environments due to climate change,
99 agriculture, industry and other anthropogenic effects. Hybrid genotypes that are incompatible in
100 one environment may be more compatible in the novel environment and the increased genetic
101 diversity speeds hybrid adaptation to a novel environment, tipping the scales between costs and
102 benefits. Simulations assuming polygenic trait basis show that in a wide range of scenarios,
103 later generation hybrids tend to have higher fitness compared to parental species in a novel
104 environment, even if they suffer from incompatibilities (Kulmuni, Wiley and Otto, 2023).

105

106 Furthermore, if hybrid incompatibilities are not lethal, they can be purged in later hybrid
107 generations, assuming hybrid populations avoid extinction in the early generations (Bank,
108 Bürger and Hermisson, 2012; Ayala-López and Bank, 2025). The speed of purging depends on
109 the strength and genomic architecture of the incompatibilities (Blanckaert, Bank and Hermisson,
110 2020). The simplest case is a two-locus incompatibility between derived (D) alleles, where the
111 ancestral (A) alleles are still available. If the parents are A_1A_1/D_2D_2 and D_1D_1/A_2A_2 then F1
112 hybrids will have A_1D_1/A_2D_2 genotypes. Genotypes containing both D1 and D2 alleles have
113 reduced fitness and appear at F1 but also in further hybrid generations and A_1A_1/A_2A_2 rapidly
114 takes over in an isolated hybrid population. Purging can happen faster in isolated hybrid
115 populations, where gene flow from parental to hybrid populations does not occur, meaning
116 incompatibilities are not re-introduced. For example, despite numerous intrinsic incompatibilities
117 that impact the majority of the genome, isolated wood ant hybrid populations have persisted for
118 decades (Heidbreder *et al.*, 2026). Detailed investigations on one hybrid population show that
119 hybrids tend to fix one or the other parental ancestry at barrier loci, consistent with purging of
120 the incompatibilities (Heidbreder *et al.*, 2026). Since purging of incompatibilities can happen
121 over time, fitness of hybrid populations can also vary over generations. Despite low hybrid
122 fitness in early generations, later generation hybrids may show higher fitness.

123

124 **Hybridization may increase under conditions of global change, which could fuel** 125 **adaptation or extinctions**

126 Global change challenges species around the world. Today, organisms face multiple stressors
127 at a higher frequency than several decades ago, thus posing challenges to natural populations.
128 Such biotic and abiotic stressors include increased pesticide or pathogen loads, invasive
129 species, climate change including extreme events, and habitat degradation and loss (Hof *et al.*,
130 2011; Eggleton, 2020; Wagner, 2020), all fueling biodiversity loss (Vellend *et al.*, 2017;
131 Eggleton, 2020; Jaureguiberry *et al.*, 2022). It is thus essential to understand and predict how
132 species and hybrid populations respond to and persist under global change.

133 Several authors have suggested that global change leads to increased rates of hybridization
134 (Hoffmann and Sgrò, 2011; Ottenburghs, 2021). This is because global change pushes
135 populations to migrate to more suitable areas. Similarly, agriculture and global trade also
136 transport plants and animals across the world. Both bring previously isolated populations or
137 species into contact thus providing opportunities for hybridization. Furthermore, pollution may

138 alter the environment in ways that disrupt prezygotic isolating mechanisms (Grabenstein and
139 Taylor, 2018). A systematic evaluation of the impact of global change on rates of hybridization
140 across taxa is lacking. Yet, both historical and contemporary data underline the potential for
141 elevated rates of hybridization in response to climate change or other aspects of global change
142 (Table 1). It is difficult to link global change directly as the cause for elevated hybridization rates,
143 but several examples of increased hybridization or number of hybrid individuals coinciding with
144 global change do exist (see Grabenstein and Taylor, 2018; Arce-Valdés and Sánchez-Guillén,
145 2022) for previous syntheses).

146 The effect of Pleistocene climate oscillations facilitating periods of allopatry and sympatry and
147 so divergence and gene flow, respectively, is well known (e.g. (Morgan *et al.*, 2010; Musher *et*
148 *al.*, 2020). Contemporary examples include eutrophication in perialpine lakes, which coincides
149 with increased success of F1 hybrid *Daphnia* (Keller *et al.*, 2008). Increased rates of
150 hybridization in swordtail fish are associated with water pollution, which is assumed to impact
151 assortative mating (Moran *et al.*, 2026). Range shifts coincident with the start of climate change
152 have driven hybridisation between Atlantic puffin populations (Kersten *et al.*, 2023). An
153 increased rate of bidirectional gene flow in wood ants coincides with climate warming after the
154 last glacial maximum based on demographic modeling (Portinha *et al.*, 2022). Furthermore, in
155 the past 20 years, the wood ant hybrids have expanded 200 km northwards, coinciding with the
156 expansion of climatic conditions suitable for hybrids (Krapf *et al.*, 2025). Lastly, hybridization
157 between black-capped and mountain chickadees positively correlates with human habitat
158 disturbances (Grabenstein *et al.*, 2023). Table 1 collates examples that demonstrate cases
159 where past or present changes in the environment or climate have potentially facilitated
160 hybridization (see also Table 1 in Arce-Valadés and Sánchez-Guillén 2022). However, the rate
161 of environmental change at present is ten to hundreds times faster than before the
162 Anthropocene, and could thus lead to higher rates of hybridization compared with previous
163 climatic changes. Alternatively, the current pace of change could lead to extinction of
164 populations before opportunities for hybridization arise.

165 Hybridization induced by global change could fuel adaptation to global change and/or lead to
166 increased rates of extinctions. Generally, species can respond to the new conditions by
167 behavioral changes, phenotypic plasticity, and adaptation via genomic changes, or a
168 combination thereof (Donelson *et al.*, 2023). Because behavioral and phenotypic plasticity are
169 finite, costly, and limited by the genomic makeup of an organism, many species need to adapt
170 genetically, in order to persist. Hybridization can allow a quick increase in genetic variation,

171 which could promote adaptation to global change. Under novel environments generated by
172 global change, it is likely that neither parental nor hybrid populations are well adapted, and the
173 increased variation among hybrids may make hybrid lineages better candidates for persisting in
174 changing conditions. This may be especially true if hybrids have increased plasticity or selection
175 favors those hybrid genotypes that have broader or more adaptive plastic responses. However,
176 this is only possible if the hybrid populations persist and can overcome potential hybrid
177 incompatibilities. Below, we focus on the impact of hybridization on fitness, plasticity, and
178 behavior under conditions of global change. Previous review and opinion papers have
179 discussed the impact of climate change on the erosion of species barriers and persistence of
180 parental lineages (Vallejo-Marín and Hiscock, 2016; Grabenstein and Taylor, 2018; Larson,
181 Tinghitella and Taylor, 2019), but here we draw attention to the role of hybrid populations or
182 lineages themselves and selective pressures acting on them. Using recent examples, we
183 discuss cases where hybrid populations are favoured or selected against under conditions of
184 global change and highlight gaps in our knowledge where more information is needed to predict
185 the persistence of hybrid lineages in conditions of global change.

186

187 **More studies on fitness of later generation hybrids in conditions of global change are**
188 **needed**

189 Several studies on fitness of early-generation hybrids under conditions of global change exist.
190 These studies show that hybridization can positively or negatively affect fitness and phenotypes
191 in the context of global change. For example, under increasing temperatures, some hybrid
192 populations can survive better than parental species: For instance, F1 hybrid poplar trees had a
193 higher survival compared to both parental species under dry condition (Hultine *et al.*, 2020) as
194 well as a higher survival than one of the parental species in a common-garden experiment
195 performed in warm conditions (Hord *et al.*, 2025). Similarly, gene flow between populations in an
196 annual wildflower had a positive effect on fitness when tested in a common garden experiment
197 in an unexpectedly warm year (Bontrager and Angert, 2019). Benefits have been demonstrated
198 in early-generation hybrids in a wide variety of other environments induced by global change,
199 such as increased fitness of F2 yeast hybrids in increasing salt concentrations (Stelkens *et al.*,
200 2014), greater tolerance to reduced dissolved oxygen in F1 hybrids of invasive shrimps
201 (Jermacz *et al.*, 2025), and greater tolerance to pesticides in F1 and F2 hybrids of plant bugs
202 (Wazir and Shad, 2022).

203

204 Detrimental examples also exist. For example, F1 hybrids of ascidians (Chordata, Tunicata)
205 survived a narrower range of experimental temperatures compared to parental species,
206 indicating that hybrids are less likely to persist and disperse to novel habitats (Hudson, McQuaid
207 and Rius, 2021). However, the low fitness of early-generation hybrids living in environments
208 induced by global change, does not necessarily reflect long-term hybrid fitness (Mitchell *et al.*,
209 2019; Kulmuni, Wiley and Otto, 2023), as purging of incompatibilities and deleterious alleles is
210 expected over time. However, the rate at which these alleles are purged and incompatibilities
211 overcome has rarely been experimentally evaluated (although several theoretical studies exist;
212 e.g.(Bank, Bürger and Hermisson, 2012; Blanckaert, Bank and Hermisson, 2020).

213

214 Only a small number of studies have investigated fitness of later generation hybrids under
215 conditions of global change. Yet, some evolve and resequence studies on hybridized lineages
216 have demonstrated increased heat tolerance of later generation hybrids under heat stress
217 despite evidence for intrinsic incompatibilities (Griffiths, Kawji and Kelly, 2021; Poikela *et al.*,
218 2026). These studies suggest that under strong heat selection the benefits of gene flow
219 outweigh the costs of hybrid incompatibilities. Similar results have been found for trees, where
220 introgression is associated with increased tolerance to selection pressures induced by warmer,
221 drier climates (Hord *et al.*, 2025). Overall, studies comparing hybrid fitness and phenotypes over
222 multiple generations in conditions of global change are lacking. Such multiple-generation
223 studies are needed to reveal the impact of environment dependent incompatibilities and to
224 understand the scenarios where incompatibilities can be purged over time. In other words, these
225 studies help to predict if hybridization could fuel adaptation to global change and whether the
226 costs of hybridization could be overcome under conditions of global change. Genetic
227 architecture and severity of incompatibilities will impact the likelihood of overcoming the cost of
228 incompatibilities. We predict that hybrid populations or lineages may be better equipped to
229 adapt to global change compared to parental species when the architecture of incompatibilities
230 is simple and the environment is novel enough for hybrid populations to leverage increased
231 genetic diversity and adapt rapidly to the novel environment. The resulting persistent hybrid
232 lineage might take many different forms - from adaptive introgression of a few alleles to
233 something that is closer to a 50:50 ancestry mix. Furthermore, the persistence of these hybrid
234 lineages also depends on the spatial and reproductive isolation from the parental lineages.

235

236

237 **Hybridization can increase phenotypic plasticity accelerating adaptation to global**
238 **change**

239 The multifarious nature and strong selective pressure associated with global change blend
240 processes acting on ecological and evolutionary timescales (Carroll *et al.*, 2007). The fate of
241 hybrid lineages in rapidly changing climates thus depends both on genetic adaptation as well as
242 on phenotypic plasticity. When environments are temporally and spatially heterogeneous,
243 natural selection typically favours higher phenotypic plasticity (Snell-Rood and Ehlman, 2021).
244 An important question is thus whether hybrids and hybrid lineages have higher phenotypic
245 plasticity.

246
247 Outcrossed populations and early-generation interspecies hybrids have more genetic and
248 phenotypic variation and show more transgressive phenotypic values (Rieseberg, Archer and
249 Wayne, 1999). Higher genetic variation does not necessarily result in higher plasticity: when a
250 trait is more genetically variable, plasticity is, by definition, lower since $V_P = V_G + V_E$, where V_P
251 is phenotypic variance, V_G is genetic variance, and V_E is environmental variance. A positive
252 relationship between heterozygosity and plasticity is also not supported in the literature
253 (Gillespie and Turelli, 1989; Scheiner, 1993). However, increased genetic variation due to
254 recombination of parental genotypes should lead to an increase in the breadth of genotype by
255 environment ($G \times E$) interactions (Via and Lande, 1985; Scheiner, 1993). This increase in the
256 *variation* in plasticity should be particularly important in heterogeneous environments. Increased
257 $G \times E$ could be a mechanism explaining some cases of increased plasticity and performance in
258 hybrids between *Daphnia* clones (Yampolsky and Scheiner, 1994), hybrid maize (Liu *et al.*,
259 2021), as well as the success of hybrid lineages in extreme environments, such as salt-tolerant
260 sunflowers (Gross *et al.*, 2004).

261
262 In addition, outcrossing and hybridization can recombine regulatory networks, e.g. when
263 developmental switch genes and other regulatory loci that control plasticity (Schlichting and
264 Pigliucci, 1993) are coupled with new protein coding genes. A potential manifestation of this are
265 high rates of plasticity in gene expression, such as in a recent study in mussels (Schwartz *et al.*,
266 2024): up to 25% of the genes in hybrid mussels showed gene expression plasticity in relation
267 to temperature variation beyond what was seen in the parental lineages. These types of
268 transgressive gene expression patterns (i.e. expression levels outside parental ranges) can
269 allow plastic responses to novel environmental conditions (Lensink, Monroe and Kliebenstein,
270 2025). Similarly, in allopolyploid plants (i.e., interspecific hybrid with more than two sets of

271 chromosomes), combinations of different parental genomes fix heterozygosity and result in high
272 genomic plasticity, including in the epigenome (Leitch and Leitch, 2008). As a result, polyploids
273 may use gene expression profiles of both parents resulting in a higher diversity of expressed
274 phenotypes across environments and fitness benefits in heterogeneous environments due to
275 increased variation in trait means and trait plasticity (Shimizu-Inatsugi *et al.*, 2017; Wei *et al.*,
276 2019). Recombining parental genomes in hybrids provides multiple molecular routes towards
277 higher genetic variance for plasticity, i.e. higher $G \times E$, which may increase the opportunity for
278 short-term adaptive responses in changing environments. In turn, higher phenotypic plasticity
279 may positively influence gene flow and thus the likelihood of hybridization. This is because more
280 plastic species tend to have broader distributions (Hollander, 2008) and adaptive plasticity
281 increases the likelihood of coexistence in heterogeneous environments (Pérez-Ramos *et al.*,
282 2019).

283

284 Higher $G \times E$ may contribute to the higher resilience and performance of hybrids, especially in
285 more heterogeneous environments. Does it also contribute to long-term persistence of the
286 hybrid lineages in changing environments? Phenotypic plasticity is potentially important for
287 global change adaptation. When comparing among wild and laboratory populations, for which
288 genomic and plasticity information was available, the amount of genetic variation in plastic
289 responses to the environment ($G \times E$) was found to be an important predictor of species'
290 vulnerabilities to global change (Kelly, 2019). Selection can sort that variation efficiently. For
291 example, Mongolian pine trees with high gene flow between mountain and dune habitats show
292 increased plasticity in environmental stress tolerance. These trees also showed divergence in
293 locally adaptive traits related to water transport and mechanical support despite gene flow
294 (Wuyuntana *et al.*, 2025). This example illustrates how increased genetic variation following
295 hybridization can be sorted by selection so that plasticity is maintained for traits that contribute
296 to stress responses, while traits that contribute to local adaptation are canalized. Similarly, a
297 study resurrecting ancestral *Daphnia* lineages from dormant propagules found that ancestral
298 genetic variation in predator-induced plasticity was the basis for predator-mediated selection.
299 The outcomes of selection were rapid shifts in *Daphnia* behavior and life history while
300 maintaining high variance in plasticity (Landy *et al.*, 2020).

301

302 Thus, elevated plasticity in hybrids can be maintained by selection and contribute to short-term
303 benefits. Two caveats are that 1) there are no meta-analyses or systematic reviews for the role
304 of elevated hybrid plasticity in adapting to global change and so evidence, although available

305 across taxa and environments, is somewhat anecdotal and 2) the long-term fate of hybrid
306 plasticity is poorly understood. Whether plasticity promotes persistence of the hybrid lineage on
307 the long term depends on whether adaptive phenotypic plasticity can be assimilated
308 (Waddington, 1953; Lande, 2009) or allows the lineage to survive long enough so that they can
309 genetically adapt in other phenotypic dimensions (Visser, 2008). Plasticity can also hinder
310 adaptation when it buffers against selection pressures (Price, Qvarnström and Irwin, 2003; De
311 Jong and De Jong, 2005).

312

313 Theoretically, assimilation will happen if the plastic response results in higher genetic and
314 phenotypic variation (Lande, 2009). This has been documented for several species, including in
315 the context of climate change (Chevin, Collins and Lefèvre, 2013) and is likely attributable to the
316 release of cryptic genetic variance in novel environments (Le Rouzic and Carlborg, 2008;
317 Husby, Visser and Kruuk, 2011). Similar to parental species, whether an initial increase in
318 plasticity following hybridization increases evolvability and adaptive potential depends on
319 genomic architectures and selection pressures. Consider the following contrasting examples:
320 Wild-cultivated fish hybrids showed initial increased phenotypic variation and plasticity.
321 However, after 11 years in the environment of the wild ancestor, plasticity decreased back to
322 ancestral magnitude. Phenotypes and performance converged with those of the wild ancestor
323 (Harbicht, Wilson and Fraser, 2014). This is likely due to strong directional selection resulting in
324 convergent evolution in the hybrid towards one of the parental lines. In contrast, several
325 examples in polyploids plants show long term persistence of elevated plasticity, genetic
326 variation, and broader environmental tolerance (Shimizu-Inatsugi *et al.*, 2017; Wei *et al.*, 2019).
327 The polyploid architectures here fix heterozygosity and selection favors the hybrid lineage itself,
328 because it has higher gene expression plasticity than its ancestors. In addition, fluctuating
329 selection (like that imposed by a changing climate) likely contributes to the maintenance of
330 genetic diversity and promotes plasticity. Comparing these two examples, illustrates an
331 important point: the degree to which parental genomes can recombine in the hybrid lineage and
332 whether selection acts directionally towards parental phenotypes versus fluctuates to maintain
333 genetic variation for plasticity jointly influence the long-term fate of hybrids and underlines the
334 importance of studying hybrid fitness through time and space.

335

336

337

338 **The impact of hybridization on behavior in the conditions of global change is largely**
339 **unknown**

340 In order to understand reproductive isolating barriers, much focus has been devoted to hybrid
341 phenotypes and fitness. Yet, a potentially relevant aspect of hybridization in the context of
342 global change is behavior. By definition, behaviour is a form of phenotypic plasticity (West-
343 Eberhard, 1989), yet it is an extremely plastic trait that can be more diverse and nuanced than
344 traits such as morphology or physiology (West-Eberhard, 1989). Due to its high plasticity, the
345 probability of applying a favourable behavior under changing environments is also higher than
346 for example generating a favourable morphology. A behavior is also immediate action and can
347 be modified or reversed more rapidly than other plastic traits (West-Eberhard, 1989). Further,
348 like other plastic traits, behavior allows for extended waiting time required for genetic
349 adaptation. Compared to parental species, hybrids may display similar, intermediate, and novel
350 behaviors, combine behavioral elements from both parents, or lack parental behaviours (Payne,
351 2024). Novel or combined behaviors may help hybrids persist in novel habitats due to global
352 change, but they can also hinder their persistence.

353 Divergent migration behaviours (i.e., timing, routes, age) in hybrids can adversely impact their
354 fitness and survival. For example, intermediate departures of F1 hybrid birds (Väli *et al.*, 2018),
355 earlier and intermediate emigration of F1 and backcrossed hybrid fish (Kovach *et al.*, 2015;
356 O'Toole *et al.*, 2015; Ramesh *et al.*, 2021; Bourret *et al.*, 2022), or different migration routes in
357 hybrid birds (F1 to later generations; (Scordato *et al.*, 2020; Justen, Lee-Yaw and Delmore,
358 2021) compared to parental species can lead to reduced amount and quality of food reducing
359 hybrids' fitness. If changes in migration behavior are further coupled with reduced cognitive
360 abilities or mechanistically flawed behaviours (e.g. time-consuming and flawed transport of nest
361 material; Dilger 1962) in hybrids of varying generations (e.g., diminished learning and memory
362 of food locations; (McQuillan *et al.*, 2018; Rice and McQuillan, 2018; Alario *et al.*, 2023), this
363 may further negatively affect hybrids' fitness and survival. Such intermediate, combined, or
364 novel behaviors in hybrids can lead to reduced fitness, population sizes, and bottlenecks, that
365 can be even more pronounced with unpredictable and extreme weather events under global
366 change.

367 However, behavioral changes in hybrids can also contribute positively to fitness in conditions of
368 global change. For example, hybrid fish are more aggressive and bolder than parental species
369 (F1 hybrids: Einum and Fleming, 1997; Johnsson and Abrahams, 2011; later generation:
370 (D'Amore, Popescu and Morris, 2019), possibly allowing them to rapidly expand to new habitats.

371 F1 hybrid mice were more efficient at learning and had better memory compared to their inbred
372 parents (Smart, 1970; Sloin *et al.*, 2022), which could help survival in novel environment.
373 Further, later-generation hybrid birds produce songs from both parental species (Curry,
374 Rossano and Reudink, 2007), which may give males the functional advantage to deter rivals of
375 both parental species (Robbins, Braun, Tobey *et al.*, 1986). Such behavioral changes can allow
376 hybrids to attain higher food quality or mates, occupy different ecological niches, or compete
377 with their parental species thus elevating their fitness.

378 Overall, studies on the effects of hybridization on the behavior under global change are limited.
379 This may be due to the fact that detecting behavioral differences among parental species and
380 their hybrids can be challenging as well as time-consuming. Studying behavioral changes in
381 hybrids in the context of global change adds an additional layer of difficulty. Yet, the mentioned
382 examples suggest that hybrids may be intermediate in hard-wired (*i.e.*, genetically-determined)
383 behaviors such as migration (Liedvogel, Åkesson and Bensch, 2011) or transporting nesting
384 material (Dilger 1962). At the same time, hybrids may have a broader and possibly more
385 nuanced repertoire in behaviours that are mainly determined by environmental or other cues
386 than parental species - assuming that parental species have adapted to different habitats.
387 Whether mixed, intermediate, or novel behaviors are beneficial or detrimental to hybrids, or both
388 when present at the same time, is difficult to predict with this limited number of studies and the
389 general high level of behavioral plasticity. Nevertheless, we predict that mixed, novel, or
390 intermediate behaviors in hybrid lineages can significantly impact the persistence of hybrids,
391 especially under novel environments such as expected under global change. Overall, behavior
392 can be viewed as one aspect of an individual's phenotype (West-Eberhard, 1989). Moving away
393 from the focus on hybrid viability and sterility, and expanding studies to the various aspects of
394 hybrid phenotype, like behavior, allows a more nuanced understanding of hybrid fitness and
395 whether hybrids are likely to persist and adapt in the context of global change.

396 **Caveats and conclusions**

397 Here we have mostly ignored the fact that the fate of hybrids also depends on demographics
398 and interaction with the parental lineages. Hybridization in species declining towards extinction
399 increases outbreeding depression and has the potential to erode local adaptation, while
400 hybridization in species on the rise following an invasion increases adaptive genetic variation
401 and adaptive plasticity (Colautti *et al.*, 2017). Also, the past demographic history of the species
402 can mediate the benefits of hybridization. Species with small effective population size
403 accumulate slightly deleterious mutations, due to inefficiency of selection removing them.

404 Hybridization can facilitate purging these deleterious mutations, as has been inferred e.g. in
405 ants (Nouhaud et al., 2022) and humans (Juric, Aeschbacher and Coop, 2016). Note, purging of
406 slightly deleterious mutations that accumulated within a species is different to purging of
407 incompatibilities. To predict the fate of hybrids it is important to integrate the effect of
408 hybridization on the distribution of genetic variation across the geographic distribution of the
409 hybrid population in relation to dynamics in selection and phenotypic diversity. Interaction
410 between hybridization and demographics can partially be tested using natural hybrid systems,
411 especially those that are spatially distributed along a chronosequence, such as is the case for
412 volcanic islands, or along latitudinal and elevation gradients (i.e., space-for-time approach).
413 However, experimental evolution of hybrids in different environmental and demographic
414 contexts would be important to complement the research on natural systems. Experimental
415 evolution approaches could, in principle, freely vary a complex array of factors that shape the
416 long-term fate of plasticity and genetic diversity in hybrids and their contribution to global
417 change adaptation. Experimental evolution approaches could also take into account how
418 competitive or mating interactions between hybrid and parental lineages impact the persistence
419 of hybrid lineages under conditions of global change.

420
421 In conclusion, global change is predicted to facilitate hybridization but whether and how the
422 hybrid lineages persist and shape biodiversity remains unknown. However, the fact that traces
423 of past hybridization and gene flow characterize the history of many taxa, suggests that the
424 impact of hybridization on biodiversity is pervasive. At the moment the costs and benefits of
425 hybridization in the context of current global change are unknown because hybrid fitness,
426 phenotypes, plasticity, and behavior are rarely investigated in later generation hybrids and in
427 environmental conditions that simulate global change. We predict that the benefits of
428 hybridization can outweigh the costs in scenarios where hybrid incompatibilities can be purged,
429 and the environment is sufficiently different from the parental environment, giving hybrids an
430 advantage due to increased genetic diversity and plasticity to outcompete the parental species.
431 In terms of persistence of biodiversity, extinction of parental species represents a loss, but
432 persistence of hybrid lineages preserves (at least partial) parental genetic diversity. This may be
433 a more desirable long-term outcome from a conservation perspective than the extinction of both
434 parental species and hybrid lineages.

435
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Ecosystem	Taxa	Change	Evidence for increased hybridization or hybrids due to global change	Reference	Link
Freshwater	Daphnia	Eutrophication in perialpine lakes	Abundance of F1 hybrids in lakes with highest trophic state in the past	Keller et al. 2008	https://pmc.ncbi.nlm.nih.gov/articles/PMC2453521/
Freshwater	Xiphophorus swordtail fish	Change in water quality	Ocurrence of hybrids and reduced assortative mating in low water quality coinciding with urban area	Moran et al. 2025	https://www.biorxiv.org/content/10.1101/2025.04.22.649978v1
Freshwater	Trout	Climate change	Increasing summer temperature and decreasing spring percipitation is linked with hybridization	Muhlfeld et al. 2014	https://www.nature.com/articles/nclimate2252
Freshwater/ marine	Stickleback fish	Accidental introduction of the invasive signal crayfish	After crayfish introduction, hybrids have increased in number	Taylor et al. 2005	https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-294X.2005.02794.x
Marine	Atlantic puffins subspecies	Climate change	Genomics detects recent hybrids due to sudden southward expansion	Kersten et al. 2023	https://www.science.org/doi/10.1126/sciadv.adh1407
Marine	Blue whales	Climate change and/or whaling	Whaling likely reduced the number of organisms and recent climatic changes likely facilitating range expansions led to hybridization	Attard et al 2012	https://onlinelibrary.wiley.com/doi/full/10.1111/mec.12025
Terrestrial	Black-capped and mountain chickadees	Human habitat disturbance	significantly more hybrids in areas with higher human disturbance	Grabenstein et al. 2022	https://onlinelibrary.wiley.com/doi/10.1111/gcb.16476
Terrestrial	Banksia plants	human habitat disturbance (roadways, tracks, abandoned mine pits, railway lines, firebreaks)	significantly more hybrids in areas with higher human disturbance	Lamont et al. 2003	https://academic.oup.com/jeb/article/16/4/551/7323372#430377291
Terrestrial	Butterflies	Climate Change	Northward movement of one parent due to a warming climate likely lead to Increased introgression	Kunte et al., 2011	10.1371/journal.pgen.1002274
Terrestrial	Butterflies	warming climate	Shifting climate conditions in spring maximum temperature and summer minimum temperature due to climate change likely contributed to hybridization	Jahner et al. 2011	https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1558-5646.2011.01481.x

Terrestrial	Butterflies	warming climate	A warming climate likely led to the northward shift of the host plant (<i>Aristolochia</i>), which likely allowed hybridization between the butterfly species	Mullen et al. 2008	10.1111/j.1558-5646.2008.00366.x
Terrestrial	Damselflies	warming climate	Climate change facilitated expansion of one parent, establishing a sympatric zone between parental species which likely led to hybridization	Sánchez-Guillén	http://www.biomedcentral.com/1471-2148/11/210
Terrestrial	Formica wood ants	warming climate	Northward expansion of hybrids coincides with expansion of suitable and warmer climatic conditions	Krapf et al. 2025	https://www.biorxiv.org/content/10.1101/2025.09.25.678544v2
Terrestrial	Ants	Introduction and warming climate	The unintended introduction of both species led to expansion in North America, while a warming climate facilitated their spread and likely led to hybridisation events	Callcott and Colli	https://www.jstor.org/stable/3495821 ; https://academic.oup.com/ee/article-abstract/31/1/127/3778
Terrestrial	Termites	Human activity	Human activity introduced both invasive termites, and in the introduced habitat, swarming overlapped in observation years 2013 and 2014	Chouvenc et al. 2014	https://doi.org/10.1371/journal.pone.0120745
Terrestrial	Grasshoppers	Human habitat disturbance	Deforestation ca 800 years ago led to hybridisation	Sivyer et al., 2011	10.1111/icad.12289
Terrestrial	Grasshoppers	Human habitat disturbance and drought	A construction of a dam and subsequent habitat changes as well as a prolonged drought have allowed range overlap and hybridization	Brust et al. 2008	https://www.jstor.org/stable/20621954
Terrestrial	Grasshoppers	Drought and climate change	Ongoing climate change and frequent extreme weather events such as droughts can decrease population sizes of <i>C. montanus</i> possibly leading to more frequent hybridization events.	Rohde et al., 2011	10.1111/1365-2435.12834
Terrestrial	Tomato	Trade	Hybridization between native and introduced species coincides with human colonization and trade	Gibson et al. 2021	https://doi.org/10.7554/eLife.64165