

Hybridization due to changing species distributions:

adding problems or solutions to conservation of biodiversity during global change?

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ABSTRACT

Background: Due to increasing global change, the rate of hybridization seems to be increasing.

Question: Is hybridization adding problems or solutions to the effects of global change on biodiversity?

Methods: We divided ourselves into two independent groups. Each group listed topics it thought appropriate. We then compared and combined the lists, extracting a natural structure of the topics. We next divided ourselves into three specialized subgroups and discussed the topics in more depth. In a final plenary meeting, we brought ideas together, discussed open topics, identified consensus or differences of opinion, and prepared a preliminary report.

Results: Our lists of topics were highly similar, suggesting that we missed only a few topics. We agreed that it is important to consider hybridization in both its genetic and ecological contexts and with explicit attention paid to phylogenetic and biogeographic history. It is also necessary to distinguish between underlying processes and resulting consequences. Knowledge of the consequences of hybridization is more developed in genetics than in ecology. We suggest that hybridization adds problems (loss of biodiversity, ecosystem degradation) as well as solutions (new adaptive variation, ecosystem robustness) to global change challenges. Which of these applies in a given case depends on its evolutionary and environmental context, and on the objectives of conservation management. We provide five groups of questions to stimulate further research.

54 A major goal in conservation is to maintain current biodiversity and the conditions and
55 processes that support it. In a world that is rapidly changing due to human actions, this
56 is an increasingly challenging task. Loss and alteration of habitats, climate change,
57 eutrophication, and introduction of exotic species are some of the greatest current
58 anthropogenic threats to biodiversity. One relatively underappreciated way in which
59 these factors can impact biodiversity, and the one that is the focus of this paper, is by
60 hybridization.

61 Hybridization involves the combination of evolutionarily divergent gene pools, e.g.,
62 populations, ecotypes or species. While hybridization has been viewed by some as a

63 nuisance (Mayr 1942), upsetting the natural order of things, it is in fact a natural
64 process that may have been common in the evolutionary history of many organisms.
65 [Darwin \(1859\)](#) already pointed to those intermediate forms as being relevant to the
66 study of evolution, but it was not until the 20th century that the role of interspecific
67 hybridization in evolution began to be studied ([Anderson and Stebbins 1954](#)) and the
68 suggestion was made that hybridization can importantly contribute to novel
69 evolutionary trajectories ([Lewontin and Birch 1966](#)). However, global change may be
70 accelerating the rate and impact of hybridization in an unprecedented way, by
71 changing species distributions and the fate of hybrids. For example, introduced exotic
72 species may come into contact with closely-related species with which they hybridize.
73 Alteration of habitat may also cause “hybridization of the environment” where
74 ecologically segregated species come into greater contact, facilitating hybridization,
75 and may create novel habitats in which hybrids thrive (Anderson 1948, Anderson and
76 Stebbins 1954). There is great potential for ongoing hybridization between domestic
77 species and wild progenitors or other related species and weedy hybridized relatives of
78 crops cause considerable agricultural losses and rapidly gain genes with useful traits
79 such as herbicide resistance from their domestic relatives. And finally, climate change
80 may cause changes in species distributions followed by novel contact and hybridization
81 between previously isolated species.

82 Hybridization can affect biodiversity in many different ways, from the disappearance of
83 one or both parental species to the introgression of beneficial adaptive genetic
84 variation from one species to another to the generation of novel hybrid species
85 (Abbott et al. 2013). Hence, hybridization can be seen as causing additional problems

86 to the challenges for biodiversity conservation posed by global change, but also as
87 providing partial solutions. The extent and consequences of hybridization will vary with
88 the length of divergent evolutionary history between the hybridizing species and
89 spatial factors, necessitating consideration of the phylogeographic relationships and
90 levels of relatedness as part of the study of process and outcome of hybridization.
91 Hybridization generates novel interactions from genetic through to ecosystem levels
92 and trigger a range of interacting processes leading to multiple ecological and
93 evolutionary outcomes. Therefore it is important to understand the different contexts
94 in which hybridization occurs and impacts on biodiversity and, where possible and
95 desired, to take appropriate actions to manage the resulting consequences at the
96 individual, population, species, community and ecosystem level.

97 Ecologists, evolutionary biologists, conservation biologists and policy makers should
98 benefit from a broader understanding of how human impacts are changing the
99 frequency, forms and outcomes of hybridization and its ecological and evolutionary
100 impacts in natural systems. This paper aims to increase attention to and understanding
101 of these issues, and particularly, how global change impacts hybridization and its
102 consequences on biodiversity generation and conservation. We also highlight how the
103 evaluation of the conservation impacts of hybridization depends on who is doing the
104 evaluation and the criteria being used.

105 We first introduce the processes involved in hybridization. We then look at the
106 consequences that hybridization can have. Next, we discuss the effects that different
107 viewpoints and objectives can have on our perception of hybridization and its
108 importance, and end by listing a number of open research questions. We look at

109 processes and consequences in three different contexts: a genetic one, one of space
110 and time, and an ecological one. In this way, we attempt to convey the breadth,
111 richness and complexity surrounding hybridization, as well as the challenges that lie
112 ahead in studying and understanding the importance of hybridization in response to
113 global change.

114

115 **Processes involved in hybridization**

116 In its broadest sense, hybridization can be defined as reproductive interactions
117 between individuals representing lineages that show some degree of evolutionary
118 divergence. Within this broad definition, hybridization occurs at many different levels
119 of divergence in terms of evolutionary time, phenotypic distinctiveness and the
120 genomic regions showing divergence. For example, two subspecies of *Antirrhinum*
121 snapdragon flowers (*A. majus pseudomajus* and *A. m. striatum*) hybridize in the
122 Pyrenees and show narrow hybrid zones for distinctive flower colors controlled by a
123 few genes under selection, but are hardly differentiated across the rest of the genome
124 (Whibley et al 2006). At the other extreme, some fish species that diverged up to 20
125 million years ago (MYA) can still hybridize ([Bolnick and Near 2005](#)). Below we examine
126 (i) genetic processes affecting the genomes of hybridizing populations, (ii) the role that
127 the amount of genomic divergence, evolutionary time (or time since hybridization) and
128 geographical space have on determining which of these genetic processes will occur,
129 and (iii) the ecological effects of hybridization, that can extend towards all directly or
130 indirectly interacting populations and species.

131

Genetic context

132 Evaluating the effects of hybridization in a genetic context is fundamental because
133 interactions between genomes of hybridizing taxa can make for a range of different
134 outcomes. These are briefly reviewed in text box 1. Studies of local adaptation and
135 hybridization include challenges of distinguishing neutral and adaptive genetic
136 variation and finding evidence for fitness effects at both the individual and population
137 level. Which of these genetic processes will occur depends on the extent of adaptive
138 and overall genomic divergence between hybridizing taxa and the effects of time and
139 space.

140

141

TEXTBOX 1

142

Heterosis is the fitness gain frequently observed in hybrids as a result of increased
143 heterozygosity after combining alleles from both parents, reversing the effects of
144 inbreeding depression due to the accumulated load of mildly deleterious alleles
145 ([Hochholdinger and Hoecker 2007](#)). Heterosis can also result from deregulation of
146 gene expression leading to enhanced growth (Syed and Chen 2004, Song et al. 2010).

147

In most cases heterozygosity and heterosis rapidly dissipate in later generation
148 hybrids; however, if hybridization is recurrent, hybrid populations can maintain
149 elevated heterosis for longer. Alternatively, heterozygosity and associated heterosis
150 can be “fixed” in hybrid individuals that undergo polyploidization or reproduce

151

asexually.

152 *Hybrid speciation* can occur when hybrid offspring are or become reproductively
153 isolated from both parental species. The occurrence of allopolyploidy or chromosomal
154 inversions, by creating a barrier to gene exchange, may facilitate hybrid speciation. In
155 addition, hybrids may differ phenotypically and ecologically from the parental forms
156 and even show traits that lie outside the range of their parents (*transgressive*
157 *segregation*: Rieseberg et al. 1999, Stelkens & Seehausen 2009). This can add
158 behavioral or ecological reproductive barriers to intrinsic genetic reproductive barriers
159 when present (Selz et al. 2014). Moreover, it provides evolutionary novelty that could
160 enable adaptation to new niches (Gross & Rieseberg 2005, Tobler & Carson 2010). In
161 the case of allopolyploid hybrid speciation, the effect of heterosis could be fixed which
162 could benefit the hybrid species.

163 *Adaptive introgression* occurs when genetic variation that is moved from one species
164 to another by hybridization increases individual fitness. In such a situation, selection is
165 extremely efficient at promoting gene flow even across strong reproductive barriers
166 (Arnold and Martin 2009, Dasmahapatra et al 2012). This process could be relatively
167 important for adaptation, as occasional hybridization between taxa that are
168 phylogenetically and geographically sufficiently close might be more common than the
169 occurrence of rare new adaptive mutations within taxa. Introgression is particularly
170 advantageous in the case of complex adaptations that are either multigenic or require
171 multiple changes within genes, and which are even less likely to evolve *de novo* (Kim et
172 al. 2008). The common view that evolution occurs by selection on newly arising
173 mutations might be biased if adaptation involving novel changes within taxa is easier

174 to detect than adaptation involving introgression of standing variation between close
175 relatives.

176 *Outbreeding depression* occurs when the hybrids are less fit than the parental forms
177 and develops as populations become locally adapted, and offspring produced by
178 parents from different populations have reduced ecological performance and
179 associated fitness. Gene flow is crucial in determining the extent of local adaptation
180 that can build across populations (Lenormand 2002): local adaptation tends to be
181 compromised by gene flow because of the potential introduction of maladaptive
182 genetic variation (but see Edelaar et al. 2008, Edelaar and Bolnick 2012). Local
183 adaptation can be considered a mild form of reproductive isolation whose persistence
184 depends on the balance between divergent selection and gene flow.

185 *Hybrid breakdown or hybrid incompatibility* frequently results following hybridization
186 between more divergent taxa and is of great biological interest because it reflects the
187 processes of speciation in action (Feder et al. 2012, Abbott et al. 2013). Multi locus
188 incompatibilities such as Bateson-Dobzhansky-Muller (BDM) incompatibilities between
189 different interacting sets of coadapted genes steadily accumulate between diverging
190 species (Coyne and Orr 1997, Bolnick and Near 2005, Matute et al. 2010, Moyle and
191 Nakazato 2010, Stelkens et al. 2010, Singhal and Moritz 2013). Chromosomal
192 rearrangements also facilitate the isolation of genomes and divergent evolution in
193 hybridizing systems because the rearranged regions cause unbalanced genomic
194 representation and incompatibility when this region recombines in hybrids, thus
195 protecting small genomic regions from recombination (Kirkpatrick and Barton 2006,
196 Feder and Nosil 2009). Hybrid breakdown or intrinsic low hybrid fitness can be

197 asymmetric depending on the direction of the cross (Turelli and Moyle 2007) or occur
198 in later generations after F1 hybrid formation, allowing introgression even if hybrids
199 are highly unfit.

200 *Genetic homogenization or swamping* can occur when hybrids are fitter than the
201 parental species, but also when they are equally fit or even less fit. If there are no
202 strong barriers to hybridization (e.g. assortative mating by habitat, time or mating
203 preference or selection against hybrids), then the proportion of hybrids can increase
204 with each generation as new F1 hybrids and hybrid backcrosses to the parental species
205 are produced until over time, no non-hybrid parental genotypes are left (Hegde et al.
206 2006). If one of the two species is numerically dominant, then the final hybrid
207 population will genetically resemble that species more. If one of the two hybridizing
208 species, e.g. a non-native invading species, continuously receives genetic input from
209 non-hybridizing conspecific populations, then the genetic homogenization will have a
210 directional component and over time leave little obvious trace of the second parent
211 involved in the hybridization (swamping; Prentis et al. 2007).

212

213 *Spatial and temporal context*

214 Taxa differ in the rate of potential hybridization and introgression in response to
215 changes in species distributions or in habitat conditions. Hybridization takes place in a
216 spatio-temporal context that reflects the evolutionary history of the hybridizing
217 parental populations/species. Thus, hybridization can occur among closely related
218 sympatric or parapatric taxa within adaptive radiations, allopatric sister species that

219 have experienced extensive divergence, or distantly related (non-sister) species (Figure
220 1). The time since populations began diverging and the extent and cause of divergence
221 will have a large impact on the outcome of any hybridization event. Hybridization
222 among younger taxa is more likely to lead to adaptive introgression or the formation
223 of hybrid swarms, as intrinsic genetic incompatibilities may be absent or rare. Here,
224 reproductive barriers likely depend more on ecological aspects such as resource or
225 habitat use, such that hybridization happens after habitat alteration. If species have
226 closely occurring geographical distributions, then natural hybridization could occur
227 after contact is established (in secondary sympatry or primary hybrid zones), for
228 example after natural range expansions due to historic changes in climate (Figure 1).
229 As species are spatially more separated, the smaller is the probability that natural
230 range expansions or long-distance colonization events will bring species into contact,
231 and thus the less likely it is that these species will hybridize. Likewise, the longer two
232 populations have diverged, the smaller the probability that hybridization will be
233 successful, and the greater the probability that hybridization will lead to reproductive
234 interference, or even that reproductive interactions no longer occur at all and genetic
235 coexistence is possible (Figure 1). The likelihood and tempo of this decrease in
236 hybridization varies widely between different groups of organisms. For example,
237 allopolyploid plants most likely arise between species pairs that diverged between 4
238 and 8 MYA as this is the window between hybrid sterility and cross-incompatibility of
239 progenitors (Levin 2012, 2013), whereas fish often hybridize down to 20 MYA without
240 polyploidization of hybrids (Bolnick and Near 2005). Most taxa are probably naturally
241 subject to episodes of hybridization and introgression in their evolutionary history. The

242 critical question is to what extent the frequency and/or distribution (taxonomic,
243 geographical) of such episodes is being changed by humans?

244 *Ecological context*

245 Hybridization affects ecosystem biodiversity and functioning through the production of
246 a hybrid population or even a novel hybrid species, or because of changes in genetic
247 differentiation and numbers (even extinction) of the hybridizing parental species.
248 These effects can extend towards all directly or indirectly interacting populations and
249 species. To assess the likely higher-level impacts of hybridization in multispecies
250 systems (communities, food webs, mutualistic networks, ecosystems), it is necessary
251 to consider at least three bodies of ecological theory: food web or network theory
252 (trophic interactions, competition and mutualisms), theory on biodiversity-ecosystem
253 functioning (primary and secondary production, nutrient cycling, resilience of
254 community and ecosystems) and theory on ecosystem services (Figure 2). Ultimately,
255 these will need to be combined with evolutionary and metacommunity theories to
256 incorporate the spatial, temporal and genetic components, and the resulting eco-
257 evolutionary dynamics to improve our currently limited understanding (Leitch et al.,
258 2014). The focus of hybridization studies to date has mostly been on isolated nodes in
259 the network (e.g. what are population consequences for the parents and hybrids?),
260 rather than on the interactions or the system as a whole (e.g., how do the hybrids
261 operate within the “rewired” food web?; Figure 3).

262

263 **Consequences of hybridization**

264 *Genetic context*

265 Restoring heterosis to combat inbreeding depression and improve population viability
266 can be a potential tool for the conservation of critically endangered species. As such,
267 controlled hybridization of the rare Florida panther *Puma concolor coryi* and the
268 related Texas cougar *P. c. cougar* was implemented to increase the genetic diversity
269 of the former, leading to a rapid demographic recovery (Hedrick 1995). This process
270 seems also to occur naturally, e.g. alleviation of locally expressed inbreeding
271 depression is thought to be favoring introgression from mainland sparrows into
272 Mandarte Island sparrows (*Melospiza melodia*) in British Columbia (Keller et al. 1994).
273 Allopolyploidy is frequent in plants because it both restores meiotic function
274 (homologous chromosome pairing) and fixes heterosis in new hybrids, which could
275 confer fitness advantages over parental species. A number of successfully established
276 allopolyploid plant species have arisen during the last century following accidental or
277 deliberate human-mediated introductions of parental species, for example new
278 *Tragopogon* species in North America derived from introduced European parental
279 species (Soltis et al. 2004), and *Senecio cambrensis* and *Spartina anglica* in the UK both
280 due to hybridization between native and introduced parentals (Abbott and Lowe 2004,
281 Ainouche et al. 2009). North American *Helianthus* sunflowers are a classic case of
282 multiple hybrid speciation events. Some of these events are 100,000s years old
283 predating human interference, while others are recent and probably have a human
284 component to them such as alteration of habitats or introductions of domesticated
285 sunflower across North America bringing species into contact (Rieseberg et al. 1999,
286 Gross and Rieseberg 2005). Hybrid asexual races of *Leuciscus* minnows in Iberia (Alves

287 et al. 2001) and *Poeciliopsis* minnows in South America (Vrijenhoek 1993) are
288 analogous examples in animals. Heterosis as a process promoting hybridization and
289 introgression will have important impacts on biodiversity, in some cases decreasing it
290 when hybrids with superior fitness replace parents and other ecosystem components
291 (see Ecological context), and in other cases increasing it due to the emergence of new
292 hybrid taxa.

293 Adaptive introgression has occurred naturally, probably as a common natural process.
294 Its historic presence can be inferred from evolutionary signatures, e.g. *Heliconius*
295 butterfly mimetic wing color supergenes show signals of elevated gene flow between
296 species (Dasmahapatra et al 2012). By its very nature, adaptive introgression can also
297 be detected as a response to current conditions. For example, strong selection has
298 been implicated in the spread of warfarin pesticide resistance alleles from the Algerian
299 mouse, *Mus spretus*, to domestic mouse, *M. musculus domesticus* through
300 introgression (Song et al 2011). Because adaptive introgression could increase the
301 viability of individuals and happen over just a few generations, in a world of increasing
302 global change and hybridizing contact we may see more and more examples of
303 introgression following hybridization as an adaptive response to altered selection
304 pressures. For some species, adaptive introgression might be one way by which
305 decline towards extinction could be reversed, as a form of evolutionary rescue. For
306 example, in the past, *in-situ* survival of endemic species through periods of climate
307 change appears to have been facilitated by hybridization (Becker et al. 2013).
308 Introgression can be cryptic where the phenotypic appearance of the original taxa are

309 maintained leading to underestimates of the evolutionary importance of hybridization
310 (Ward et al. 2012).

311 Negative outcomes will ensue where hybridization disrupts local adaptation resulting
312 in maladapted hybrids and outbreeding depression. For example, Ibex from southern
313 latitudes have a different reproductive timing compared to Ibex from more northern
314 latitudes, and the introduction of southern individuals to a northern population led to
315 the production of hybrids that reproduced at sub-optimal times and the extinction of
316 the northern population (Turcek 1951). Hybrid incompatibilities that have evolved *in*
317 *situ* can make species resistant to introgression with co-occurring relatives, particularly
318 if reinforcing selection against hybridization then occurs (Servedio and Noor 2003).
319 However, hybridization frequency due to human environmental disturbance might
320 cross a threshold beyond which hybridizing barriers are ineffective and taxa rapidly
321 converge (Seehausen et al 2008, Gilman and Behm 2011, Vonlanthen et al. 2012).
322 Equally, environmental change can alter adaptive landscapes and erode pre-existing
323 local adaptation, up to the point that local populations become more vulnerable to
324 introgression and are swamped. When a non-native species is numerically dominant
325 over a native species, hybridization can result in the genetic dilution and eventual
326 extinction of the native species, even when certain reproductive barriers are in place.
327 In fact, even if no introgression occurs because of complete sterility of F1 hybrids,
328 hybridization can still lead to population declines and extinction (Prentis et al 2007).
329 Producing sterile hybrids is a form of the Allee effect as this kind of hybridization can
330 be viewed as wasted reproductive output with greater negative effects on the rarer
331 hybridizing species (Huxel 2004). A dramatic example of extinction despite hybrid

332 incompatibility is provided by a moving hybrid zone in Spain whereby diploid annual
333 mercury plants, *Mercurialis annua*, are taking over the range of hexaploid annual
334 mercury due to pollen swamping (Buggs and Pannell 2006).

335 *Spatial and Temporal context*

336 As outlined above, the spatio-temporal context of hybridization affects the outcomes
337 of hybridization (Figure 1). Similarly, this context determines which aspects of global
338 change might play a role in increasing hybridization between which kinds of species.
339 Habitat alteration by human activities can be expected to be more relevant in
340 promoting hybridization among younger taxa, which are not yet separated by strong
341 genetic incompatibilities. Habitat alteration can bring taxa with previously overlapping
342 geographic distributions together in a disturbed habitat, or enable range expansion
343 which brings previously allopatric taxa into contact. Human-induced climate change
344 can also lead to geographic distribution changes, causing previously isolated taxa to
345 come into contact. Natural long-distance colonizations or large-scale range expansion
346 are typically rare, but human activities (accidental transport, deliberate introduction)
347 are now greatly increasing the movement of taxa, resulting in the establishment of
348 non-native and invasive species, and enhanced probabilities for hybridization among
349 evolutionarily more divergent taxa. Finally, human-mediated introductions can also
350 lead to introductions of hybrid material to new areas/environments leading to the
351 origin of new taxa, as in the case of the recently originated homoploid hybrid species
352 *Senecio squalidus* (Abbott et al. 2009).

353 Investigations of clades showing adaptive radiations are particularly informative about
354 the impacts of human disturbance and consequent changes in hybridization frequency

355 on patterns of biodiversity. Recent ecological radiations such as those of fish in
356 postglacial lake systems show predominantly extrinsic post-zygotic and prezygotic
357 reproductive isolation based on divergent ecological adaptations and are thus sensitive
358 to changes in niche structure and new species introductions (Vonlanthen et al. 2012).
359 Range shifts in response to climate change or human introductions can bring species
360 into hybridizing contact that have not evolved effective hybridizing barriers, in which
361 cases rampant introgression is both expected and observed (Rosenfield et al. 2004,
362 Munoz-Fuentes et al. 2007). In other cases, deliberate introductions of relatively
363 evolutionarily divergent species into systems that contain pairs of reproductively
364 isolated sympatric species can promote merging of otherwise isolated sympatric taxa
365 as has occurred following stocking of trout, *Salmo trutta*, from recently recolonized
366 glaciated northern Europe to refugial southern Europe that contained a greater
367 diversity of hitherto reproductively isolated trout species (Giuffra et al. 1994, Keller et
368 al. 2012, Seehausen unpubl.).

369 Hybridization between introduced and native species can generate novel biodiversity
370 on extremely short time and spatial scales when favored by selection. New ecotypes of
371 hybrid sculpins in the Rhine-Scheldt river systems are a good example of evolutionary
372 novelty in response to human disturbance. Canals now link parental drainage systems
373 and a novel hybrid ecotype has emerged that has invaded highly disturbed, warm and
374 oxygen-poor waters of the main channel of the Rhine when both parental species are
375 restricted to little hillside streams (Nolte et al. 2005). Allopolyploid speciation can be
376 an extremely rapid adaptive consequence of hybridization such as the new
377 allopolyploid *Tragopogon* goatsbeard species described above that have established

378 successfully in North America where the introduced progenitors hybridized, but not in
379 Europe where the same native progenitors coexist in a stable ecological context (Soltis
380 et al. 2004). Historical examples also exist such as the Hawaiian Silversword radiation
381 (endemic genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia*) during the last 5-6 Myrs
382 which has arisen from early hybridization between North American immigrants
383 (Barrier et al 1999). Another striking example of historic hybridization following long-
384 distance dispersal is between *Senecio flavus* (Namibia) and *S. glaucus* (North Africa)
385 that led to the origin of the allopolyploid *S. mohavensis* within the last 1 Myrs
386 (Coleman et al. 2001, 2003).

387 The frequency of dispersal events across biogeographic realms has dramatically
388 increased with the advent of human disturbance, and the hybridizing impacts of this
389 depend in part on the temporal and spatial context. For example, the current biota of
390 the Mediterranean Sea predominantly reflects a continuous history of immigration and
391 diversification since the opening of the strait of Gibraltar with the Atlantic Ocean 5
392 MYA (Bianchi and Morri 2000, Patarnello et al. 2007, Lejeusne et al 2009). In recent
393 times, the Mediterranean Sea has experienced a major influx of approximately 10 new
394 species per year from the Red Sea/Indian Ocean in the century and a half since the
395 construction of the Suez Canal reconnected these marine systems that had been
396 separate for the last 10 MYA (Galil 2009). Despite extensive recent migration, there
397 have been relatively few cases of invasion with hybridization from the Red Sea because
398 these faunas have been isolated for 10 M years. In contrast to this, one would expect a
399 new wave of Atlantic invaders responding to global change to probably lead to

400 relatively more cases of invasion with hybridization because the strait of Gibraltar
401 represents a more recent phylogenetic break.

402 *Ecological context*

403 Invasions can proceed with or without hybridization, and with or without rewiring of
404 the food web due to adaptive responses and indirect effects, as outlined in Figure 3. It
405 is clear that the range of possible ecological consequences of hybridization is large,
406 and empirical examples exist. For a hybrid population to establish it needs to occupy or
407 create a previously unoccupied niche or to replace a resident species: this can have
408 positive, neutral or negative impacts on ecosystem functioning, which can be hard to
409 predict *a priori*. A common phenomenon in biodiversity-ecosystem functioning studies
410 is that as a system loses a species, its role is replaced by an equivalent species or group
411 of species from within the resident species pool, usually via growth and/or density
412 compensation. Adding a species with a new role in a previously unoccupied niche will
413 shift ecosystem functioning, potentially enhancing overall process rates and facilitate
414 population increase. A classic example is the North American Ruddy duck, *Oxyura*
415 *jamaicensis*, which reached populations numbering in the thousands within just a few
416 decades following the escape of just seven founding individuals in the UK (Muñoz-
417 Fuentes et al. 2007). In the UK, this species was initially welcomed as a new addition to
418 the avifauna but problems arose after it spread to Spain and started to hybridize with a
419 distantly related allospecies, the endangered White-headed duck *O. leucocephala*
420 (Muñoz-Fuentes et al. 2007). If hybrids are simply a blend of the ecological traits of the
421 parent species it might be easier to predict ecosystem-level consequences; but if it has
422 unique characteristics not found in either parent species (e.g. due to transgressive

423 segregation) then reliable predictions become increasingly difficult, or impossible
424 (Woodward et al. 2013, Leitch et al. 2014). Some cases of diversification following
425 transgressive hybrid expression are known but it is not yet clear whether this is the
426 rule rather than the exception (Rieseberg et al 1999; Selz et al. 2013, Selz et al. 2014).

427 One way to better understand the ecosystem consequences of hybridization could be
428 to map the provisioning of ecosystem services and the taxonomic and functional traits
429 of native, invasive and hybrid taxa onto food webs to study the network context and
430 ramifications at higher ecosystem levels that have not been considered before. This
431 contrasts with the traditional treatment of nodes in food webs as fixed entities rather
432 than being transmutable (Reiss et al 2009). Particular attention should be directed to
433 hybridization in keystone species, such as top predators occupying highly connected
434 nodes in the food web or ecosystem engineers, as these are good candidates to cause
435 the strongest ecosystem effects. There are many examples of invasive species acting as
436 keystones, especially where they colonize a previously isolated area such as oceanic
437 islands or large lakes. Invasives also tend to be generalists, so they can rapidly forge
438 many new links when colonizing a food web, and many of them are high in the food
439 chain, exploiting a vacant niche in which they have few or no predators. While
440 probably rare in absolute numbers compared to invaders at lower food web levels,
441 some of these high trophic level invaders are hybrids, such as the invasive Nile perch in
442 Lake Victoria, which is a hybrid between *Lates niloticus* of Lake Albert and *L. longispinis*
443 of Lake Turkana (Harrison 1991). Clearly, invasion and hybridization at the top of the
444 food web will have very different consequences for ecosystem processes and services
445 than at lower trophic levels, where hybridization could be especially pronounced

446 (Leitch et al 2014). There are several examples of invasive-hybrid consumer species at
447 intermediate trophic levels, especially among vertebrates and in freshwaters. For
448 example, in the UK hybridization between native Crucian carp *Carassius carassius* and
449 introduced goldfish *C. auratus* is rampant, with few if any genetically pure stocks of the
450 resident species left (Wheeler 2000). These fishes can have powerful effects on
451 ecosystem functioning, with the potential to trigger regime shifts from a clear-water,
452 vegetation-rich state to a turbid-water, vegetation-poor state in shallow lakes
453 (Richardson and Whoriskey 1992). Native cyprinids hybridize readily in many
454 freshwaters, with bream-roach, roach-dace and other combinations appearing
455 regularly, yet these have not become invasive in mainland Europe. Nonetheless, there
456 is a potential threat from newly introduced cyprinids forming hybrids that become
457 invasive, especially in areas where the community is not already saturated. For
458 example, the lacustrine fish fauna of Ireland has been invaded by hybrids between
459 introduced roach (*Rutilus rutilus*), and introduced bream (*Abramis brama*), which show
460 overlapping trophic positions but with hybrids expressing the greatest flexibility in diet
461 (Toscano et al. 2010, Hayden et al. 2011).

462

463 **Evaluating the impact of hybridization: the importance of different viewpoints and**
464 **objectives**

465 The evaluation of the effects of hybridization depends on who is doing the evaluation,
466 and more specifically in which context and with which objectives the effects are
467 compared. While this is perhaps self-evident, in many cases discussions can become
468 heated and unfocused because people are measuring impacts with different tools,

469 scales, units and dimensions. For example, someone who is simply documenting and
470 studying hybridization as a genetic phenomenon might be more interested in
471 documenting frequency and outcomes of hybridization and might not have a strong
472 opinion on the need for managing invaders and hybrids, compared with others whose
473 priorities are to prevent or limit the global extinction of a native species due to
474 competition with new invasive hybrids.

475 We argue that in many cases, value judgments about hybridization being negative or
476 positive should be reserved or at least placed into its proper context, especially as
477 characteristics can be affected in contrasting directions. While one might assume that
478 actions to conserve one species automatically benefit the rest of the ecological
479 network in which it is embedded under the “optimist’s scenario”, this is not necessarily
480 the case when the complexity of the network is better understood (Pocock et al. 2012)
481 As another example, Beefalo (hybrids between native bison, *Bison bison*, and
482 introduced domestic cattle, *Bos taurus*) in North America represent an improved
483 provisioning service because of increased meat production per capita, but at the same
484 time of a reduced cultural-aesthetic service being provided by a hybrid: ecotourists are
485 willing to pay a premium to see wild Bison but hybridity, especially if visibly evident,
486 diminishes that appeal (Halbert et al 2005). This becomes increasingly important when
487 making management decisions. For example, depending on whether the focus is on
488 maintaining evolutionary history or ecological functioning, one might set priorities
489 differently. We might be particularly concerned about loss of phylogenetically distinct
490 allospecies because this means loss of a great deal of evolutionary history: in that case
491 the relative importance of human impacts is greatest at larger

492 phylogenetic/biogeographic distances (Figure 1). If one is more concerned about the
493 conservation of functional diversity and its relevance to ecosystem functioning, then
494 loss of recently ecologically diverged taxa from adaptive radiations may be of more
495 concern (Becker et al. 2013). Even though distinct functional phenotypes can re-
496 evolve, this is unlikely to happen on a timescale relevant to current human society.

497 Using fixed criteria to value the occurrence of hybridization is becoming increasingly
498 difficult. For example, one could state that native species have a greater conservation
499 value than non-native species and their hybrid progenitors, whereby non-nativeness is
500 defined as having arrived in historic times to a region due to human activity. But what
501 if a new species arrived because it changed its distribution in response to human-
502 induced climate change: is that a natural range expansion making it a newly acquired,
503 native species that should be protected, or range expansion indirectly due to human
504 activity, making it a non-native species that should be eliminated? And what if this new
505 species starts to hybridize with a native one and genetic material is introgressing: does
506 that threaten the genetic integrity of the original native species, or could it be an
507 adaptive response to the changed climate, enabling the native species to persist?
508 Alternatively, is the presence of hybrids in a vacant niche preferable to an overall loss
509 in diversity if a native parental species has already gone extinct? While considerable
510 progress is being made to address these issues in individual cases, opposing solutions
511 are often possible depending on one's background and ideas on 'how things should
512 be'.

513

514 **Open questions/areas for further research**

515 Although we have outlined how aspects of genetics, ecology, and space and time
516 combine to give a wide diversity of outcomes and consequences of hybridization, our
517 knowledge on this is still very unbalanced. For example, the genetic principles of
518 hybridization are now relatively well-known, but insight into the relevance of
519 hybridization and local adaptation for ecosystem functioning is far sketchier. We
520 therefore conclude by identifying questions for further research.

521 • Is there a relationship between historical dynamics and current vulnerability to
522 changed frequency of hybridization? In other words, can we predict differences in
523 the resilience and negative impact of hybridization between refugial (stable) and
524 non-refugial (unstable) species, between communities with strong or shallow co-
525 evolutionary histories (evolutionary assembly versus colonization assembly), or
526 between high or low latitude? Do these factors influence how likely a hybrid is to
527 exhibit transgressive and possibly disruptive characteristics?

528 • What is the rate of introgression as a function of phylogenetic and/or biogeographic
529 distance (Figure 1) and how are the evolutionary consequences of such
530 introgression affected by human-mediated habitat modifications such as agro-
531 ecosystems and aquaculture? What are the conditional probabilities of successful
532 invasion following successful hybridization; i.e. how many failures are we missing in
533 the “ghost of hybridization past”?

534 • Was introgression elevated during periods of past rapid change and can we detect
535 the evolutionary consequences such as diversity increases or decreases at such
536 times and variation across biomes or latitudes? It is important to understand
537 natural background levels of hybridization as a baseline against which to assess the

538 hybridization in response to rapid global change. Comparative genomics
539 approaches could be promising in this regard if we could identify and estimate the
540 prevalence and size of introgressed chromosome segments to measure past
541 hybridization.

542 • How can we integrate the likelihood and impacts of hybridization into ecological
543 network theory? Do hybrid invasions predominantly affect ecological network
544 structure without affecting biodiversity or do they tend to affect biodiversity
545 without altering ecosystem structure? Can we identify nodes, trophic levels, or
546 interaction types that are most vulnerable to hybridization (Figure 2, 3)?

547 • How do we reconcile contrasting ecosystem services provided by new hybrids (e.g.
548 food production versus cultural-aesthetic values)? Given that most regulatory
549 ecosystem services such as carbon sequestration and nutrient cycling are done by
550 microbes at the base of the food web, should we be most concerned with
551 identifying, predicting and managing hybridization impacts on cultural-aesthetic,
552 supporting or provisioning services?

553

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567

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760 **Figure legends**

761

762 *Figure 1.* Placing aspects of hybridization in a phylogenetic context. A schematic
763 phylogeny indicates the types of potentially hybridizing taxa, and how the likelihood of
764 natural events that may drive hybridization diminishes with phylogenetic depth.
765 Phylogenetic relatedness impacts on ecological and evolutionary outcomes of
766 hybridization (top and bottom). Red arrows indicate how human facilitation of
767 hybridization increases with phylogenetic depth, while at the same time increasing the
768 evolutionary history at risk of being lost.

769

770 *Figure 2.* A schematic food web from a generic freshwater ecosystem, mapping
771 hypothetical propensity of hybridization (horizontal bars; n/a refers to groups where
772 the species concept is often not applicable) onto ecosystem services (left), taxonomy
773 (centre) and trophic position (right). V: vertebrate predator, F = fish, C: carnivorous
774 invertebrate, O: omnivorous invertebrate, D: detritivore, hD/Hd: herbivore-detritivore,
775 H: herbivore, AH: aquatic hyphomycete, L: leaf-litter, P: plant, A: algae. Ecosystem
776 service delivery within the food web is indicated in italic text. In this schematic cultural
777 and provisioning services may be provided by both top predators (e.g., ornithological
778 ecotourism, recreational angling and fisheries production) and primary producers
779 (aesthetically valuable water plants of conservation concern), whereas regulatory
780 services (e.g., carbon sequestration, water purification and toxicant degradation etc)
781 tend to be restricted primarily to the lower trophic levels.

782

783 *Figure 3.* Potential changes to species interaction networks in response to invasion and
784 hybridization. Boxes show different examples of potential outcomes of invasion and
785 hybridization in a schematic food web. Species are indicated by colored circles, while
786 interactions between species are separated as direct (solid lines) or indirect (dashed
787 lines), and as pre-existing (black) or new (red). The invading species (dark red) and the
788 novel hybrid (dark orange) exhibit a similar ecology to a native species (pale yellow) at
789 the top level in the interaction network. Invasion outcomes range from invasion
790 failure, to establishment of the new species, coexistence, hybridization and species
791 replacement. This may lead to increased biodiversity, or species turnover with no
792 change in biodiversity, and a range of possible indirect effects, such as altered
793 apparent competition among prey that share predators. Note that additional scenarios
794 can arise where the invader and hybrids cause species extinctions by removing prey
795 nodes from the network, but these other more extreme conditions are not shown
796 here. Also the invader will have different effects depending on its trophic position.
797 Here we have highlighted a top predator invasion as an example because these can
798 have especially powerful cascading effects, via top-down control.
799

secondary contact without hybridisation

hybrid speciation / reproductive interference (no introgression)

introgression / merging / hybrid speciation

habitat alteration

young species,
e.g. adaptive radiation

common natural
range expansions

older allospecies

rare natural range
expansions;
long distance colonization

fully isolated species

exceedingly rare natural
range expansions;
biotic interchange

distantly related species

evolutionary history at risk of being lost

increasing relative role of human facilitation

also genetic processes

only ecological processes





