



ADAPTATION TO BIOINVASIONS: WHEN DOES IT OCCUR?

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Abstract:	<p>The presence of alien species represents a major cause of habitat degradation and biodiversity loss worldwide, constituting a critical environmental challenge of our time. Despite sometimes experiencing reduced propagule pressure, leading to a reduced genetic diversity and an increased chance of inbreeding depression, alien invaders are often able to thrive in the habitats of introduction, giving rise to the so-called "genetic paradox" of biological invasions. The adaptation of alien species to the new habitats is therefore a complex aspect of biological invasions, encompassing genetic, epigenetic, and ecological processes. Albeit numerous studies and reviews investigated the mechanistic foundation of the invaders' success and aimed to solve the genetic paradox, still remains a notable oversight regarding the temporal context in which adaptation takes place. Given the profound knowledge and management implications, this neglected aspect of invasion biology should receive more attention when examining invaders' ability to thrive in the habitats. Here, we discuss the adaptation mechanisms exhibited by alien species with the purpose of highlighting the timing of their occurrence during the invasion process. We analyse each stage of the invasion separately, providing evidence that adaptation mechanisms play a role in all of them. However, these mechanisms vary across the different stages of invasion, and are also influenced by other factors, such as the transport speed, the reproduction type of the invader, and the presence of human interventions. Finally, we provide insights into the implications for management and identify knowledge gaps, suggesting avenues for future research that can shed light on species adaptability. This, in turn, will contribute to a more comprehensive understanding of biological invasions.</p>

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27 **ABSTRACT**

28 The presence of alien species represents a major cause of habitat degradation and biodiversity loss
29 worldwide, constituting a critical environmental challenge of our time. Despite sometimes
30 experiencing reduced propagule pressure, leading to a reduced genetic diversity and an increased
31 chance of inbreeding depression, alien invaders are often able to thrive in the habitats of
32 introduction, giving rise to the so-called “genetic paradox” of biological invasions. The adaptation
33 of alien species to the new habitats is therefore a complex aspect of biological invasions,
34 encompassing genetic, epigenetic, and ecological processes. Albeit numerous studies and reviews
35 investigated the mechanistic foundation of the invaders’ success and aimed to solve the genetic
36 paradox, still remains a notable oversight regarding the temporal context in which adaptation takes
37 place. Given the profound knowledge and management implications, this neglected aspect of
38 invasion biology should receive more attention when examining invaders’ ability to thrive in the
39 habitats. Here, we discuss the adaptation mechanisms exhibited by alien species with the purpose of
40 highlighting the timing of their occurrence during the invasion process. We analyse each stage of
41 the invasion separately, providing evidence that adaptation mechanisms play a role in all of them.
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43 other factors, such as the transport speed, the reproduction type of the invader, and the presence of
44 human interventions. Finally, we provide insights into the implications for management and
45 identify knowledge gaps, suggesting avenues for future research that can shed light on species
46 adaptability. This, in turn, will contribute to a more comprehensive understanding of biological
47 invasions.

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50 **Keywords:** alien species, non-indigenous species, invasive species, alien species adaptation, genetic
51 paradox of invasions, adaptation, adaptation in invasions.

52 1. INTRODUCTION

53 Biological invasions are one of the main drivers of global change and pose significant threats to
54 biodiversity, ecosystems, and human well-being (Bellard et al., 2016; Shackleton et al., 2019; Pyšek
55 et al., 2020). Besides, the magnitude of alien species introduction continues to increase (Seebens et
56 al., 2017), and the negative effects they bring are expected to exacerbate further (Hulme et al.,
57 2014; Juliano & Lounibos, 2005; Haubrock et al., 2021; Fantle-Lepczyk et al., 2022).

58 However, despite their concerning impact on global biodiversity, biological invasions also offer a
59 unique opportunity to investigate population evolution within a timescale compatible with human
60 life. Indeed, the intentional or unintentional introduction of species into new habitats serves as a
61 recurring and unique experiment involving many different taxa. These experiments shed light on the
62 adaptation mechanisms of invaders, which play a role in their ability to survive, establish and
63 spread into new areas with different biotic and abiotic components (e.g. Estoup et al., 2016; Marin
64 et al., 2019). These mechanisms are particularly intriguing when the introduced population is built
65 up and becomes invasive starting from just a few initial founders.

66 Allendorf and Lundquist (2003) used the concept of “genetic paradox” to describe the contradiction
67 arising from the ability of some species to establish invasive populations starting from small
68 propagules, despite having reduced genetic variation due to demographic bottlenecks and genetic
69 drift. This reduced variation is indeed expected to lead to inbreeding depression, thus hindering the
70 ability of the introduced population to persist and evolve in the new environment (Allendorf &
71 Lundquist, 2003). While many possible explanations have been proposed to unravel the genetic
72 paradox underlying biological invasions (Estoup et al., 2016; Marin et al., 2019; Stapley et al.,
73 2015; Hawes et al., 2016), the chronological order in which adaptation events occur still remains a
74 crucial knowledge gap.

75 Understanding when and under which evolutionary processes adaptation is mostly like to develop is
76 critical to thoroughly comprehend the invasion process. Furthermore, this understanding holds

77 significant implications for management, as it can help design strategies to effectively counter the
78 invasion process.

79 In this review, we used as reference the framework proposed by Blackburn et al. (2011), which
80 breaks down the invasion process into stages. These stages include the movement from the native
81 range towards new areas, the release or escape from confinement, the establishment of populations
82 and their subsequent spread. Each stage is characterised by a specific barrier that individuals must
83 overcome to progress to the next step.

84 While it may be intuitive to assume that the adaptation process primarily takes place in the new
85 range (as introduced organisms do not face the new habitat before), existing literature demonstrates
86 that adaptation can occur in each stage of the invasion process. Besides, adaptation in the different
87 stages is not mutually exclusive. Our purpose is to illustrate how adaptation mechanisms helping
88 invaders in overcoming their barriers can evolve during each phase of the invasion process
89 described by Blackburn et al. (2011), and even earlier in the native range of the invader. Moreover,
90 we aim to highlight the management and research implications resulting from a full understanding
91 of the adaptation timeframe.

92 In this review, we firstly explain the main adaptation mechanisms occurring during invasions,
93 subdivided into three main phases of the invasion process. First, the (future) invader is in its native
94 geographic range, where it naturally lives. Second, the transport: the invading organisms leave their
95 native range, transit across geographical barriers and reach a non-native environment; this stage also
96 includes the captivity and/or cultivation phases in the new range. Third, the establishment and
97 spread of the introduced population in the new area. Then we analyse how adaptation can develop
98 within each specific stage, providing concrete examples and insights into the implications for
99 effective management. Finally, we discuss how future research efforts should attempt to disentangle
100 the role of each stage in the adaptation of invaders.

101 A comprehensive awareness of these invasion dynamics can significantly enhance our ability to
102 effectively address the challenges posed by invasive alien and protect biodiversity and ecosystems.

103

104 2. PRE-ADAPTATION IN BIOLOGICAL INVASIONS

105 The definition of “pre-adaptation” here adopted is “*adaptation to an environmental circumstance of*
106 *the new range which evolved in the native range and which, thus, both the introduced and native-*
107 *source populations are able to display*”.

108 Pre-adaptation is a prevalent feature in biological invasions, and it can be driven by a variety of
109 mechanisms. First, introduced organisms tend to derive from populations living in native
110 environments that resemble the recipient ones (Peterson, 2003; Dlugosch & Parker, 2007; Cope et
111 al., 2019). When the ecological characteristics of the donor and recipient areas sufficiently match,
112 invading organisms do not face an adaptive challenge, as their success in the novel habitat does not
113 require further adaptations (Estoup et al., 2016), and their ability to establish, thus, mainly hinges on
114 their dispersal abilities. However, if native and recipient environments significantly differ for one or
115 more variables, various other pre-adaptation mechanisms can intervene to help the invaders
116 overcome the constraints of the new environmental conditions.

117 2.1 Phenotypic plasticity

118 The most investigated pre-adaptation mechanism is **phenotypic plasticity**, both in animals (e.g.
119 Kistner et al., 2012; Lucek et al., 2014) and plants (e.g. Lamarque et al., 2013; Colomer-Ventura et
120 al., 2015; Elst et al., 2016). Despite not consistently being adaptive (Ghalambor et al., 2007; Lande,
121 2009; Davidson et al., 2011), phenotypic plasticity can facilitate invasion by allowing the
122 introduced organisms to adjust towards the new optimal phenotype in the first phases of invasion
123 (Ghalambor et al., 2007; Lande, 2009). In fact, many authors propose plasticity as a possible driver
124 of invasion success (Geng et al., 2016; Hahn et al., 2012; Liao et al., 2019). Although the term
125 "plasticity" is typically used to describe morpho-physiological characteristics, it also encompasses

126 behavioral traits. In the context of biological invasions, this aspect is particularly significant for
127 mammals (Gil-Fernández et al., 2020; Chow et al., 2021; Kowalczyk & Zalewski, 2009; Zalewski
128 & Bartoszewicz, 2012, but see also Sol et al., 2002). An example of behavioral plasticity can be
129 observed in the shelter preferences exhibited by invasive raccoon dogs (*Nyctereutes procyonoides*)
130 in Poland (Kowalczyk & Zalewski, 2009). This species responds to predation risk and harsh
131 climatic conditions by changing its preferential use of different shelter types during the year.
132 winter, raccoon dogs prefer burrows and hollow trees, as they offer less visibility from predators
133 and thermoregulation advantages. However, during reproduction and pups-rearing season, they
134 prefer hollow trees and dense vegetation, as burrows contemplate a major contact risk with the host,
135 pups-predator, species (i.e. badger, Kowalczyk & Zalewski, 2009).

136 Phenotypic plasticity is a product of the evolutionary history of the species, and environmental
137 fluctuations are known to facilitate its evolution (Meyers et al., 2005; Lee & Gelembiuk, 2008;
138 Kristensen et al., 2018); it would thus be spontaneous to think of it as a common, equal feature of
139 the invading and the native-source populations, as it turned out to be for many alien species
140 (Colomer-Ventura et al., 2015; Palacio-Lopez & Gianoli, 2011). Nevertheless, it must be
141 emphasized that plasticity can also increase after the colonization event as the result of the invasion
142 process (Liao et al., 2019; Davidson et al., 2011; Mounger et al., 2021). An explanation for this
143 apparent contradiction has been proposed by Lande (2009): following a sudden environmental
144 change, selection will shape individuals' phenotypes towards a new optimal state, and this can result
145 in an increase in plasticity. Afterwards, genetic assimilation of the new optimal phenotype will scale
146 back the phenotypic plasticity by replacing it (Lande, 2009; Lande, 2015). A temporary increase in
147 plasticity during the invasion has been observed, for example, in the fungal pathogen
148 *Seiridium cardinale* (Garbelotto et al., 2015). A fluctuation in the behavioral plasticity pattern may
149 also occur within a single generation through individual learning (Wright et al., 2010). The new
150 environment will thus induce plastic (and sometimes adaptive) responses in the invaders through a
151 series of mechanisms, such as epigenetic modifications, which we discuss later in this review. If

152 plasticity evolves in the new environment to approach the new optimal phenotype, it should not be
153 considered a pre-adapted trait.

154 2.2 Anthropogenically Induced Adaptation to Invade (AIAI)

155 Pre-adaptation can result from anthropization and human activities. Hufbauer et al. (2011)
156 introduced the model of **Anthropogenically Induced Adaptation to Invade** (AIAI). According to
157 the authors, human-altered habitats within the native range can make the (future) invader adapt to a
158 set of characteristics typical of anthropogenically-altered habitats, which the species could find
159 again in the introduction range. Furthermore, the presence of organisms in anthropogenic areas
160 increases the likelihood of their transportation to new geographical regions, thereby increasing the
161 probability of their settlement there. Therefore, the already-adapted invaders do not need to face a
162 significant adaptive challenge to succeed in the anthropized introduction area. Once introduced,
163 they can even expand and adapt to natural habitats (Hufbauer et al., 2011). The AIAI model
164 probably fits the invasion of the gram-negative phytopathogen *Xylella fastidiosa* in Europe. This
165 bacterium is native to America, where the introduction of coffee cultivation (i.e. anthropogenic
166 disturbance) allowed it to infect coffee plants (Marcelletti & Scortichini, 2016). Subsequently, the
167 trade of coffee plants transported the bacterium to European countries, where – presumably after
168 being initially adapted to coffee plants – it turned to other host species, such as *Olea europaea*
169 (Marcelletti & Scortichini, 2016). The AIAI model could probably also describe the invasion of
170 many marine, hull-fouling, alien species. In fact, harbours, marinas and their artificial substrates can
171 host many biofouling organisms, which can colonize boat hulls and be transported to other marinas
172 around the world (Ulman et al., 2017; Ferrario et al., 2017). However, it is worth emphasizing that
173 the AIAI scenario is not easy to document, as it requires demonstrating (i) the adaptation of a
174 population to human-altered habitats within its native range, and evidence that (ii) the introduced
175 population originates from the native human-altered habitat and (iii) such population is more

176 adaptable compared to populations living in natural areas in the native range (Hufbauer et al.,
177 2011).

178

179 *2.3 Resistance characteristics and life-history traits*

180 Pre-adaptation can also result from the **innate characteristics of resistance** to environmental
181 constrain or the invaders' **life-history traits**. These general “predictors of invasion success” are
182 several and diverse, and they have been investigated across a wide range of organisms. These traits
183 encompass factors such as heat (Bates et al., 2013) and salinity tolerance (Piscart et al., 2011),
184 immune response (Møller & Cassey, 2004), germination speed (Schlaepfer et al., 2009), time until
185 reproduction (Schlaepfer et al., 2009), fecundity and reproductive rate (Jenkins & Keller, 2011;
186 Epifanio, 2013; Cappellini et al. 2015; Cardeccia et al., 2018). A noteworthy example within this
187 conceptual framework is the pre-adapted trait of tolerance to inbreeding depression, which has been
188 observed in the invasive ant *Brachyponera chinensis*. Native populations of this species already
189 exhibit a sib-mating behaviour, which may have helped them to purge deleterious alleles over
190 generations, thus predisposing this species to invade (Eyer et al., 2018).

191

192 *2.4 Exaptation*

193 A further form of pre-adaptation could be the so-called “**exaptation**”. Exapted traits are features
194 that did not originally evolve for their current role but were coopted afterwards (Gould & Vrba,
195 1982). In the context of biological invasions, the evolution of traits that will assume a new adaptive
196 function in the introduction range (i.e. exaptation) has been proposed (Hufbauer et al., 2011).
197 However, despite being theoretically possible, this mechanism has to date no evidence. In addition,
198 it would be challenging to demonstrate that a particular structure/gene plays two different roles in
199 the native and introduction range.

200

201 Finally, it is important to emphasize that current literature does not always report a causal
202 explanation for the observed presence of pre-adapted traits in invaders (e.g. Everatt et al., 2012).
203 More research is required to elucidate the factors driving the ability of some organisms to thrive in
204 sometimes very different environments although their evolutionary history has – at least apparently
205 – not posed selective pressures in that direction.

206

207 **3. ADAPTATION DURING TRANSPORT**

208 Once taken from their range, organisms can be transported to other areas through many vectors,
209 including ships, trains, and aircrafts (Hulme et al., 2008). After arriving in a non-native range,
210 however, invaders may face a captivity or cultivation phase before being escaping or being released
211 (Blackburn et al., 2011). In both transport and captivity/cultivation phases, organisms can face
212 admixture and bottlenecks that shape their genetic pool, potentially increasing their fitness and
213 making them adapted to the future environmental conditions they will encounter in the introduction
214 range.

215

216 *3.1 Genetic admixture during transport*

217 During invasions (and, at least potentially, during both the captivity and cultivation phases), **genetic**
218 **admixture** between genetically-differentiated individuals of the same species can increase the
219 genetic diversity of a potential invader (Rius & Darling, 2014). However, admixture and the
220 resulting increase in genetic diversity do not always lead to higher fitness of the invaders or, in
221 general, to an increased invasiveness of the introduced population (Chapple et al., 2012; Irimia et
222 al., 2021). This could have different explanations, including the presence of Dobzhansky-Muller
223 incompatibilities (Dobzhansky, 1936; Muller, 1942). To understand such incompatibilities, consider
224 two allopatric populations with identical genotypes at two loci (AABB). One population evolves the
225 allele A' , which over generations goes to fixation ($A'A'BB$); the other evolves the allele B' , which
226 goes to fixation as well ($AAB'B'$). Both populations are viable and fertile, but when they come into

227 contact and mix, two alleles that do not share a common evolutionary history (A' and B') can
228 become present in the same heterozygote genotypes ($AA'BB'$), potentially leading to the
229 production of non-viable or sterile individuals. Still, in some cases, genetic admixture between
230 individuals with different genetic backgrounds has proved to be advantageous for invaders. This can
231 happen because of increased levels of adaptive potential (Facon et al., 2011b; Rius & Darling, 2014;
232 Kleunen et al., 2015; Calfee et al., 2020), or even because of a reduction of Allee effects when
233 mating availability is limited (Mesgaran et al., 2016). The outcome of a crossing between different
234 populations (whether positive, negative or neutral) might vary even within a single species, as
235 demonstrated with the invasive forb *Centaurea solstitialis* (Irimia et al., 2021), making the role of
236 admixture in invasion biology very elusive. Nevertheless, it must be emphasized that current
237 literature is primarily focused on demonstrating admixture between already-introduced organisms
238 (as discussed in section 4.2), overlooking its potential role in captivity/cultivation phases.
239 Admixture can even occur between different species, usually congeneric (Ainouche et al., 2009;
240 Kovach et al., 2015; but see also Haynes et al., 2011). This seems to be important in plants, where
241 hybrids are usually invasive (Ainouche et al., 2009; Pandit et al., 2006). Albeit it might not always
242 be clear whether hybridization occurred during the cultivation phase or in the new environment,
243 some evidences suggest a possible role of cultivation in this regard. For example, the Oxford
244 ragwort *Senecio squalidus* has a hybrid origin, resulting from a cross between *S. aethnensis* and *S.*
245 *chrysanthemifolius*, two Italian species. *Senecio squalidus* is believed to have arisen through
246 hybridization in the gardens of Badminton (UK), where both *S. aethnensis* and *S.*
247 *chrysanthemifolius* were cultivated at the end of the 17th century. After escaping cultivation, the
248 species then rapidly spread throughout the UK (Nevado et al., 2020). Despite other species (or
249 populations of a species) might share similar evolutionary histories, demonstrating the occurrence
250 of hybridization events giving rise to ecologically-dominant invaders is rather challenging, as it
251 would require at least a partial a priori knowledge of the invasion history of the species.

252 Nevertheless, whether hybridization in captivity/cultivation might promote invasions should be
253 properly assessed.

254

255 *3.2 Founder events and genetic bottlenecks*

256 The collection, transport, and captivity/cultivation of organisms can also expose populations to
257 **founder effects** and **genetic bottlenecks** that will shape their genetic pools. In fact, both domestic
258 animals and cultivated plants often have a reduced genetic diversity due to bottlenecks that occurred
259 at the time of the founders collection and genetic drift occurring during the initial period of
260 domestication when the population sizes are typically small (Makino et al., 2018; Tamburino et al.,
261 2020). These genetic bottlenecks may act as a brake for invaders expansion, as they are well known
262 to originate populations with reduced genetic variability, increased inbreeding depression and
263 subsequent reduced ability to adapt (Hoelzel et al., 2008; Thévenon et al., 2002). However, despite
264 being generally negative for populations, bottlenecks have occasionally proved to promote
265 biological invasions. Genetic bottlenecks can, for example, lead to a decrease in intraspecific
266 competition. An example of increased ability to invade is given by Tsutsui et al. (2000), who
267 demonstrated that introduced populations of the invasive Argentine ant (*Linepithema humile*) in
268 California showed less intraspecific aggression compared to native ones ones, and highlighted a
269 negative correlation between genetic similarity and the levels of aggression between colonies, in
270 both native and introduction areas. Thus, they suggested that a reduction of genetic diversity of the
271 introduced populations, resulting from bottleneck events during introduction led to a reduction of
272 the intraspecific aggression among those populations. The decrease in intraspecific aggression leads
273 to lower territoriality costs and thus allows the formation of increased colony size, making these
274 colonies interspecifically-dominant (Tsutsui et al., 2000). In fact, loss of intraspecific aggression is
275 expected to allow a growth in colonies size and the formation of super-colonies (i.e. colonies made
276 up of several interconnected nests), thus enhancing ants interspecific competitive ability (Suarez et
277 al., 2008).

278 Moreover, inbreeding depression aroused by genetic bottlenecks can lead to purging of genetic
279 load, in particular reducing highly recessive alleles (Wang et al., 1999; Grossen et al., 2020).
280 However, it is not always clear in which phase the purging of deleterious alleles can occur
281 (Barringer et al., 2012), and in the context of biological invasions, to date, there is no evidence of a
282 pre-introduction bottleneck leading to this purging process.

283

284 *3.3 Selection and physiological adaptive responses*

285 Albeit the evolution of invading propagules during transport is commonly attributed to stochastic
286 events (i.e. genetic bottlenecks), a recent review (Briski et al., 2018) emphasized the role that
287 **selection** may play between the collection of organisms and their introduction elsewhere. The
288 authors highlighted that specific selective pressures acting on transported individuals can promote
289 the development of resistance traits. For example, the exposure of the travelling propagule to
290 elevated temperatures, food scarcity or ultraviolet light, could lead to populations that are more
291 prone to survive these stressors upon introduction (Briski et al., 2018). It is important to underlie
292 that the different conditions experienced during transport can also influence the invasion success by
293 enabling **physiological** (and/or epigenetic) **adaptive responses** in the invading organisms, rather
294 than merely genetic changes at the population level. For example, slow moving vessels are often
295 expected to let hull-fouling species gradually adapt to changing water temperature and salinity;
296 these conditions of absence of sharp disturbance might also allow the formation of larger colonies
297 (Campbell & Hewitt, 2015). In such scenarios, disentangling the role of physiological adaptations,
298 genetic changes, and epigenetic changes is not easy, and it is highly likely that all these factors
299 contribute to the development of resistance characteristics during the slow transportation process.
300 Hence, the transport process can be a key step for some biological invasions, as it might both
301 sharply alter the genetic pool of the transferred organisms and make them physiologically adapted
302 to succeed in the invasion process.

303

304 4. ADAPTATION IN THE NEW HABITAT

305 In the new range introduced organisms can undergo adaptation, as the new environmental
306 conditions can favour genetic and non-genetic modifications, and human actions (e.g. multiple
307 introductions, habitat alteration, climate change) can favor the process of adaptation itself (Raitos
308 et al., 2010; Fukasawa et al., 2013; Rius et al., 2014; Negi et al., 2016; Marin et al., 2018). This
309 dynamic interaction between invasive species and their changing environments can lead to the
310 development of new traits that enhance their survival and competitiveness in the invaded
311 ecosystem.

312

313 *4.1 Epigenetics and Transposable Elements (TEs)*

314 In this phase of the invasion process, the role of **transposable elements** (TEs) activity and
315 **epigenetic modifications** can be crucial. Both TEs activity and epigenetic modifications are, in
316 fact, known to be stimulated by novel or stressful environments, and these two mechanisms can act
317 independently or together, since both are sensible to environmental changes. Moreover, epigenetic
318 changes can alter TEs mobility and expression, as to contrast the potentially deleterious
319 consequences of TEs activity, the genome has evolved many epigenetic mechanisms aimed at
320 reducing their activity (Marin et al., 2019; Slotkin & Martienssen, 2007). On the other side, TEs
321 activity may mediate epigenetic regulation as well (Negi et al., 2016). Thus, TEs activity and
322 epigenetic modifications may contribute to the success of invasions by facilitating both adaptive
323 evolution and phenotypic plasticity (Marin et al., 2019).

324 TEs are mobile repeated DNA segments that can move in the genome and induce mutations,
325 thereby altering gene regulation. Despite their possible negative consequences on individuals (as
326 their increase is generally negatively correlated with the individual fitness), TEs can also produce
327 new genetic and phenotypic variation on which selection can act (Slotkin & Martienssen, 2007;
328 Negi et al., 2016). In fact, in native populations, TEs are expected to constitute a great but hidden
329 variation, as their activity is well regulated by a complex epigenetic system (Slotkin & Martienssen,

2007; Marin et al., 2019). However, when organisms face a new environment and experience new stressors, this hidden genetic variation is released. This happens because stress can directly trigger TEs activity and reduce TEs epigenetic silencing mechanisms, indirectly triggering TEs activity. The increase of TEs activity is expected to add to the population new variability on which selection can act, thus favouring long term adaptive responses (Slotkin & Martienssen, 2007; Negi et al., 2016; Lanciano & Mirouze, 2018). This pattern has been shown, for example, in invasive populations of the ant *Cardiocondyla obscurior* (Errbii et al., 2021). The role of TEs in biological invasions has been reviewed by Stapley et al. (2015) and Marin et al. (2019); however, to date, there is no evidence of a direct causal correlation between increase in TEs activity due to new habitat-related stress and the success of an invasion.

As for epigenetics, although the ability of populations to evolve is generally considered limited by the existing genetic variation, environmental changes and stress can generate epigenetic modifications, which can, in turn, alter gene expression to trigger adaptive responses to the new conditions. This happens in a wide range of organisms, including animals and plants (Marin et al., 2019; Hawes et al., 2018; Mounger et al., 2021).

In fact, phenotypic modifications following environmental changes have often been attributed to changes in gene expression consequent to an alteration of the epigenetic patterns (e.g. Gao et al., 2010). For example, epigenetic modifications following a stress phase can make plants resistant to the same stress: if the stress recurs in the future, the plant is able to give a more effective response to contrast it. These epigenetic changes are rapid, reversible and can even be inheritable across generations (Mauch-Mani et al., 2017; Gao et al., 2010). Furthermore, epigenetic modifications may be able to enhance phenotypic plasticity and generate heritable variation on a shorter timescale than mutations in DNA nucleotide sequences (Hawes et al., 2018; Mounger et al., 2021). A common approach to study the role of epigenetic mechanisms in the success of biological invasions involves comparing methylation patterns of different populations of the same species from different colonized geographical areas. Although this method does not directly examine the relationship

356 between epigenetic modifications and traits variation, it allows to explore how environmental cues
357 shape methylation patterns (Marin et al., 2019). For example, in China, DNA differential
358 methylation patterns are thought to be responsible for the invasion success of the plant
359 *Chenopodium ambrosioides* in metal-contaminated sites (Zhang et al., 2022). However, it is worth
360 emphasizing that the correlation between epigenetic variation and the occupied environment is not
361 universal, as epigenetic markings do not always converge in populations occupying similar
362 environments (Marin et al., 2019). Besides, the molecular mechanisms underlying epigenetically-
363 induced adaptation are still not clear, and further research investigating the effects of epigenetic
364 changes on plasticity genes would be required to fulfill this knowledge gap (Mounger et al., 2021).

365

366 *4.2 Admixture in the new range*

367 Albeit **genetic admixture** between genetically-differentiated individuals of the same species can
368 occur in cultivation/captivity phases (as explained in section 3.1), its role in invasion biology has
369 mainly been explored when it takes place between wild populations in the introduction range
370 (Kolbe et al., 2008; Chun et al. 2009; Rius & Darling, 2014; Calfee et al., 2020), where it can give
371 the invaders levels of diversity higher than the ones in the native populations.. As previously
372 explained, this process does not always increase the success of invaders (Chapple et al., 2012;
373 Irimia et al., 2021). Nonetheless, a growing body of literature suggests a possible adaptive role of
374 genetic admixture between genetically-differentiated populations occurring in the new ranges
375 (Facon et al., 2011b; Rius et al., 2014; Kleunen et al. 2015; Calfee et al., 2020).

376 Even in the wild introduction range, admixture can occur between the invading species and a native
377 counterpart (Ainouche et al., 2009; Kovach et al., 2015), or even with another established alien
378 (Haynes et al., 2011). This process becomes particularly critical when it occurs between wild
379 populations, as it can lead to rapid displacement of native species due to the spread of exotic
380 genotypes (Huxel, 1999), posing a major risk in conservation biology. Similarly to admixture
381 between populations of the same species, even hybridization is usually counter selected (Kovach et

382 al., 2015). However, in certain instances, this process might favor the invader (San Jose et al.,
383 2023), probably because it provides alleles that are already adapted to the local environment.

384

385 *4.3 Habitat alteration in the new range*

386 Lastly, in the introduction range, **human alteration of natural habitats** can often increase the
387 likelihood of invasion, enhancing the fitness of invaders and reducing the native species' (Fukasawa
388 et al., 2013). These human-induced alterations can encompass changes in both communities
389 composition and abiotic factors.

390 For example, the prevalence of the alien squirrel *Sciurus carolinensis* over the native *S. griseus* in
391 California has been attributed to the better adaptation of the former to fragmented hardwood forests
392 (Jessen et al., 2018). On a broader scale, seawater warming due to climate change has been
393 observed to facilitate the spread of alien invaders, for example, in the Mediterranean Sea (Raitsos et
394 al., 2010).

395

396

397 **5. ADAPTATION ALONG THE INVASION PROCESS AND IMPLICATIONS**

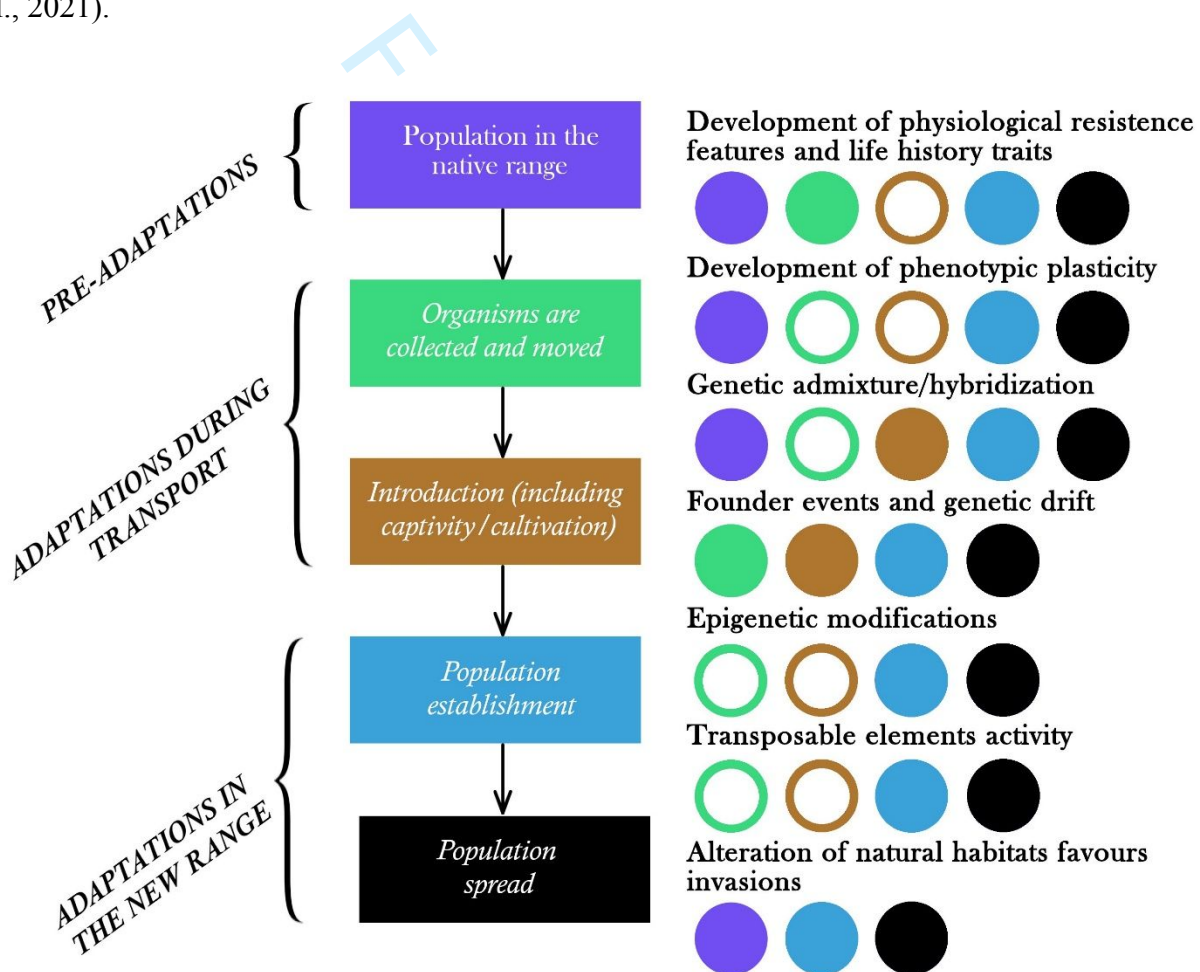
398 Mechanisms of adaptation during invasions numerous and multifaced, encompassing genetic,
399 epigenetic, and ecological processes (Estoup et al., 2016). Literature investigating adaptation during
400 invasions has traditionally focused on finding mechanistic solutions to the genetic paradox of
401 invasions (Stapley et al., 2015; Estoup et al., 2016; Hawes et al., 2016; Marin et al., 2019).

402 However, there has been a general lack of interest in determining the timeframe during which
403 adaptation is most likely to occur.

404

405 Some mechanisms of adaptation can't be avoided, as they arise from natural and innate instances of
406 the species, while others might involve, at least in part human intervention.

407 In Figure 1 we provide an overview of the primary adaptation mechanisms that occur during
 408 invasions, categorized within the invasion framework proposed by Blackburn et al. (2011), with the
 409 addition of a native range stage. However, it should be emphasized that these mechanisms, albeit
 410 typically treated as separated, are often interconnected and reliant on one another. For example, TEs
 411 activity and epigenetic modifications can mutually influence each other (Slotkin & Martienssen,
 412 2007; Negi et al., 2016; Marin et al., 2019), and epigenetic modifications can be the basis for the
 413 development of phenotypic plasticity and resistance characteristics (Hawes et al., 2018; Mounger et
 414 al., 2021).



415 Figure 1. The invasion process is divided into the invasion stages proposed by Blackburn et al. (2011), with
 416 the addition of a native range stage. For each stage, circles on the right indicate the mechanisms of
 417 adaptation that may play a role. Full circles indicate literature supporting the mechanism occurrence
 418 whereas empty circles indicate a potential role in the stage, but absence of supporting literature. Examples
 419 are provided within the text where available (full circles).
 420

421

422 Albeit it is theoretically possible that epigenetic changes arisen in the native range may facilitate a
423 future invasion, due to their responsive and reversible nature, their importance primarily stems from
424 their ability to provide rapid adaptive responses to the changing environmental conditions (Hawes
425 et al., 2018). Since their formation is elicited by the new environmental stress (Hawes et al., 2018;
426 Marin et al., 2018), it is most likely to take place between stage 1 and stage 5 (Fig. 1). However,
427 available literature is mainly focused on investigating epigenetic changes that occur in the new
428 range (Hawes et al., 2018), and to the best of our knowledge, there are no studies that have analysed
429 changing epigenetic patterns before organisms are already introduced. Similarly, even TEs activity
430 is induced by environmental stress, and changing frequencies of insertions are usually attributed to
431 the novel environmental conditions of the new range (Marin et al., 2018).

432 Regarding both epigenetic and TEs insertions changes, once organisms are picked up, prevention is
433 no longer possible. To avoid the development of these adaptation mechanisms in invaders, the only
434 possible approach is to prevent the collection and transportation of organisms to other locations.

435 Genetic admixture between genetically differentiated organisms (as well as hybridization) could
436 theoretically occur in each stage of an invasion (Fig. 1). While admixture between already-
437 introduced organisms has often been investigated, literature exploring the role that the process may
438 have before introduction, particularly during cultivation/captivity phases, is still scarce. Besides,
439 some authors proposed that admixture could also occur within the native range (Gillis et al., 2009).

440 We acknowledge that this could be the case of species introduced through hull-fouling or ballast
441 waters. For example, the serpulid *Hydroides elegans* has a cosmopolitan distribution, showing a
442 low genetic differentiation between populations worldwide. The constant genetic flow between
443 populations of the species has been attributed to its biofouling nature, which allows it to be easily
444 transported across the globe (Pettengill et al., 2007). In such cases, it is highly probable that
445 admixture between individuals in the native range may occur even before introduction.

446 Understanding when admixture occurs along the invasion process can have significant management
447 implications, as different stages of the process may require distinct approaches to control this

448 phenomenon. For instance, in ongoing invasion processes where admixture between new
449 individuals and established invaders can generate heterosis in the introduced population (e.g. Facon
450 et al., 2011; Kleunen et al., 2015), it is crucial for authorities to focus on preventing or managing
451 introductions of individuals from additional native-source populations.

452 It may be the case, for example, of the ladybug *Harmonia axyridis*, for which it has been proposed
453 that the invasiveness may be enhanced through hybridization between invading individuals and
454 pest-control ones occurring in the introduction range (Facon et al., 2011b). Understanding the phase
455 and mechanisms of adaptation that underpin the success of an invader could, in such cases, lead to
456 significant implications for the management and trade of the species. Thus, we believe that future
457 research should attempt to fulfill the knowledge gaps regarding the time admixture (as well as
458 hybridization) takes place. This knowledge can be invaluable for informed decision-making and
459 management strategies in the context of invasive species.

460
461 Alteration of natural habitats, both in the native and the introduction range, can favor invasions. In
462 the native range, this process can lead to the AIAI (Hufbauer et al., 2011; see section 2.2), while in
463 the invaded range it can favor the spread of alien opportunistic species (Jessen et al., 2018).

464 Albeit some factors of environmental change (such as the presence of urban centers or global
465 climatic changes) may be challenging to control, this underscores that human actions and projects
466 should be opportunely conceived to impede the spread of alien species. For example, the
467 introduction of artificial substrates and the destruction of naturally occurring ones in coastal and
468 estuarine habitats might enhance alien species' advantage over native counterparts (Tyrrel & Byers,
469 2007). This highlights the need for careful design and planning of underwater facilities to mitigate
470 the impact on native ecosystems. In fact, if properly designed, human-made structures could serve
471 as a barrier to the expansion of invaders, impairing their ability to adapt upon arrival in the new
472 range. For instance, to prevent alien flora colonisation, it has been proposed that road construction
473 and management in natural reserves should consider the following factors (Tyser & Worley, 1992):

- 474 -utilizing original topsoil for filling in the roadside ditches;
- 475 -avoid considering the project complete until native vegetation is fully established on the roadside;
- 476 -monitoring the presence of alien species on the roadside;
- 477 -using seeds of native species to re-establish native flora on the roadside.

478

479 Similar planning and administrative implications have the potential to prevent the establishment of
480 invaders in various other types of infrastructures (e.g. parks, seaports, railways). Therefore, research
481 efforts should aim to uncover and understand these critical management aspects.

482

483 **6. CONCLUSION**

484 Here we established a coherent sequence in which adaptation of invading species can occur in the
485 different stages of the invasion process. By structuring these stages logically, we provide
486 valuable insights into effective management strategies and highlight the importance of research
487 efforts that incorporate temporal considerations into the study of biological invasions.

488 We believe that this neglected aspect of invasions deserves thorough consideration, as it could carry
489 significant implications for the management of alien invaders. Neglecting the temporal aspects
490 could, indeed, hinder a comprehensive understanding of invasion dynamics: the
491 study of explanations underlying the genetic paradox (Estoup et al., 2016) may be pointless if we do
492 not account the temporal scale at which adaptation takes place. On the other hand, when studying
493 adaptation of invaders, focusing only on a few phases of the invasion process could lead to an
494 underestimation of the actual invasion risk. Therefore, we propose that future research should delve
495 into this overlooked aspect of invasion biology, trying not only to elucidate potential solutions to
496 the genetic paradox, but also discern the phases of the invasion process in which adaptation occurs.
497 This comprehensive approach will allow a deeper understanding of invasive species' population
498 dynamics, and contribute to their effective management.

499

500 **AUTHOR CONTRIBUTIONS**

501 **Alessandro Nota**: Conceptualization; investigation; project administration; supervision;
502 visualization; writing – original draft. **Sandro Bertolino**: Investigation; validation; writing – review
503 & editing. **Francesco Tiralongo**: Validation; writing – review & editing. **Alfredo Santovito**:
504 Conceptualization; writing – review & editing.

505

506 **CONFLICT OF INTEREST STATEMENT**

507 The authors declare that they have no conflict of interest.

508

509 **BIBLIOGRAPHY**

510 Ainouche, M. L., Fortune, P. M., Salmon, A., Parisod, C., Grandbastien, M.-A., Fukunaga, K., Ricou, M., &

511 Misset, M.-T. (2009). Hybridization, polyploidy and invasion: Lessons from *Spartina* (Poaceae).

512 *Biological Invasions*, 11(5), 1159–1173. <https://doi.org/10.1007/s10530-008-9383-2>

513 Allendorf, F. W., & Lundquist, L. L. (2003). Introduction: Population Biology, Evolution, and Control of

514 Invasive Species. *Conservation Biology*, 17(1), 24–30.

515 Ancel Meyers, L., Ancel, F. D., & Lachmann, M. (2005). Evolution of genetic potential. *PLoS Computational*

516 *Biology*, 1(3), e32. <https://doi.org/10.1371/journal.pcbi.0010032>

517 Banks, N. C., Paini, D. R., Bayliss, K. L., & Hodda, M. (2015). The role of global trade and transport network

518 topology in the human-mediated dispersal of alien species. *Ecology Letters*, 18(2), 188–199.

519 <https://doi.org/10.1111/ele.12397>

520 Barringer, B. C., Kulka, E. A., & Galloway, L. F. (2012). Reduced inbreeding depression in peripheral relative

521 to central populations of a monocarpic herb. *Journal of Evolutionary Biology*, 25(6), 1200–1208.

522 <https://doi.org/10.1111/j.1420-9101.2012.02510.x>

- 523 Bartlett, J. C., Convey, P., & Hayward, S. A. L. (2020). Surviving the Antarctic Winter—Life stage cold
524 tolerance and ice entrapment survival in the invasive chironomid midge *Eretmoptera murphyi*. *Insects*,
525 11(3), Article 3. <https://doi.org/10.3390/insects11030147>
- 526 Bates, A. E., McKelvie, C. M., Sorte, C. J. B., Morley, S. A., Jones, N. A. R., Mondon, J. A., Bird, T. J., & Quinn,
527 G. (2013). Geographical range, heat tolerance and invasion success in aquatic species. *Proceedings of*
528 *the Royal Society B: Biological Sciences*, 280(1772), 20131958.
529 <https://doi.org/10.1098/rspb.2013.1958>
- 530 Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology*
531 *Letters*, 12(2), 20150623. <https://doi.org/10.1098/rsbl.2015.0623>
- 532 Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson,
533 D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*,
534 26(7), 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- 535 Briski, E., Chan, F. T., Darling, J. A., Lauringson, V., MacIsaac, H. J., Zhan, A., & Bailey, S. A. (2018). Beyond
536 propagule pressure: Importance of selection during the transport stage of biological invasions.
537 *Frontiers in Ecology and the Environment*, 16(6), 345–353. <https://doi.org/10.1002/fee.1820>
- 538 Calfee, E., Agra, M. N., Palacio, M. A., Ramírez, S. R., & Coop, G. (2020). Selection and hybridization shaped
539 the rapid spread of African honey bee ancestry in the Americas. *PLOS Genetics*, 16(10), e1009038.
540 <https://doi.org/10.1371/journal.pgen.1009038>
- 541 Campbell, M. L., & Hewitt, C. L. (2011). Assessing the port to port risk of vessel movements vectoring non-
542 indigenous marine species within and across domestic Australian borders. *Biofouling*, 27(6), 631–644.
543 <https://doi.org/10.1080/08927014.2011.593715>
- 544 Capellini, I., Baker, J., Allen, W. L., Street, S. E., & Venditti, C. (2015). The role of life history traits in
545 mammalian invasion success. *Ecology Letters*, 18(10), 1099–1107. <https://doi.org/10.1111/ele.12493>

- 546 Cardeccia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B., Gollasch, S., Minchin, D., Narščius, A., Olenin, S.,
547 & Ojaveer, H. (2018). Assessing biological invasions in European seas: biological traits of the most
548 widespread non-indigenous species. *Estuarine, Coastal and Shelf Science*, 201, 17–28.
549 <https://doi.org/10.1016/j.ecss.2016.02.014>
- 550 Chapple, D. G., Miller, K. A., Kraus, F., & Thompson, M. B. (2013). Divergent introduction histories among
551 invasive populations of the delicate skink (*Lampropholis delicata*): Has the importance of genetic
552 admixture in the success of biological invasions been overemphasized? *Diversity and Distributions*,
553 19(2), 134–146. <https://doi.org/10.1111/j.1472-4642.2012.00919.x>
- 554 Chow, P. K. Y., Clayton, N. S., & Steele, M. A. (2021). Cognitive Performance of wild eastern gray squirrels
555 (*Sciurus carolinensis*) in rural and urban, native, and non-native environments. *Frontiers in Ecology and*
556 *Evolution*, 9. <https://www.frontiersin.org/articles/10.3389/fevo.2021.615899>
- 557 Chun, Y. J., Fumanal, B., Laitung, B., & Bretagnolle, F. (2010). Gene flow and population admixture as the
558 primary post-invasion processes in common ragweed (*Ambrosia artemisiifolia*) populations in France.
559 *New Phytologist*, 185(4), 1100–1107. <https://doi.org/10.1111/j.1469-8137.2009.03129.x>
- 560 Colomer-Ventura, F., Martínez-Vilalta, J., Zuccarini, P., Escolà, A., Armengot, L., & Castells, E. (2015).
561 Contemporary evolution of an invasive plant is associated with climate but not with herbivory.
562 *Functional Ecology*, 29(11), 1475–1485. <https://doi.org/10.1111/1365-2435.12463>
- 563 Cope, R. C., Ross, J. V., Wittmann, T. A., Watts, M. J., & Cassey, P. (2019). Predicting the risk of biological
564 invasions using environmental similarity and transport network connectedness. *Risk Analysis*, 39(1),
565 35–53. <https://doi.org/10.1111/risa.12870>
- 566 Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity
567 than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, 14(4), 419–431.
568 <https://doi.org/10.1111/j.1461-0248.2011.01596.x>
- 569 Dlugosch, K. M., & Parker, I. M. (2007). Molecular and quantitative trait variation across the native range of
570 the invasive species *Hypericum canariense*: Evidence for ancient patterns of colonization via pre-

- 571 adaptation? *Molecular Ecology*, 16(20), 4269–4283. <https://doi.org/10.1111/j.1365->
- 572 [294X.2007.03508.x](https://doi.org/10.1111/j.1365-294X.2007.03508.x)
- 573 Dobzhansky, Th. (1936). Studies on Hybrid Sterility. II. Localization of sterility factors in *Drosophila*
- 574 *pseudoobscura* hybrids. *Genetics*, 21(2), 113–135.
- 575 Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., Gonzalez, P., Grosholz, E.
- 576 D., Ibañez, I., Miller, L. P., Sorte, C. J. B., & Tatem, A. J. (2016). Global threats from invasive alien
- 577 species in the twenty-first century and national response capacities. *Nature Communications*, 7(1),
- 578 Article 1. <https://doi.org/10.1038/ncomms12485>
- 579 Elst, E. M., Acharya, K. P., Dar, P. A., Reshi, Z. A., Tufto, J., Nijs, I., & Graae, B. J. (2016). Pre-adaptation or
- 580 genetic shift after introduction in the invasive species *Impatiens glandulifera*? *Acta Oecologica*, 70,
- 581 60–66. <https://doi.org/10.1016/j.actao.2015.12.002>
- 582 Epifanio, C. E. (2013). Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: a review. *Journal of*
- 583 *Experimental Marine Biology and Ecology*, 441, 33–49. <https://doi.org/10.1016/j.jembe.2013.01.010>
- 584 Errbii, M., Keilwagen, J., Hoff, K. J., Steffen, R., Altmüller, J., Oettler, J., & Schrader, L. (2021). Transposable
- 585 elements and introgression introduce genetic variation in the invasive ant *Cardiocondyla obscurior*.
- 586 *Molecular Ecology*, 30(23), 6211–6228. <https://doi.org/10.1111/mec.16099>
- 587 Estoup, A., Ravigné, V., Hufbauer, R., Vitalis, R., Gautier, M., & Facon, B. (2016). Is there a genetic paradox
- 588 of biological invasion? *Annual Review of Ecology, Evolution, and Systematics*, 47(1), 51–72.
- 589 <https://doi.org/10.1146/annurev-ecolsys-121415-032116>
- 590 Everatt, M. J., Worland, M. R., Bale, J. S., Convey, P., & Hayward, S. A. L. (2012). Pre-adapted to the
- 591 maritime Antarctic? – Rapid cold hardening of the midge, *Eretmoptera murphyi*. *Journal of Insect*
- 592 *Physiology*, 58(8), 1104–1111. <https://doi.org/10.1016/j.jinsphys.2012.05.009>
- 593 Eyer, P.-A., Matsuura, K., Vargo, E. L., Kobayashi, K., Yashiro, T., Suehiro, W., Himuro, C., Yokoi, T., Guénard,
- 594 B., Dunn, R. R., & Tsuji, K. (2018). Inbreeding tolerance as a pre-adapted trait for invasion success in

- 595 the invasive ant *Brachyponera chinensis*. *Molecular Ecology*, 27(23), 4711–4724.
596 <https://doi.org/10.1111/mec.14910>
- 597 Facon, B., Crespin, L., Loiseau, A., Lombaert, E., Magro, A., & Estoup, A. (2011). Can things get worse when
598 an invasive species hybridizes? The harlequin ladybird *Harmonia axyridis* in France as a case study.
599 *Evolutionary Applications*, 4(1), 71–88. <https://doi.org/10.1111/j.1752-4571.2010.00134.x>
- 600 Facon, B., Genton, B. J., Shykoff, J., Jarne, P., Estoup, A., & David, P. (2006). A general eco-evolutionary
601 framework for understanding bioinvasions. *Trends in Ecology & Evolution*, 21(3), 130–135.
602 <https://doi.org/10.1016/j.tree.2005.10.012>
- 603 Facon, B., Hufbauer, R. A., Tayeh, A., Loiseau, A., Lombaert, E., Vitalis, R., Guillemaud, T., Lundgren, J. G., &
604 Estoup, A. (2011). Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Current*
605 *Biology: CB*, 21(5), 424–427. <https://doi.org/10.1016/j.cub.2011.01.068>
- 606 Fantle-Lepczyk, J. E., Haubrock, P. J., Kramer, A. M., Cuthbert, R. N., Turbelin, A. J., Crystal-Ornelas, R.,
607 Diagne, C., & Courchamp, F. (2022). Economic costs of biological invasions in the United States. *The*
608 *Science of the Total Environment*, 806(Pt 3), 151318. <https://doi.org/10.1016/j.scitotenv.2021.151318>
- 609 Ferrario, J., Caronni, S., Occhipinti-Ambrogi, A., & Marchini, A. (2017). Role of commercial harbours and
610 recreational marinas in the spread of non-indigenous fouling species. *Biofouling*, 33(8), 651–660.
611 <https://doi.org/10.1080/08927014.2017.1351958>
- 612 Fukasawa, K., Miyashita, T., Hashimoto, T., Tataru, M., & Abe, S. (2013). Differential population responses of
613 native and alien rodents to an invasive predator, habitat alteration and plant masting. *Proceedings of*
614 *the Royal Society B: Biological Sciences*, 280(1773), 20132075.
615 <https://doi.org/10.1098/rspb.2013.2075>
- 616 Garbelotto, M., Rocca, G. D., Osmundson, T., di Lonardo, V., & Danti, R. (2015). An increase in transmission-
617 related traits and in phenotypic plasticity is documented during a fungal invasion. *Ecosphere*, 6(10),
618 art180. <https://doi.org/10.1890/ES14-00426.1>

- 619 Geng, Y., van Klinken, R. D., Sosa, A., Li, B., Chen, J., & Xu, C.-Y. (2016). The relative importance of genetic
620 diversity and phenotypic plasticity in determining invasion success of a clonal weed in the USA and
621 China. *Frontiers in Plant Science*, 7. <https://www.frontiersin.org/articles/10.3389/fpls.2016.00213>
- 622 Ghalambor, C. K., MCKAY, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive
623 phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional*
624 *Ecology*, 21(3), 394–407. <https://doi.org/10.1111/j.1365-2435.2007.01283.x>
- 625 Gil-Fernández, M., Harcourt, R., Newsome, T., Towerton, A., & Carthey, A. (2020). Adaptations of the red
626 fox (*Vulpes vulpes*) to urban environments in Sydney, Australia. *Journal of Urban Ecology*, 6(1),
627 juaa009. <https://doi.org/10.1093/jue/juaa009>
- 628 Gillis, N. K., Walters, L. J., Fernandes, F. C., & Hoffman, E. A. (2009). Higher genetic diversity in introduced
629 than in native populations of the mussel *Mytella charruana*: evidence of population admixture at
630 introduction sites. *Diversity and Distributions*, 15(5), 784–795. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2009.00591.x)
631 [4642.2009.00591.x](https://doi.org/10.1111/j.1472-4642.2009.00591.x)
- 632 Glémin, S. (2003). How are deleterious mutations purged? Drift versus nonrandom mating. *Evolution;*
633 *International Journal of Organic Evolution*, 57(12), 2678–2687. [https://doi.org/10.1111/j.0014-](https://doi.org/10.1111/j.0014-3820.2003.tb01512.x)
634 [3820.2003.tb01512.x](https://doi.org/10.1111/j.0014-3820.2003.tb01512.x)
- 635 Goubert, C., Henri, H., Minard, G., Valiente Moro, C., Mavingui, P., Vieira, C., & Boulesteix, M. (2017). High-
636 throughput sequencing of transposable element insertions suggests adaptive evolution of the invasive
637 Asian tiger mosquito towards temperate environments. *Molecular Ecology*, 26(15), 3968–3981.
638 <https://doi.org/10.1111/mec.14184>
- 639 Gould, S. J., & Vrba, E. S. (1982). Exaptation—A missing term in the science of form. *Paleobiology*, 8(1), 4–
640 15. <https://doi.org/10.1017/S0094837300004310>
- 641 Grossen, C., Guillaume, F., Keller, L. F., & Croll, D. (2020). Purging of highly deleterious mutations through
642 severe bottlenecks in Alpine ibex. *Nature Communications*, 11(1), Article 1.
643 <https://doi.org/10.1038/s41467-020-14803-1>

- 644 Hahn, M. A., Kleunen, M. van, & Müller-Schärer, H. (2012). Increased phenotypic plasticity to climate may
645 have boosted the invasion success of polyploid *Centaurea stoebe*. *PLOS ONE*, *7*(11), e50284.
646 <https://doi.org/10.1371/journal.pone.0050284>
- 647 Haubrock, P. J., Turbelin, A. J., Cuthbert, R. N., Novoa, A., Taylor, N. G., Angulo, E., Ballesteros-Mejia, L.,
648 Bodey, T. W., Capinha, C., Diagne, C., Essl, F., Golivets, M., Kirichenko, N., Kourantidou, M., Leroy, B.,
649 Renault, D., Verbrugge, L., & Courchamp, F. (2021). Economic costs of invasive alien species across
650 Europe. *NeoBiota*, *67*, 153–190. <https://doi.org/10.3897/neobiota.67.58196>
- 651 Hawes, N. A., Fidler, A. E., Tremblay, L. A., Pochon, X., Dunphy, B. J., & Smith, K. F. (2018). Understanding
652 the role of DNA methylation in successful biological invasions: a review. *Biological Invasions*, *20*(9),
653 2285–2300. <https://doi.org/10.1007/s10530-018-1703-6>
- 654 Haynes, G., Gongora, J., Gilligan, D., Grewe, P., Moran, C., & Nicholas, F. (2012). Cryptic hybridization and
655 introgression between invasive cyprinid species *Cyprinus carpio* and *Carassius auratus* in Australia:
656 Implications for invasive species management. *Animal Conservation*, *15*, 83–94.
657 <https://doi.org/10.1111/j.1469-1795.2011.00490.x>
- 658 HOELZEL, A. R. (1999). Impact of population bottlenecks on genetic variation and the importance of life-
659 history; a case study of the northern elephant seal. *Biological Journal of the Linnean Society*, *68*(1–2),
660 23–39. <https://doi.org/10.1111/j.1095-8312.1999.tb01156.x>
- 661 Hufbauer, R. A., Facon, B., Ravigné, V., Turgeon, J., Foucaud, J., Lee, C. E., Rey, O., & Estoup, A. (2012).
662 Anthropogenically induced adaptation to invade (AIAI): Contemporary adaptation to human-altered
663 habitats within the native range can promote invasions. *Evolutionary Applications*, *5*(1), 89–101.
664 <https://doi.org/10.1111/j.1752-4571.2011.00211.x>
- 665 Hulme, P. E. (2014). Invasive species challenge the global response to emerging diseases. *Trends in*
666 *Parasitology*, *30*(6), 267–270. <https://doi.org/10.1016/j.pt.2014.03.005>
- 667 Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J.,
668 Pyšek, P., Roques, A., Sol, D., Solarz, W., & Vilà, M. (2008). Grasping at the routes of biological

- 669 invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, 45(2), 403–
670 414. <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- 671 Huxel, G. R. (1999). Rapid displacement of native species by invasive species: effects of hybridization.
672 *Biological Conservation*, 89(2), 143–152. [https://doi.org/10.1016/S0006-3207\(98\)00153-0](https://doi.org/10.1016/S0006-3207(98)00153-0)
- 673 Irimia, R. E., Hierro, J. L., Branco, S., Sotes, G., Cavieres, L. A., Eren, Ö., Lortie, C. J., French, K., Callaway, R.
674 M., & Montesinos, D. (2021). Experimental admixture among geographically disjunct populations of an
675 invasive plant yields a global mosaic of reproductive incompatibility and heterosis. *Journal of Ecology*,
676 109(5), 2152–2162. <https://doi.org/10.1111/1365-2745.13628>
- 677 Jenkins, C., & Keller, S. R. (2011). A phylogenetic comparative study of preadaptation for invasiveness in the
678 genus *Silene* (Caryophyllaceae). *Biological Invasions*, 13(6), 1471–1486.
679 <https://doi.org/10.1007/s10530-010-9907-4>
- 680 Jessen, T., Wang, Y., & Wilmers, C. C. (2018). Habitat fragmentation provides a competitive advantage to an
681 invasive tree squirrel, *Sciurus carolinensis*. *Biological Invasions*, 20(3), 607–618.
682 <https://doi.org/10.1007/s10530-017-1560-8>
- 683 Juliano, S. A., & Lounibos, L. P. (2005). Ecology of invasive mosquitoes: Effects on resident species and on
684 human health. *Ecology Letters*, 8(5), 558. <https://doi.org/10.1111/j.1461-0248.2005.00755>
- 685 Kistner, E. J., & Dybdahl, M. F. (2013). Adaptive responses and invasion: The role of plasticity and evolution
686 in snail shell morphology. *Ecology and Evolution*, 3(2), 424–436. <https://doi.org/10.1002/ece3.471>
- 687 Kolbe, J. J., Larson, A., Losos, J. B., & de Queiroz, K. (2008). Admixture determines genetic diversity and
688 population differentiation in the biological invasion of a lizard species. *Biology Letters*, 4(4), 434–437.
689 <https://doi.org/10.1098/rsbl.2008.0205>
- 690 Kovach, R. P., Muhlfeld, C. C., Boyer, M. C., Lowe, W. H., Allendorf, F. W., & Luikart, G. (2015). Dispersal and
691 selection mediate hybridization between a native and invasive species. *Proceedings of the Royal*
692 *Society B: Biological Sciences*, 282(1799), 20142454. <https://doi.org/10.1098/rspb.2014.2454>

- 693 Kowalczyk, R., & Zalewski, A. (2011). Adaptation to cold and predation—Shelter use by invasive raccoon
694 dogs *Nyctereutes procyonoides* in Białowieża Primeval Forest (Poland). *European Journal of Wildlife*
695 *Research*, 57(1), 133–142. <https://doi.org/10.1007/s10344-010-0406-9>
- 696 Kristensen, T. N., Ketola, T., & Kronholm, I. (2020). Adaptation to environmental stress at different
697 timescales. *Annals of the New York Academy of Sciences*, 1476(1), 5–22.
698 <https://doi.org/10.1111/nyas.13974>
- 699 Lamarque, L. J., Porté, A. J., Eymeric, C., Lasnier, J.-B., Lortie, C. J., & Delzon, S. (2013). A test for pre-
700 adapted phenotypic plasticity in the invasive tree *Acer negundo* L. *PLOS ONE*, 8(9), e74239.
701 <https://doi.org/10.1371/journal.pone.0074239>
- 702 Lanciano, S., & Mirouze, M. (2018). Transposable elements: all mobile, all different, some stress responsive,
703 some adaptive? *Current Opinion in Genetics & Development*, 49, 106–114.
704 <https://doi.org/10.1016/j.gde.2018.04.002>
- 705 Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and
706 genetic assimilation. *Journal of Evolutionary Biology*, 22(7), 1435–1446.
707 <https://doi.org/10.1111/j.1420-9101.2009.01754.x>
- 708 Lande, R. (2015). Evolution of phenotypic plasticity in colonizing species. *Molecular Ecology*, 24(9), 2038–
709 2045. <https://doi.org/10.1111/mec.13037>
- 710 Lee, C. E., & Gelembiuk, G. W. (2008). Evolutionary origins of invasive populations. *Evolutionary*
711 *Applications*, 1(3), 427–448. <https://doi.org/10.1111/j.1752-4571.2008.00039.x>
- 712 Liao, Z.-Y., Scheepens, J. F., Li, W.-T., Wang, R.-F., Zheng, Y.-L., & Feng, Y.-L. (2019). Biomass reallocation and
713 increased plasticity might contribute to successful invasion of *Chromolaena odorata*. *中科院*, 256(x).
714 <https://doi.org/10.1016/j.flora.2019.05.004>

- 715 Lucek, K., Sivasundar, A., & Seehausen, O. (2014). Disentangling the role of phenotypic plasticity and genetic
716 divergence in contemporary ecotype formation during a biological invasion. *Evolution*, 68(9), 2619–
717 2632.
- 718 Makino, T., Rubin, C.-J., Carneiro, M., Axelsson, E., Andersson, L., & Webster, M. T. (2018). Elevated
719 proportions of deleterious genetic variation in domestic animals and plants. *Genome Biology and*
720 *Evolution*, 10(1), 276–290. <https://doi.org/10.1093/gbe/evy004>
- 721 Marcelletti, S., & Scortichini, M. (2016). *Xylella fastidiosa* CoDiRO strain associated with the olive quick
722 decline syndrome in southern Italy belongs to a clonal complex of the subspecies *pauca* that evolved
723 in Central America. *Microbiology (Reading, England)*, 162(12), 2087–2098.
724 <https://doi.org/10.1099/mic.0.000388>
- 725 Marin, P., Genitoni, J., Barloy, D., Maury, S., Gibert, P., Ghalambor, C. K., & Vieira, C. (2020). Biological
726 invasion: The influence of the hidden side of the (epi)genome. *Functional Ecology*, 34(2), 385–400.
727 <https://doi.org/10.1111/1365-2435.13317>
- 728 Mesgaran, M. B., Lewis, M. A., Ades, P. K., Donohue, K., Ohadi, S., Li, C., & Cousens, R. D. (2016).
729 Hybridization can facilitate species invasions, even without enhancing local adaptation. *Proceedings of*
730 *the National Academy of Sciences*, 113(36), 10210–10214. <https://doi.org/10.1073/pnas.1605626113>
- 731 Møller, A. P., & Cassey, P. (2004). On the relationship between T-cell mediated immunity in bird species and
732 the establishment success of introduced populations. *Journal of Animal Ecology*, 73(6), 1035–1042.
733 <https://doi.org/10.1111/j.0021-8790.2004.00879.x>
- 734 Mounger, J., Ainouche, M. L., Bossdorf, O., Cavé-Radet, A., Li, B., Parepa, M., Salmon, A., Yang, J., &
735 Richards, C. L. (2021). Epigenetics and the success of invasive plants. *Philosophical Transactions of the*
736 *Royal Society B: Biological Sciences*, 376(1826), 20200117. <https://doi.org/10.1098/rstb.2020.0117>
- 737 Muller, H. J. (1942). Isolating mechanisms, evolution, and temperature. *Biology Symposia*, 6, 71–124.

- 738 Negi, P., Rai, A. N., & Suprasanna, P. (2016). Moving through the stressed genome: emerging regulatory
739 roles for transposons in plant stress response. *Frontiers in Plant Science*, 7, 1448.
740 <https://doi.org/10.3389/fpls.2016.01448>
- 741 Nevado, B., Harris, S. A., Beaumont, M. A., & Hiscock, S. J. (2020). Rapid homoploid hybrid speciation in
742 British gardens: The origin of Oxford ragwort (*Senecio squalidus*). *Molecular Ecology*, 29(21), 4221–
743 4233. <https://doi.org/10.1111/mec.15630>
- 744 Palacio-López, K., & Gianoli, E. (2011). Invasive plants do not display greater phenotypic plasticity than their
745 native or non-invasive counterparts: a meta-analysis. *Oikos*, 120(9), 1393–1401.
746 <https://doi.org/10.1111/j.1600-0706.2010.19114.x>
- 747 PANDIT, M. K., TAN, H. T. W., & BISHT, M. S. (2006). Polyploidy in invasive plant species of Singapore.
748 *Botanical Journal of the Linnean Society*, 151(3), 395–403. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8339.2006.00515.x)
749 [8339.2006.00515.x](https://doi.org/10.1111/j.1095-8339.2006.00515.x)
- 750 Peterson, A. T. (2003). Predicting the geography of species' invasions via ecological niche modeling. *The*
751 *Quarterly Review of Biology*, 78(4), 419–433. <https://doi.org/10.1086/378926>
- 752 Pettengill, J. B., Wendt, D. E., Schug, M. D., & Hadfield, M. G. (2007). Biofouling likely serves as a major
753 mode of dispersal for the polychaete tubeworm *Hydroides elegans* as inferred from microsatellite loci.
754 *Biofouling*, 23(3–4), 161–169. <https://doi.org/10.1080/08927010701218952>
- 755 Piscart, C., Kefford, B. J., & Beisel, J.-N. (2011). Are salinity tolerances of non-native macroinvertebrates in
756 France an indicator of potential for their translocation in a new area ? *Limnologica*, 41, 107.
757 <https://doi.org/10.1016/j.limno.2010.09.002>
- 758 Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F.,
759 Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A.,
760 Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., ... Richardson, D. M. (2020). Scientists' warning on
761 invasive alien species. *Biological Reviews of the Cambridge Philosophical Society*, 95(6), 1511–1534.
762 <https://doi.org/10.1111/brv.12627>

- 763 Raitzos, D. E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A. M., Theocharis, A.,
764 & Papathanassiou, E. (2010). Global climate change amplifies the entry of tropical species into the
765 eastern Mediterranean Sea. *Limnology and Oceanography*, 55(4), 1478–1484.
766 <https://doi.org/10.4319/lo.2010.55.4.1478>
- 767 Rius, M., & Darling, J. A. (2014). How important is intraspecific genetic admixture to the success of
768 colonising populations? *Trends in Ecology & Evolution*, 29(4), 233–242.
769 <https://doi.org/10.1016/j.tree.2014.02.003>
- 770 San Jose, M., Doorenweerd, C., & Rubinoff, D. (2023). Genomics reveals widespread hybridization across
771 insects with ramifications for species boundaries and invasive species. *Current Opinion in Insect*
772 *Science*, 58, 101052. <https://doi.org/10.1016/j.cois.2023.101052>
- 773 Schlaepfer, D. R., Glättli, M., Fischer, M., & van Kleunen, M. (2010). A multi-species experiment in their
774 native range indicates pre-adaptation of invasive alien plant species. *New Phytologist*, 185(4), 1087–
775 1099. <https://doi.org/10.1111/j.1469-8137.2009.03114.x>
- 776 Shackleton, R. T., Shackleton, C. M., & Kull, C. A. (2019). The role of invasive alien species in shaping local
777 livelihoods and human well-being: A review. *Journal of Environmental Management*, 229, 145–157.
778 <https://doi.org/10.1016/j.jenvman.2018.05.007>
- 779 Slotkin, R. K., & Martienssen, R. (2007). Transposable elements and the epigenetic regulation of the
780 genome. *Nature Reviews. Genetics*, 8(4), 272–285. <https://doi.org/10.1038/nrg2072>
- 781 Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal*
782 *Behaviour*, 63(3), 495–502. <https://doi.org/10.1006/anbe.2001.1953>
- 783 Stapley, J., Santure, A. W., & Dennis, S. R. (2015). Transposable elements as agents of rapid adaptation may
784 explain the genetic paradox of invasive species. *Molecular Ecology*, 24(9), 2241–2252.
785 <https://doi.org/10.1111/mec.13089>

- 786 Suarez, A. V., Holway, D. A., & Tsutsui, N. D. (2008). Genetics and behavior of a colonizing species: the
787 invasive Argentine ant. *The American Naturalist*, 172(S1), S72–S84. <https://doi.org/10.1086/588638>
- 788 Tamburino, R., Sannino, L., Cafasso, D., Cantarella, C., Orrù, L., Cardi, T., Cozzolino, S., D'Agostino, N., &
789 Scotti, N. (2020). Cultivated tomato (*Solanum lycopersicum* L.) Suffered a severe cytoplasmic
790 bottleneck during domestication: implications from chloroplast genomes. *Plants (Basel, Switzerland)*,
791 9(11), 1443. <https://doi.org/10.3390/plants9111443>
- 792 Thevenon, S., & Couvet, D. (2002). The impact of inbreeding depression on population survival depending
793 on demographic parameters. *Animal Conservation*. <https://doi.org/10.1017/S1367943002001075>
- 794 Tsutsui, N. D., Suarez, A. V., Holway, D. A., & Case, T. J. (2000a). Reduced genetic variation and the success
795 of an invasive species. *Proceedings of the National Academy of Sciences*, 97(11), 5948–5953.
796 <https://doi.org/10.1073/pnas.100110397>
- 797 Tsutsui, N. D., Suarez, A. V., Holway, D. A., & Case, T. J. (2000b). Reduced genetic variation and the success
798 of an invasive species. *Proceedings of the National Academy of Sciences*, 97(11), 5948–5953.
799 <https://doi.org/10.1073/pnas.100110397>
- 800 Tyrrell, M. C., & Byers, J. E. (2007). Do artificial substrates favor nonindigenous fouling species over native
801 species? *Journal of Experimental Marine Biology and Ecology*, 342(1), 54–60.
802 <https://doi.org/10.1016/j.jembe.2006.10.014>
- 803 Tyser, R. W., & Worley, C. A. (1992). Alien flora in grasslands adjacent to road and trail corridors in Glacier
804 National Park, Montana (U.S.A.). *Conservation Biology*, 6(2), 253–262.
- 805 Ulman, A., Ferrario, J., Occhpinti-Ambrogi, A., Arvanitidis, C., Bandi, A., Bertolino, M., Bogi, C.,
806 Chatzigeorgiou, G., Çiçek, B. A., Deidun, A., Ramos-Esplá, A., Koçak, C., Lorenti, M., Martinez-Laiz, G.,
807 Merlo, G., Princisgh, E., Scribano, G., & Marchini, A. (2017). A massive update of non-indigenous
808 species records in Mediterranean marinas. *PeerJ*, 5, e3954. <https://doi.org/10.7717/peerj.3954>

- 809 van Kleunen, M., Röckle, M., & Stift, M. (2015). Admixture between native and invasive populations may
810 increase invasiveness of *Mimulus guttatus*. *Proceedings of the Royal Society B: Biological Sciences*,
811 282(1815), 20151487. <https://doi.org/10.1098/rspb.2015.1487>
- 812 Wang, J. (2000). Effects of population structures and selection strategies on the purging of inbreeding
813 depression due to deleterious mutations. *Genetical Research*, 76(1), 75–86.
814 <https://doi.org/10.1017/S0016672399004450>
- 815 Wang, J., Gaughan, S., Lamer, J. T., Deng, C., Hu, W., Wachholtz, M., Qin, S., Nie, H., Liao, X., Ling, Q., Li, W.,
816 Zhu, L., Bernatchez, L., Wang, C., & Lu, G. (2020). Resolving the genetic paradox of invasions:
817 Preadapted genomes and postintroduction hybridization of bigheaded carps in the Mississippi River
818 Basin. *Evolutionary Applications*, 13(2), 263–277. <https://doi.org/10.1111/eva.12863>
- 819 Westphal, M. I., Browne, M., MacKinnon, K., & Noble, I. (2008). The link between international trade and
820 the global distribution of invasive alien species. *Biological Invasions*, 10(4), 391–398.
821 <https://doi.org/10.1007/s10530-007-9138-5>
- 822 Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and
823 species invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution*, 22(4), 393–404.
824 <https://doi.org/10.1080/03949370.2010.505580>
- 825 Zalewski, A., & Bartoszewicz, M. (2012). Phenotypic variation of an alien species in a new environment: The
826 body size and diet of American mink over time and at local and continental scales. *Biological Journal of*
827 *the Linnean Society*, 105(3), 681–693. <https://doi.org/10.1111/j.1095-8312.2011.01811.x>
- 828 Zhang, H., Tang, Y., Li, Q., Zhao, S., Zhang, Z., Chen, Y., Shen, Z., & Chen, C. (2022). Genetic and epigenetic
829 variation separately contribute to range expansion and local metalliferous habitat adaptation during
830 invasions of *Chenopodium ambrosioides* into China. *Annals of Botany*, 130(7), 1041–1056.