

REVIEW

Adaptation to bioinvasions: When does it occur?

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Abstract

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 crucial 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 of introduction. 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 analyze 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.

KEYWORDS

adaptation, adaptation in invasions, alien species, genetic paradox of invasions, invasive species

1 | INTRODUCTION

Biological invasions are one of the main drivers of global change and pose significant threats to biodiversity, ecosystems, and human well-being (Bellard et al., 2016; Pyšek et al., 2020; Shackleton et al., 2019). Besides, the magnitude of alien species introduction continues to increase (Seebens et al., 2017), and the negative effects they bring

are expected to exacerbate further (Fantle-Lepczyk et al., 2022; Haubrock et al., 2021; Hulme, 2014; Juliano & Lounibos, 2005).

However, despite their concerning impact on global biodiversity, biological invasions also offer a unique opportunity to investigate population evolution within a timescale compatible with human life. Indeed, the intentional or unintentional introduction of species into new habitats serves as a recurring and unique experiment involving

many different taxa. These experiments shed light on the adaptation mechanisms of invaders, which play a role in their ability to survive, establish, and spread into new areas with different biotic and abiotic components (e.g., Estoup et al., 2016; Marin et al., 2020). In this context, due to the genetic flexibility of invasive species, the genetic sources of variation and adaptive potential have a pivotal role and should be integrated in the study of biological invasions (Prentis et al., 2008). Indeed, these mechanisms are particularly intriguing when the introduced population is built up and becomes invasive starting from just a few initial founders.

Allendorf and Lundquist (2003) used the concept of “genetic paradox” to describe the contradiction arising from the ability of some species to establish invasive populations starting from small propagules, despite having reduced genetic variation due to demographic bottlenecks and genetic drift. This reduced variation is indeed expected to lead to inbreeding depression, thus hindering the ability of the introduced population to persist and evolve in the new environment (Allendorf & Lundquist, 2003). Recent studies (e.g., Kim et al., 2023) emphasize the importance of temporal analyses in invasion biology, highlighting how temporal data collections can provide insights into the progressive stages of invasion, and offering a coherent description of how and when adaptive changes occur. However, while the analysis of adaptation mechanisms during biological invasions has traditionally focused on resolving the genetic paradox, and many possible explanations have been proposed (Estoup et al., 2016; Hawes et al., 2018; Marin et al., 2020; Stapley et al., 2015), the importance of time has often been overlooked, and the chronological order in which adaptation events occur still remains a crucial knowledge gap. The temporal perspective is, nevertheless, crucial for effectively managing invasive species and mitigating their impacts (Kim et al., 2023). Indeed, understanding when and under which evolutionary processes adaptation is most likely to develop is indeed critical to comprehend the potential opportunities and challenges invasive species may face during the invasion process, helping delineate effective management strategies.

Here, we used as reference the frameworks proposed by Blackburn et al. (2011) and Daly et al. (2023), which break down the invasion process into stages. These stages include the movement from the native range toward new areas, the release or escape from confinement, the establishment of populations, and their subsequent spread. Each stage is characterized by a specific barrier that individuals must overcome to progress to the next step. Our review focuses on various types of adaptations, including physiological and behavioral plasticity-related processes, as well as genetic (transposable element activity, genetic admixture, and hybridization) and epigenetic mechanisms. Moreover, we discuss the role that the human-altered environment can play in promoting the invasiveness of some organisms. While it may be intuitive to assume that the adaptation process primarily takes place in the new range (as introduced organisms do not face the new habitat before), existing literature demonstrates that adaptation can occur in each stage of the invasion process. Besides, adaptation in the different stages is not mutually exclusive. Our purpose was to illustrate how adaptation

mechanisms helping invaders in overcoming their barriers can evolve during each phase of the invasion process described by Blackburn et al. (2011), and even earlier in the native range of the invader. This pre-introduction adaptation underscores the complexity of invasion dynamics and the importance of considering evolutionary processes within the native range as part of the management strategies (Rey et al., 2012). Moreover, we aim to highlight the management and research implications resulting from a full understanding of the adaptation timeframe.

In this review, we firstly explain the main adaptation mechanisms occurring during invasions, subdivided into the three main phases of the invasion process (Daly et al., 2023): first, the (future) invader is in its native geographic range, where it naturally lives; second, the transport: the organisms leave their native range, transit across geographical barriers and reach a non-native environment; this stage also includes the captivity and/or cultivation phases in the new range; and third, the establishment and spread of the introduced population in the new area. Then, we analyze how adaptation can develop within each specific stage, providing concrete examples and insights into the implications for effective management. Finally, we discuss how future research efforts should attempt to disentangle the role of each stage in the adaptation of invaders. A comprehensive awareness of these invasion dynamics can significantly enhance our ability to effectively address the challenges posed by invasive alien and protect biodiversity and ecosystems.

The bibliographic research was conducted using Google Scholar, employing the keywords “invasive species,” “alien species,” “non-indigenous species,” “adaptation,” “invasion success,” and “genetic paradox,” in different combinations. The resulting articles and their references were selected based on their relevance to the study's aims.

2 | PRE-ADAPTATION IN BIOLOGICAL INVASIONS

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

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

2.1 | Phenotypic plasticity

The most investigated pre-adaptation mechanism is *phenotypic plasticity*, both in animals (e.g., Kistner & Dybdahl, 2013; Lucek et al., 2014) and plants (e.g., Colomer-Ventura et al., 2015; Elst et al., 2016; Lamarque et al., 2013). Despite not consistently being adaptive (Davidson et al., 2011; Ghalambor et al., 2007; Lande, 2009), phenotypic plasticity can facilitate invasion by allowing the introduced organisms to adjust toward the new optimal phenotype in the first phases of invasion (Ghalambor et al., 2007; Lande, 2009). In fact, many authors propose plasticity as a possible driver of invasion success (Geng et al., 2016; Hahn et al., 2012; Liao et al., 2019). Although the term “plasticity” is typically used to describe morphophysiological characteristics, it also encompasses behavioral traits. In the context of biological invasions, this aspect is particularly significant for mammals (Chow et al., 2021; Gil-Fernández et al., 2020; Kowalczyk & Zalewski, 2011; Zalewski & Bartoszewicz, 2012, but see also Sol et al., 2002). An example of behavioral plasticity can be observed in the shelter preferences exhibited by invasive raccoon dogs (*Nyctereutes procyonoides*) in Poland (Kowalczyk & Zalewski, 2011). This species responds to predation risk and harsh climatic conditions by changing its preferential use of different shelter types during the year. In winter, raccoon dogs prefer burrows and hollow trees, as they offer less visibility from predators and thermoregulation advantages. However, during reproduction and pups-rearing season, they prefer hollow trees and dense vegetation, as burrows contemplate a major contact risk with the host, pups-predator, species (i.e., badger, Kowalczyk & Zalewski, 2011).

Phenotypic plasticity is a product of the evolutionary history of the species, and environmental fluctuations are known to facilitate its evolution (Ancel Meyers et al., 2005; Kristensen et al., 2020; Lee & Gelembiuk, 2008); it would thus be spontaneous to think of it as a common, equal feature of the introduced and the native-source populations, as it turned out to be for many alien species (Colomer-Ventura et al., 2015; Palacio-López & Gianoli, 2011). Nevertheless, it must be emphasized that plasticity can also increase after the colonization event as the result of the invasion process (Davidson et al., 2011; Liao et al., 2019; Mounger et al., 2021). An explanation for this apparent contradiction has been proposed by Lande (2009): Following a sudden environmental change, selection will shape individuals' phenotypes toward a new optimal state, and this can result in an increase in plasticity. Afterward, genetic assimilation of the new optimal phenotype will scale back the phenotypic plasticity by replacing it (Lande, 2009, 2015). A temporary increase in plasticity during the invasion has been observed, for example, in the fungal pathogen *Seiridium cardinale* (Garbelotto et al., 2015). A fluctuation in the behavioral plasticity pattern may also occur within a single generation through individual learning (Wright et al., 2010). The new environment will thus induce plastic (and sometimes adaptive) responses in the invaders through a series of mechanisms, such as epigenetic modifications, which we discuss later in this review. If plasticity evolves in the new environment to approach the new optimal phenotype, it should not be considered a pre-adapted trait.

2.2 | Anthropogenically induced adaptation to invade

Pre-adaptation can result from anthropization and human activities. Hufbauer et al. (2012) introduced the model of *anthropogenically induced adaptation to invade* (AIAI). According to the authors, human-altered habitats within the native range can make the (future) invader adapt to a set of characteristics typical of anthropogenically altered habitats, which the species could find again in the introduction range. Therefore, land use change, urban development, and agricultural intensification could also enhance the process of invasions through this scheme, as the presence of organisms in anthropogenic areas increases the likelihood of their transportation to new geographical regions, thereby increasing the probability of their settlement there. Therefore, the already-adapted invaders do not need to face a significant adaptive challenge to succeed in the anthropized introduction area. Once introduced, they can even expand and adapt to natural habitats (Hufbauer et al., 2012). The AIAI model probably fits the invasion of the gram-negative phytopathogen *Xylella fastidiosa* in Europe. This bacterium is native to America, where the introduction of coffee cultivation (i.e., anthropogenic disturbance) allowed it to infect coffee plants (Marcelletti & Scortichini, 2016). Subsequently, the trade of coffee plants transported the bacterium to European countries, where—presumably after being initially adapted to coffee plants—it turned to other host species, such as the olive tree *Olea europaea* (Marcelletti & Scortichini, 2016). The AIAI model could probably also describe the invasion of many marine, hull-fouling, alien species. In fact, harbors, marinas, and their artificial substrates can host many biofouling organisms, which can colonize boat hulls and be transported to other marinas around the world (Ferrario et al., 2017; Ulman et al., 2017). However, it is worth emphasizing that the AIAI scenario is not easy to document, as it requires demonstrating (i) the adaptation of a population to human-altered habitats within its native range, and evidence that (ii) the introduced population originates from the native human-altered habitat and (iii) such population is more adaptable compared with populations living in natural areas in the native range (Hufbauer et al., 2012).

2.3 | Resistance characteristics and life-history traits

Pre-adaptation can also result from the *innate characteristics of resistance* to environmental constrain or the invaders' *life-history traits*. These general “predictors of invasion success” are several and diverse, and they have been investigated across a wide range of organisms. These traits encompass factors related to the dimension of the invader's ecological niche (Díaz et al., 2023), such as heat (Bates et al., 2013) and salinity tolerance (Piscart et al., 2011), immune response (Møller & Cassey, 2004), germination speed (Schlaepfer et al., 2010), time until reproduction (Schlaepfer et al., 2010), fecundity and reproductive rate (Cardeccia et al., 2018; Epifanio, 2013;

Jenkins & Keller, 2011). A noteworthy example within this conceptual framework is the pre-adapted trait of tolerance to inbreeding depression, which has been observed in the invasive ant *Brachyponera chinensis*. Native populations of this species already exhibit a sib-mating behavior, which may have helped them to purge deleterious alleles over generations, thus predisposing this species to invade (Eyer et al., 2018).

2.4 | Exaptation

A further form of pre-adaptation could be the so-called “exaptation.” Exapted traits are features that did not originally evolve for their current role but were coopted afterward (Gould & Vrba, 1982). In the context of biological invasions, the evolution of traits that will assume a new adaptive function in the introduction range (i.e., exaptation) has been proposed (Hufbauer et al., 2012). However, despite being theoretically possible, this mechanism has to date no evidence. In addition, it would be challenging to demonstrate that a particular structure/gene plays two different roles in the native range and in the introduction one.

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

3 | ADAPTATION DURING TRANSPORT

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

3.1 | Genetic admixture during transport

During invasions (and, at least potentially, during both the captivity and cultivation phases), *genetic admixture* between genetically differentiated individuals of the same species can increase the genetic diversity of a potential invader (Rius & Darling, 2014). However, admixture and the resulting increase in genetic diversity do not always lead to higher fitness of the invaders or, in general, to an increased invasiveness of the introduced population (Chapple et al., 2013;

Irimia et al., 2021). This could have different explanations, including the presence of Dobzhansky–Muller incompatibilities (Dobzhansky, 1936; Muller, 1942). To understand such incompatibilities, consider two allopatric populations with identical genotypes at two loci (AABB). One population evolves the allele A', which over generations goes to fixation (A'A'BB); the other evolves the allele B', which goes to fixation as well (AAB'B'). Both populations are viable and fertile, but when they come into contact and mix, two alleles that do not share a common evolutionary history (A' and B') can become present in the same heterozygote genotypes (AA'B'B'), potentially leading to the production of non-viable or sterile individuals. Still, in some cases, genetic admixture between individuals with different genetic backgrounds has proved to be advantageous for invaders. This can happen because of increased levels of adaptive potential (Calfee et al., 2020; Facon, Crespin, et al., 2011; Rius & Darling, 2014; van Kleunen et al., 2015), or even because of a reduction of Allee effects when mating availability is limited (Mesgaran et al., 2016). The outcome of a crossing between different populations (whether positive, negative, or neutral) might vary even within a single species, as demonstrated with the invasive forb *Centaurea solstitialis* (Irimia et al., 2021), making the role of admixture in invasion biology very elusive. Nevertheless, it must be emphasized that current literature is primarily focused on demonstrating admixture between already-introduced organisms (as discussed in Section 4.2), overlooking its potential role in captivity/cultivation phases. Admixture can even occur between different species, usually congeneric (Ainouche et al., 2009; Kovach et al., 2015; but see also Haynes et al., 2012). This seems to be important in plants, where hybrids are usually invasive (Ainouche et al., 2009; Pandit et al., 2006). Albeit it might not always be clear whether hybridization occurred during the cultivation phase or in the new environment, some evidence suggests a possible role of cultivation in this regard. For example, the Oxford ragwort *Senecio squalidus* has a hybrid origin, resulting from a cross between *S. aethnensis* and *S. chrysanthemifolius*, two Italian species. *Senecio squalidus* is believed to have arisen through hybridization in the gardens of Badminton (UK), where both *S. aethnensis* and *S. chrysanthemifolius* were cultivated at the end of the 17th century. After escaping cultivation, the species then rapidly spread throughout the UK (Nevado et al., 2020). Despite other species (or populations of a species) might share similar evolutionary histories, demonstrating the occurrence of hybridization events giving rise to ecologically dominant invaders is rather challenging, as it would require at least a partial a priori knowledge of the invasion history of the species. Nevertheless, whether hybridization in captivity/cultivation might promote invasions should be properly assessed.

3.2 | Founder events and genetic bottlenecks

The collection, transport, and captivity/cultivation of organisms can also expose populations to *founder effects* and *genetic bottlenecks* that will shape their genetic pools. In fact, both domestic animals and cultivated plants often have a reduced genetic diversity due to

bottlenecks that occurred at the time of the founder's collection and genetic drift occurring during the initial period of domestication when the population sizes are typically small (Makino et al., 2018; Tamburino et al., 2020). These genetic bottlenecks may act as a brake for invader expansion, as they are well known to originate populations with reduced genetic variability, increased inbreeding depression, and subsequent reduced ability to adapt (Hoelzel, 1999; Thévenon & Couvet, 2002). However, despite being generally negative for populations, bottlenecks have occasionally proved to promote biological invasions. Genetic bottlenecks can, for example, lead to a decrease in intraspecific competition. An example of increased ability to invade is given by Tsutsui et al. (2000), who demonstrated that introduced populations of the invasive Argentine ant (*Linepithema humile*) in California showed less intraspecific aggression compared with native ones, and highlighted a negative correlation between genetic similarity and the levels of aggression between colonies, in both native and introduction areas. Thus, they suggested that a reduction of genetic diversity of the introduced populations, resulting from bottleneck events during introduction, led to a reduction of the intraspecific aggression among those populations. The decrease in intraspecific aggression leads to lower territoriality costs and thus allows the formation of increased colony size, making these colonies interspecifically dominant (Tsutsui et al., 2000). In fact, loss of intraspecific aggression is expected to allow a growth in colonies' size and the formation of super-colonies (i.e., colonies made up of several interconnected nests), thus enhancing ants' interspecific competitive ability (Suarez et al., 2008).

Moreover, inbreeding depression aroused by genetic bottlenecks can lead to purging of genetic load, in particular reducing highly recessive alleles (Facon, Hufbauer, et al., 2011; Glémin, 2003; Grossen et al., 2020; Wang, 2000). However, it is not always clear in which phase the purging of deleterious alleles can occur (Barringer et al., 2012), and in the context of biological invasions, to date, there is no evidence of a pre-introduction bottleneck leading to this purging process.

3.3 | Selection and physiological adaptive responses

Albeit the evolution of propagules during transport is commonly attributed to stochastic events (i.e., genetic bottlenecks), a recent review (Briski et al., 2018) emphasized the role that *selection* may play between the collection of organisms and their introduction elsewhere. The authors highlighted that specific selective pressures acting on transported individuals can promote the development of resistance traits. For example, the exposure of the traveling propagule to elevated temperatures, food scarcity or ultraviolet light, could lead to populations that are more prone to survive these stressors upon introduction (Briski et al., 2018). It is important to underlie that the different conditions experienced during transport can also influence the invasion success by enabling *physiological* (and/or epigenetic) *adaptive responses* in the organisms, rather than merely

genetic changes at the population level. For example, slow-moving vessels are often expected to let hull-fouling species gradually adapt to changing water temperature and salinity; these conditions of absence of sharp disturbance might also allow the formation of larger colonies (Campbell & Hewitt, 2011). In such scenarios, disentangling the role of physiological adaptations, genetic changes, and epigenetic changes is not easy, and it is highly likely that all these factors contribute to the development of resistance characteristics during the slow transportation process.

Hence, the transport process can be a key step for some biological invasions, as it might both sharply alter the genetic pool of the transferred organisms and make them physiologically adapted to succeed in the invasion process.

4 | ADAPTATION IN THE NEW HABITAT

In the new range introduced organisms can undergo adaptation, as the new environmental conditions can favor genetic and non-genetic modifications, and human actions (e.g., multiple introductions, habitat alteration, and climate change) can favor the process of adaptation itself (Fukasawa et al., 2013; Marin et al., 2020; Negi et al., 2016; Raitos et al., 2010; Rius & Darling, 2014). This dynamic interaction between invasive species and their changing environments can lead to the development of new traits that enhance their survival and competitiveness in the invaded ecosystem. An important aspect of adaptation in the new range is the recognition of time lags between the introduction of an organism and its spread. These lags often span over several years or decades, reflecting the time needed for adaptations to occur. The delayed response can be attributed to the time required for genetic assimilation of advantageous traits and for ecological adjustments to the new environment (Crooks, 2005; Sakai et al., 2001). Understanding these time lags is essential to develop timely and effective management strategies, before the invader becomes fully adapted and more difficult to control. For this reason, it is crucial to comprehend which mechanisms can favor the invaders in the new range.

4.1 | Epigenetics and transposable elements

In this phase of the invasion process, the role of *transposable element* (TE) activity and *epigenetic modifications* can be crucial. Both TE activity and epigenetic modifications are, in fact, known to be stimulated by novel or stressful environments, and these two mechanisms can act independently or together, since both are sensible to environmental changes. Moreover, epigenetic changes can alter TE mobility and expression, as to contrast the potentially deleterious consequences of TE activity; the genome has evolved many epigenetic mechanisms aimed at reducing their activity (Marin et al., 2020; Slotkin & Martienssen, 2007). Instead, TE activity may mediate epigenetic regulation as well (Negi et al., 2016). Thus, TE activity and epigenetic modifications may contribute to the success

of invasions by facilitating both adaptive evolution and phenotypic plasticity (Marin et al., 2020).

TEs are mobile-repeated DNA segments that can move in the genome and induce mutations, thereby altering gene regulation. Despite their possible negative consequences on individuals (as their increase is generally negatively correlated with the individual fitness), TEs can also produce new genetic and phenotypic variation on which selection can act (Negi et al., 2016; Slotkin & Martienssen, 2007). In fact, in native populations, TEs are expected to constitute a great but hidden variation, as their activity is well regulated by a complex epigenetic system (Marin et al., 2020; Slotkin & Martienssen, 2007). However, when organisms face a new environment and experience new stressors, this hidden genetic variation is released. This happens because stress can directly trigger TE activity and reduce TE epigenetic silencing mechanisms, indirectly triggering TE activity. The increase in TE activity is expected to add to the population new variability on which selection can act, thus favoring long-term adaptive responses (Lanciano & Mirouze, 2018; Negi et al., 2016; Slotkin & Martienssen, 2007). 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. (2020); however, to date, there is no evidence of a direct causal correlation between increase in TE 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 (Hawes et al., 2018; Marin et al., 2020; 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 (Gao et al., 2010; Mauch-Mani et al., 2017). 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 the 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 between epigenetic modifications and traits variation, it allows to explore how environmental cues shape methylation patterns (Marin et al., 2020). For example, in China, DNA differential methylation patterns are thought to be responsible for the invasion success of the plant *Chenopodium ambrosioides* in metal-contained

sites (Zhang et al., 2022). Another interesting example is given by Xie et al. (2015), who studied the cold adaptation of the invasive crofton weed (*Ageratina adenophora*) in China, where it has spread north-eastward from the original, tropical, sites of colonization. Testing cold resistance in plants from geographically different populations, they concluded that this species has spread north-eastward by differentiating into increasingly cold-tolerant populations. Since the plant responses to low temperatures are primarily controlled by the C-repeat binding factor pathway, they measured the methylation levels of a positive regulator of this pathway: the *ICE1* gene. The authors found a negative correlation between *ICE1* methylation and cold tolerance, indicating that the spread of the plant was probably facilitated by lowering the methylation levels that increased *ICE1* gene expression. However, it is worth emphasizing that the correlation between epigenetic variation and the occupied environment is not universal, as epigenetic markings do not always converge in populations occupying similar environments (Marin et al., 2020). Besides, the molecular mechanisms underlying epigenetically induced adaptation are still not clear, and further research investigating the effects of epigenetic changes on plasticity genes would be required to fulfill this knowledge gap (Mounger et al., 2021).

4.2 | Admixture in the new range

Albeit *genetic admixture* between genetically differentiated individuals of the same species can occur in cultivation/captivity phases (as explained in Section 3.1), its role in invasion biology has mainly been explored when it takes place between wild populations in the introduction range (Calfee et al., 2020; Chun et al., 2010; Kolbe et al., 2008; Rius & Darling, 2014), where it can give the invaders levels of diversity higher than the ones in the native populations. As previously explained, this process does not always increase the success of invaders (Chapple et al., 2013; Irimia et al., 2021). Nonetheless, a growing body of literature suggests a possible adaptive role of genetic admixture between genetically differentiated populations occurring in the new ranges (Calfee et al., 2020; Facon, Crespín, et al., 2011; Rius & Darling, 2014; van Kleunen et al., 2015).

Even in the wild introduction range, admixture can occur between the introduced species and a native counterpart (Ainouche et al., 2009; Kovach et al., 2015), or even with another established alien (Haynes et al., 2012). This process becomes particularly critical when it occurs between wild populations, as it can lead to rapid displacement of native species due to the spread of exotic genotypes (Huxel, 1999), posing a major risk in conservation biology. Similarly to admixture between populations of the same species, even hybridization is usually counter-selected (Kovach et al., 2015). However, in certain instances, this process might favor the invader (San Jose et al., 2023), probably because it provides alleles that are already adapted to the local environment.

One interesting example is provided by Wang et al. (2020), who suggested that post-establishment hybridization between two alien bigheaded carp species might have promoted the invasion success

of their hybrids. In particular, while intrinsic genomic features (likely associated with life-history traits and evolved in the native range) might have facilitated their initial establishment, the interspecific hybridization in the introduction range might have subsequently promoted their range expansion.

4.3 | Habitat and climate alterations in the new range

Lastly, in the introduction range, *human alteration of natural habitats* can often increase the likelihood of invasion, enhancing the fitness of invaders and reducing the native species' (Fukasawa et al., 2013). These human-induced alterations can encompass changes in both communities' composition and abiotic factors. Land use changes often influence the success of invaders by altering ecosystems, as shifts from natural to urban and agricultural areas can increase ecosystem vulnerability. Urban development and agricultural intensification, for example, fragment habitats and reduce native biodiversity, creating niches that invasive species can exploit, often outcompeting native counterparts (Ficetola et al., 2010; Sánchez-Ortiz et al., 2020; Vicente et al., 2011). For example, the prevalence of the alien squirrel *Sciurus carolinensis* over the native *S. griseus* in California has been attributed to the better adaptation of the former to fragmented hardwood forests (Jessen et al., 2018). Beyond localized habitat alterations, broader environmental changes such as climate change can also affect the potential success of alien species (Raitsos et al., 2010). Directly, changes in temperature and precipitation patterns might alter the stress tolerances of invaders, expanding their potential range or enhancing their competitive advantage over native species. For instance, while introductions of species from warm to temperate areas were previously constrained by the different thermal regimes, the current trend of rising temperatures can extend the growing seasons for plant invaders and the reproductive period for animals, enabling their spread and establishment in new territories (Walther et al., 2009). Indirectly, these climatic shifts can disrupt existing ecological interactions and community structures, changing community composition, and the availability of niches, thereby facilitating the establishment of alien species (Mainka & Howard, 2010; Occhipinti-Ambrogi, 2007).

5 | ADAPTATION ALONG THE INVASION PROCESS: INTERCONNECTIONS AND IMPLICATIONS

Mechanisms of adaptation during invasions are numerous and diverse, encompassing genetic, epigenetic, and ecological processes (Estoup et al., 2016). It is important to note that most of the mechanisms here discussed pertain to successful invaders' traits, rather than to community-level or ecosystem-level influences on the invasion outcome. Of course, this does not exclude the role of the environment in influencing the success of an invasion, which is prominent

both in the native range and after introduction (see Sections 2.2 and 4.3). Literature investigating adaptation during invasions has traditionally focused on finding mechanistic solutions to the genetic paradox of invasions (Estoup et al., 2016; Hawes et al., 2018; Marin et al., 2020; Stapley et al., 2015). However, there has been a general lack of interest in determining the timeframe during which adaptation is most likely to occur. An in-depth exploration of adaptation mechanisms during the invasion process reveals the crucial role of timing in shaping the invasion dynamics, and helps to develop effective management strategies. For example, identifying when adaptation mechanisms take place during the lag phases could enable timely interventions, which may not be feasible at later stages. In Figure 1, we provide an overview of the primary adaptation mechanisms that occur during invasions, categorized within the invasion framework proposed by Blackburn et al. (2011), with the addition of a native range stage (see Table S1 for the bibliographic references for each mechanism in each stage). However, it should be emphasized that these mechanisms, albeit typically treated as separated, are often interconnected and reliant processes, influencing each other through complex genetic, epigenetic, and ecological interactions occurring along the invasion process. For example, adaptations such as phenotypic plasticity and resistance traits can result from stress-induced epigenetic modifications (Hawes et al., 2018; Mounger et al., 2021), and this can happen in both the native and introduction ranges. Similarly, both TE activity and epigenetic modifications can mutually influence each other (Marin et al., 2020; Negi et al., 2016; Slotkin & Martienssen, 2007), regardless of the involved invasion stage.

While some mechanisms of adaptation cannot be avoided, as they arise from natural and innate instances of the species, others might involve, at least in part, human intervention.

Genetic admixture between genetically differentiated organisms (as well as hybridization) could theoretically occur in each stage of an invasion (Figure 1). While admixture between already-introduced organisms has often been investigated, literature exploring the role that the process may have before introduction, particularly during cultivation/captivity phases, is still scarce. Besides, some authors proposed that admixture could also occur within the native range (Gillis et al., 2009). We acknowledge that this could be the case of species introduced through hull-fouling or ballast waters. For example, the serpulid *Hydroides elegans* has a cosmopolitan distribution, showing a low genetic differentiation between populations worldwide. The constant genetic flow between populations of the species has been attributed to its biofouling nature, which allows it to be easily transported across the globe (Pettengill et al., 2007). In such cases, it is highly probable that admixture between individuals in the native range may occur even before introduction.

Understanding when admixture occurs along the invasion process can have significant management implications, as different stages of the process may require distinct approaches to control this phenomenon. For instance, in ongoing invasion processes where admixture between new individuals and established invaders can generate heterosis in the introduced population (e.g., Facon, Crespin, et al., 2011; van Kleunen et al., 2015), it is crucial for authorities to

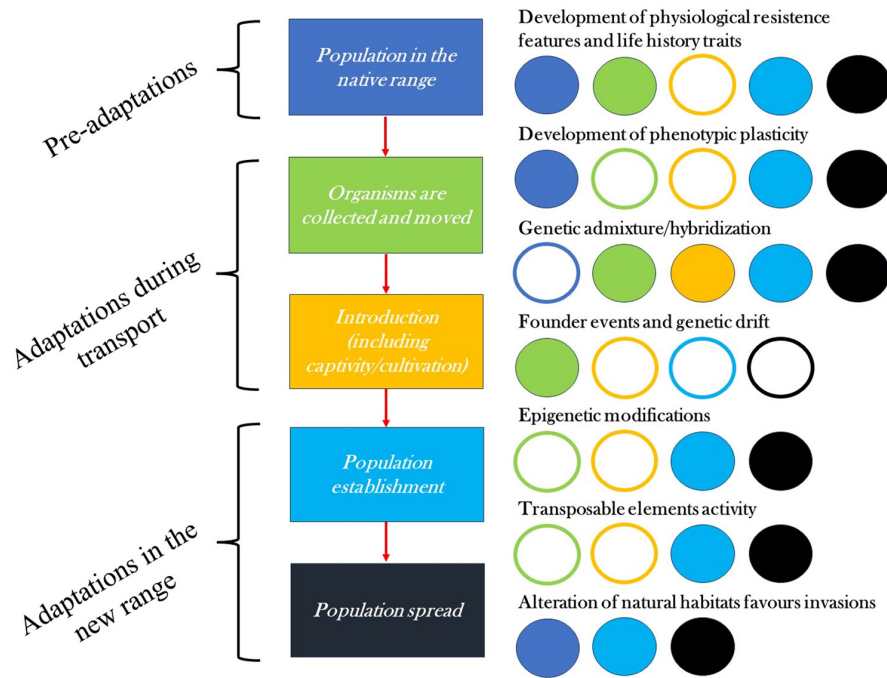


FIGURE 1 Invasion process is divided into the invasion stages proposed by Blackburn et al. (2011), with the addition of a native range stage. For each stage, circles on the right indicate the mechanisms of adaptation that may play a role in the invasion success. Full circles indicate relevant literature supporting the mechanism occurrence whereas empty circles indicate scarce or absent literature. Examples are provided within the text and in Table S1 where available.

focus on preventing or managing introductions of individuals from additional native-source populations.

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

As for epigenetics, while it is theoretically possible that epigenetic changes arising in the native range may facilitate a future invasion (due to their responsive and reversible nature), their importance primarily stems from their ability to provide rapid adaptive responses to the changing environmental conditions (Hawes et al., 2018). Since their formation is elicited by the new environmental stress (Hawes et al., 2018; Marin et al., 2020), it is most likely to take place between stage 1 and stage 5 (Figure 1). However, the available literature is mainly focused on investigating epigenetic changes that occur in the new range (Hawes et al., 2018), and to the best of our knowledge, there are no studies that have analyzed changing epigenetic patterns before organisms are already introduced. Similarly, even TE activity is induced by environmental stress, and changing frequencies of insertions are usually attributed to the novel environmental conditions of the new range (Marin et al., 2020).

Regarding both epigenetic and TE insertion changes, once organisms are picked up, prevention is no longer possible. To avoid the development of these adaptation mechanisms in invaders, the only

possible approach is to prevent the collection and transport of organisms to other locations.

Alteration of natural habitats, both in the native and the introduction range, can favor invasions. In the native range, this process can lead to the AIAI (Hufbauer et al., 2012; see Section 2.2), while in the invaded range it can favor the spread of alien opportunistic species (Jessen et al., 2018).

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

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

Similar planning and administrative implications have the potential to prevent the establishment of invaders in various other types

of infrastructures (e.g., parks, seaports, and railways). Therefore, research efforts should aim to uncover and understand these critical management aspects.

6 | CONCLUSION

Here, we established a coherent sequence in which adaptation of alien species can occur in the different stages of the invasion process. By structuring these stages logically, we provide valuable insights into effective management strategies and highlight the importance of research efforts that incorporate temporal considerations into the study of biological invasions. We believe that this neglected aspect of invasions deserves thorough consideration, as it could carry significant implications for the management of alien invaders. Neglecting the temporal aspects could, indeed, hinder a comprehensive understanding of invasion dynamics: for example, in the new range, studies on invaders' adaptation usually compare populations in the introduction range with counterparts in the native range, without providing information about the exact stage(s) in which adaptation occurred. This makes the role of timing in invasions very elusive, particularly when trying to differentiate adaptations between the establishment and the subsequent phases. The study of explanations underlying the genetic paradox (Estoup et al., 2016) may be pointless without also considering the temporal scale at which adaptation takes place. Instead, when studying adaptation of invaders, focusing only on a few phases of the invasion process could lead to an underestimation of the actual invasion risk. Therefore, we propose that future research should delve into this overlooked aspect of invasion biology, trying not only to elucidate potential solutions to the genetic paradox, but also to discern the phases of the invasion process in which adaptation occurs. Related studies considering adaptation mechanisms in the same taxa across different invasion stages could allow to discern the relative importance of each stage in the invasion outcome. This comprehensive approach will allow a deeper understanding of invasive species' population dynamics, and enhance our ability to address the challenges they pose, contributing to a more effective management.

AUTHOR CONTRIBUTIONS

Alessandro Nota: Conceptualization; investigation; project administration; visualization; writing – original draft. **Sandro Bertolino:** Investigation; validation; writing – review and editing. **Francesco Tiralongo:** Validation; writing – review and editing. **Alfredo Santovito:** Conceptualization; writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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How to cite this article: Nota, A., Bertolino, S., Tiralongo, F., & Santovito, A. (2024). Adaptation to bioinvasions: When does it occur? *Global Change Biology*, 30, e17362. <https://doi.org/10.1111/gcb.17362>