Evolution and Invasive Species

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Key Points

- Invasive species threaten ecosystems and human communities globally.
- Propagule pressure is strongly related to invasion success and influences genetic diversity during founder events.
- Invasive species can undergo rapid evolution, and traits related to survival, reproduction, and dispersal under novel conditions are under selection throughout the invasion process.
- Invasive species can drive rapid evolution in native populations, through direct interactions (e.g. predation, novel prey availability, competition) and indirect interactions (e.g. changes in abiotic conditions or community structure).
- Invasions will continue to be a global threat, and current management practices are not curbing ever-increasing invasion rates.
- Evolutionary perspectives can contribute to invasion control and ecological theory developed from the study of invasions.

Glossary

Admixture combination of individuals from previously separated source populations.
Biotic homogenization increasing genetic and taxonomic similarity between regions across the globe which is promoted by species invasions.
Continuous trait a characteristic expressed as a continuum of phenotypes, such as body size, which may be controlled by many genes.
Discrete trait a characteristic expressed as distinct phenotypes, such as blood type, which is typically controlled by few genes.
Ecosystem services material and non-material goods and other needs provided by ecosystems to humans, including food and medicine (provisioning services), nutrient cycling (supporting services), erosion control (regulating services), and esthetic inspiration and cultural identity (cultural services).
Founder event establishment of a new population by few introduced individuals and, therefore, low genetic diversity.
Invasion vector mechanism of human transport of non-native species from their native, source region to a non-native, recipient region.
Invasive species non-native species that have been introduced by humans and have established and spread in their introduced range.
Population bottleneck large reduction in population size and associated decrease in genetic diversity.
Propagule pressure the total number of introduced individuals, which is a function of number of introduction events and number of individuals released during each event.

Abstract

Invasive species threaten global biodiversity and human livelihoods. Understanding invasions will aid in their management while providing insights into ecological and evolutionary processes. Many invasive species lack an evolutionary history with species native to the invaded region, and novel selection pressures can drive rapid evolution during invasions. This article reviews the evolutionary characteristics of species that successfully invade new regions and the evolutionary impacts of this spread on both the invasive species themselves and native species in invaded communities. The number of invasions is rapidly increasing worldwide at the same time as novel genetic and genomic approaches are being developed, creating both a need and the tools to address the invasion problem.

Introduction

The study of species invasions is important both from the perspective of biodiversity conservation and because it provides general insights into ecology and evolution (Sax et al., 2005, 2007). One of the key characteristics of invasive species is that their evolutionary history with species in the invaded region is relatively short (Strauss et al., 2006a,b). To understand the role of evolution in species invasions and the ecological and management implications, it is first important to define invasive species, the steps species must undergo to become invasive, and the scope of the invasive species problem.

Background

Defining Invasive Species

Invasive species are typically defined as non-native species that have been introduced by humans and have established and spread in their introduced range (Colautti and MacIsaac, 2004). These last two characteristics—establishment and spread in the introduced range—imply impacts on native communities, as impacts are proportional to invader abundance (Bradley et al., 2019). However, impacts have been quantified for only a small proportion (Crystal-Ornelas and Lockwood, 2020) of introduced species (Roy et al., 2023; Turbelin et al., 2017; also see e.g., Williams and Smith, 2007). In some cases, when the term invasive is used more generally to describe any species that proliferates quickly and causes negative impacts, then a subset of native species could also fit this definition (Sorte et al., 2010a; Vigueira et al., 2013). This article focuses on non-native invasive species; however, some evolutionary concepts related to invasive species will also apply to native pests.

The Invasion Pathway

Species invasions occur via a step-wise process known as the invasion pathway (**Fig. 1**; see also Colautti and MacIsaac, 2004; Theoharides and Dukes, 2007). First, individuals of a species are transported by humans from the source region in their native range to the recipient region in their non-native range via an introduction vector. This transport can be either intentional (e.g., plants sold in the horticultural trade; Mack and Lonsdale, 2001) or unintentional (e.g., hitchhikers in commercial shipping vessels; Westphal et al., 2008). Second, the species is introduced if transported individuals are able to survive and reproduce in the non-native range. Third, the introduced species is considered established if it has formed a reproducing and self-sustaining population. The final step in the invasion pathway is secondary spread, in which the species extends its range beyond the original introduction site within the non-native region and becomes “invasive.”

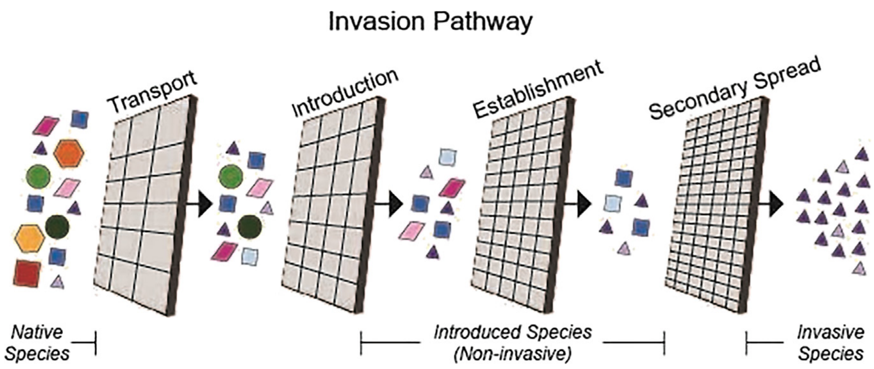

Fig. 1 In order to become invasive, native species (different shapes) must pass through four stages. Each stage acts as a filter to decrease the native species pool as well as genetic diversity (indicated by shading in the shapes) within each species. Species that are introduced but fail to undergo secondary spread in the introduced range are not considered invasive.

Whether or not a species is successful in becoming invasive depends upon its ability to pass through filters imposed by the different stages of the invasion pathway (**Fig. 1**). For example, before even arriving in their new territory, future invasive species must find—or be chosen for—transport and survive the journey. Once in the new habitat, invasion success depends on the ability to tolerate climatic conditions, attain resources, and avoid consumption in the non-native range under a novel set of abiotic and biotic conditions. The potential invasive species pool becomes sequentially narrower through the invasion pathway, leading only the minority of introduced species to become invasive (Jeschke and Strayer, 2005).

Scope of the Invasion Problem

Despite the fact that most species do not become invasive, those that do can have extremely large ecological impacts and economic costs (Pimentel et al., 2005), and the invasion problem is increasing (Butchart et al., 2010) concurrent with globalization. Documented numbers of invasive species across 21 countries have risen by about 70% since 1970 (Díaz et al., 2019) and rates of introductions and establishment are not expected to slow down in the near future (Pyšek et al., 2020; Seebens et al., 2017). These rates are in part attributed to increased global trade as well as ineffective management and policies for slowing down invasive species accumulation (Seebens et al., 2017). In 2023, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services reported 37,000 established invasive species globally (**Fig. 2**), with 3500 of these already documented as having negative impacts (Roy et al., 2023). The cost of management of—and damages by—invasive species has quadrupled every decade since 1970 and was estimated to exceed $423 billion in 2019 globally (Roy et al., 2023). Even a relatively small-scale introduction of the killer alga, *Caulerpa taxifolia*, one of the world's "100 worst" invasive species, near San Diego, California, USA, cost > $6 million for local eradication (Williams and Grosholz, 2008).

In ecological terms, invasive species have driven declines in native populations and community diversity metrics (evenness, diversity, richness) (Bradley et al., 2019). The impact of each invasive species is expected to increase directly with range size,

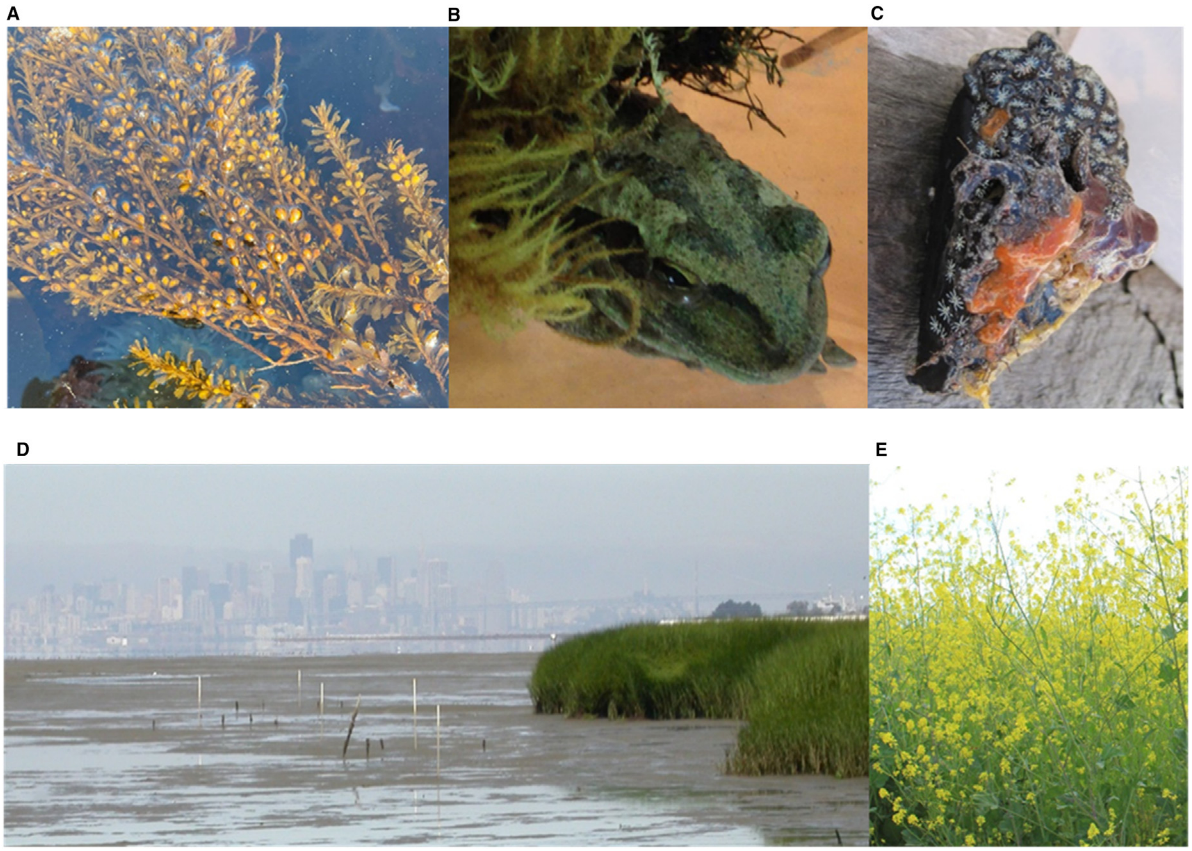

Fig. 2 Invasive species are a global issue, leading to economic, ecological, and evolutionary impacts on native ecosystems. Examples of invasive species include the (A) seaweed *Sargassum muticum*, native to the Western Pacific and broadly invasive in the Eastern Pacific and Atlantic; (B) Cuban tree frog, invasive in the USA (Florida and Hawaii) and throughout the Caribbean; (C) suite of invasive sea squirts that are now found in coastal waters worldwide and foul docks, boats, and shellfish; (D) cordgrass *Spartina alterniflora* which has hybridized with a native species, *Spartina foliosa*, and is shown here invading San Francisco Bay, California, USA; and (E) black mustard that was brought to the USA from Eurasia more than 200 years ago.

population size, and per capita effect (Parker et al., 1999). Although extinction causes are often unknown and occasionally disputed, invasive species are implicated as a leading cause of plant and animal (particularly bird and mammal) extinctions (Bellard et al., 2016a; Blackburn et al., 2019). In fact, invasive species are considered one of the primary threats to global biodiversity across terrestrial and aquatic ecosystems (Millennium Ecosystem Assessment, 2005; Sala et al., 2000) and, more specifically, to an estimated 14%−33% of vertebrate species on critically endangered species lists (Bellard et al., 2016b; Dueñas et al., 2021). Extinctions are particularly likely on islands, which have higher established invasive species richness compared to mainland regions (Dawson et al., 2017), because there is limited opportunity for native species to avoid invasive predators via adaptation (Mooney and Cleland, 2001; Pyšek et al., 2020). For example, the invasive brown tree snake appears to have driven extinctions of native birds on the island of Guam, in the tropical western Pacific Ocean (Savidge, 1987). The invasion problem is becoming exacerbated as introductions are increasing in many regions, particularly those with high human population densities (Millennium Ecosystem Assessment, 2005; Pyšek et al., 2020; Seebens et al., 2017), and leading to rapid biotic homogenization (see Olden et al., 2004; Roy et al., 2023). Contrary to previous assumptions, invasive species can persist in areas with little to no anthropogenic disturbance, including isolated and well-managed protected areas (Alexander et al., 2016; Pyšek et al., 2020; Ren et al., 2021; Rose and Hermanutz, 2004).

Invasive species also threaten human-wellness and impact the cultural services ecosystems provide. These threats include spread of infections and diseases by invasive pathogens (Pyšek et al., 2020), disruption of traditional and social relationships (Pyšek et al., 2020), and loss of access to species used for medicinal, food, and ceremonial purposes (Garibaldi and Turner, 2004; Schelhas et al., 2021). For example, rapid proliferation of an invasive water hyacinth in Lake Victoria (Eastern Africa) made fishing grounds inaccessible, hindering access to quality food and income for local communities (Mujingi Epse Cho, 2012). In the lands of the Kashaya Pomo people (California, USA), the sudden deaths of tanoak trees due to an invasive pathogen disturbed the continuation of acorn-harvesting, ceremonies, and cultural traditions (Schelhas et al., 2021). Indigenous communities have indicated that invasive species and climate change are primary threats to tribal natural resources (Schelhas et al., 2021). Clearly, invasive species pose a global threat to biodiversity, ecosystems, and human livelihoods (Roy et al., 2023).

Evolutionary Characteristics of Invasive Species

Introduced species can be prone to founder events and population bottlenecks imposed by filters in the invasion pathway, leading to declines in genetic diversity within non-native populations as compared to their native, source populations. In a review of 80 species of animals, plants, and fungi, diversity of alleles and heterozygosity were significantly lower in introduced populations than in source populations, although decreases were less than 20% (Dlugosch and Parker, 2008; also see Wares et al., 2005). Furthermore, Dlugosch and Parker (2008) found a U-shaped relationship between genetic (allelic) diversity and time since first introduction, suggesting that selection and genetic drift continue the loss of genetic diversity during the first several decades after introduction. Over longer time scales, multiple introductions and evolutionary processes can cause genetic diversity to rise again via the mechanisms discussed below. Thus, it is perhaps not surprising that a lag phase often occurs between the introduction and spread stages in the invasion pathway (see Crooks, 2005), in which population growth and subsequent spread are inhibited either by low population sizes and/or low genetic variation within the populations.

Propagule pressure—or the total number of introduced individuals—is one of the best supported correlates of invasion success (Cassey et al., 2018; Colautti et al., 2006; i.e. Kolar and Lodge, 2001; Lockwood et al., 2005; Vedder et al., 2021) and can counteract the effect of founder events on genetic diversity within introduced populations (Roman and Darling, 2007). Simberloff (2009) reviewed examples—from birds to ungulates to plants—of cases where introductions failed until the number of introduced individuals exceeded a minimum threshold. Increased propagule pressure is associated with increased population sizes and higher genetic diversity within populations (Simberloff, 2009). Furthermore, multiple introductions may lead to the formation of admixtures, new populations composed of individuals from previously separated source populations. Such introduced admixture populations can have equivalent (Dlugosch and Parker, 2008) or even increased levels of genetic diversity as compared to individual source populations (Gillis et al., 2009; Kolbe et al., 2004). For example, brown anole lizards in Florida, USA have greater genetic diversity than native Cuban populations because there were 8 different introduction events in Florida and subsequent genetic mixing (Kolbe et al., 2004).

In addition to the invasion process influencing genetic diversity, there is some evidence that genetic diversity also influences invasion success. For example, genetic diversity has been linked to the ability of the plant *Arabidopsis thaliana* to successfully establish (Crawford and Whitney, 2010) as well as to productivity and clonal spread in a perennial grass (Lavergne and Molofsky, 2007). It is important to note, however, that there are a number of counter-examples to the trends presented above. Successful invasions of a broad range of species—including a European solitary bee to North America and the North American muskrat to Europe—are thought to have derived from only one to a few introduced individuals and, thus, low initial population genetic diversity (see Simberloff, 2009). There are also examples where invasion success was associated with decreases rather than increases in genetic diversity (e.g., Schmid-Hempel et al., 2007), particularly when loss of genetic variation increased the frequency of a genotype that proved to be beneficial, leading to increase population sizes in the non-native habitat (e.g., Tsutsui et al., 2000).

Evolution of Invasive Species

Adaptive evolution in invasive species was historically expected to be limited by genetic bottlenecks, though it is now recognized that rapid adaptation is frequent among invasive species, and several mechanisms exist through which invasive populations can recover genetic diversity. More specifically, founding populations, typically composed of only a few individuals, were thought to be constrained by low genetic diversity and therefore likely struggle to adapt to novel conditions (Dlugosch and Parker, 2008; Sakai et al., 2001). However, invasive populations are capable of rapidly adapting to novel conditions (Colautti and Lau, 2016; Montesinos, 2022; van Boheemen et al., 2019), frequently within 50−150 generations and sometimes in less than 25 generations (Moran and Alexander, 2014). This is possible because "true" genetic bottlenecks (i.e., bottlenecks that would impact selectable genetic variation) are not as frequent or severe as initially expected (Dlugosch et al., 2015; Estoup et al., 2016). It appears that founder events disproportionately reduce the prevalence of either rare alleles or alleles controlling discrete traits, while the loss of variation in continuous traits is expected to be minimal (Dlugosch et al., 2015; Estoup et al., 2016). Second, as discussed above, the creation of admixtures from different source pools within the species' native range (Dlugosch and Parker, 2008; Dlugosch et al., 2015) leads to novel allele combinations or reintroduction of lost alleles. Finally, hybridization may promote invader success, either through the introduction of beneficial alleles, the masking of deleterious alleles, or the creation of novel phenotypes via recombination in the invasive population (Mesgaran et al., 2016; Moran and Alexander, 2014; Mounger et al., 2021). Hybridization writ large is what happens in admixtures within a species, through the arrival of individuals from multiple native source pools (van Kleunen et al., 2015), and also occurs between species, including between native and non-native species (Calfee et al., 2020; Grosholz, 2002; Mesgaran et al., 2016). For example, hybrids of the introduced cordgrass *Spartina alterniflora* and native species *Spartina foliosa* grow larger and are more invasive than either of the parent species in San Francisco Bay, California, USA (Grosholz, 2002, **Fig. 2**). Interestingly, there is also some evidence of synergistic interactions between invasions and hybridization, where novel selective pressures in species' invaded ranges increase the potential for hybridization (Bock et al., 2021), which could in turn facilitate further invasion.

Adaptive evolution is promoted in invasive species as they experience strong selection pressures at each stage in the invasion pathway (Bock et al., 2016; Hodgins et al., 2018). Initial transport might favor individuals that associate with and survive human transport (Horvitz et al., 2017; Medley et al., 2015) and species that are pre-adapted to the environmental conditions they experience at the point of introduction are more likely to persist and seed a new population (Liu et al., 2020; Petitpierre et al., 2012; but see Atwater et al., 2018). After introduction, high reproductive capacity may contribute to a species' ability to successfully establish (Bock et al., 2016; Hodgins et al., 2018). Finally, greater secondary spread has been associated with the ability of a species to rapidly adapt to novel environmental conditions at the edges of the invasion front (Colautti and Barrett, 2013; Oduor et al., 2016; Stuart et al., 2021; Tepolt, 2015) and their innate dispersal ability (Hodgins et al., 2018; Phillips et al., 2006). For example, cane toads with longer legs and behavioral predispositions to disperse further and in straighter lines are the first to arrive at and establish new populations in Australia (Phillips et al., 2006; Rollins et al., 2016). Due to serial interbreeding between the best-dispersing toads, these dispersal traits have become "spatially sorted" toward the invasion front, producing faster and faster offspring each generation (Rollins et al., 2016; Shine et al., 2011). As different traits are exposed to adaptive selection throughout the invasion process, it is likely that the simultaneous evolution of multiple traits is a key factor in determining invasion success and invaders' rates of spread (Alex Perkins et al., 2013).

Successful invaders are also typically capable of adapting to novel biotic pressures. In some cases, novel biotic interactions may select for increased predator defense when invasive prey species encounter novel predators (Miehls et al., 2014). On the other hand, some invasive species experience relaxed selection in the non-native habitat due, for example, to release from their native enemies or competitors (the enemy release hypothesis [ERH]; Keane and Crawley, 2002) or encounters with naïve prey (Sharpe et al., 2021). The evolution of increased competitive ability (EICA) hypothesis describes how this relaxation could allow a reallocation of resources from defense to competitive traits (Blossey and Nötzold, 1995). For example, Rotter et al. (2019) grew seeds from populations of native and invasive monkeyflowers and found that plants from invasive populations tended to be less resistant to herbivory but also grew taller and produced more flowers than native populations, indicating that a trade-off between herbivore resistance and competition traits influenced evolution. The EICA hypothesis is not, however, supported in all cases (see Felker-Quinn et al., 2013; Rotter and Holeski, 2018).

Although there are an increasing number of observations consistent with trait adaptation, it is important to note that non-genetic plasticity also contributes greatly to phenotypic variation in invasive species. There is some evidence, indicated by an analysis of 75 plant species pairs (Davidson et al., 2011), that invasive species have higher levels of phenotypic plasticity than non-invasive species, which could increase invasion success or invader dominance (Hiatt and Flory, 2020). Phenotypic plasticity is modulated by epigenetic mechanisms, which affect gene regulation but not the underlying genetic code. Of the many epigenetic mechanisms, DNA methylation is one of the best-studied in invasive species, and there is increasing evidence that it may facilitate invasion (Hawes et al., 2018 and references therein). For example, Pu and Zhan (2017) examined native and invasive populations of a marine sea squirt and found different levels of DNA methylation were correlated with differences in habitat temperature and water salinity. Critically, epigenetic mechanisms can allow individuals to respond to environmental cues even when genetic variation is low (Schrey et al., 2012; Sherman et al., 2016 and references therein), and can, thus, allow founding populations to acclimate to their recipient regions. Finally, because epigenetic modifications can themselves be selectable and heritable (Becker and Weigel, 2012; Hawes et al., 2018; Mounger et al., 2021), they may also provide an important mechanism for invasive species, particularly clonal species (Mounger et al., 2021), to adapt to novel conditions throughout the invasion process.

Finally, divergence in species' phenotypes between their native and invasive ranges may also be driven by non-selective mechanisms related to the genetic characteristics of invasive species. Genetic drift is likely in small populations, such as founder populations of invasive species or populations at the edges of an invasion front (Bélouard et al., 2019; Sakai et al., 2001). Low genetic diversity may indicate the influence of genetic drift, the random change in allele frequencies that more strongly impacts smaller populations (Bélouard et al., 2019). Areas of low genetic diversity along the invasion front can also experience "allele surfing", where alleles that are beneficial, neutral, or even deleterious strongly increase in frequency due to genetic drift (Excoffier et al., 2009; Peischl et al., 2015). Critically, these processes act independent of natural selection, and the resulting phenotypic changes may not increase fitness (e.g., Pereira et al., 2018; Colautti and Lau, 2016). Clearly, population-level differences in the characteristics of invasive species across their non-native ranges could reflect influences of myriad processes, including natural selection, hybridization, gene flow, genetic drift, and phenotypic plasticity.

Invasive Species as Drivers of Native Species Evolution

Observations across time (before and after invasion) and space (within versus outside the invaded ranges) have uncovered evidence of invasive species evolutionary impacts on native species, resulting in rapid evolution in native populations (Carroll, 2007; Lambrinos, 2004; Le Roux, 2022; Mooney and Cleland, 2001; Strauss et al., 2006b; Vellend et al., 2007). In cases where native species are able to adapt to the invasive species, the natives are less likely to be extirpated by, for example, being outcompeted. The capacity for native species to adapt in response to invasive species is dependent on factors such as their genetic diversity, population sizes, and existing adaptations (Berthon, 2015; Leger and Espeland, 2010). High genetic diversity and large population sizes increase the likelihood of heritable variation in traits that would promote enhanced competitive ability or coexistence with invasives (Hedrick, 2005; Strauss et al., 2006b). Importantly, the eco-evolutionary history of the native and invasive species influences the strength of selection, whereby a native species is likely to be able to effectively adapt when interacting with an invasive species that is similar to those that it has encountered previously in its native range (Carroll, 2011; Le Roux, 2022; Saul et al., 2013; Saul and Jeschke, 2015). Native species that have the capacity to evolve may then persist under the range of selective pressures imposed by invasive species.

Through a range of direct ecological interactions, invasive species can impose selective pressures on native species that lead to rapid evolution. Invasive species may act as novel predators to native species, requiring native species to develop anti-predator avoidance mechanisms. For example, in just 3−6 generations, the Italian agile frog exhibited shortened development time as tadpoles to avoid American red swamp crayfish predation (Melotto et al., 2020). Interestingly, the evolution of a shorter tadpole stage ran counter to selection by climatic conditions, which favored a longer tadpole stage, highlighting the relatively strong selection pressure imposed by invasive species and the subsequent disruption to local adaptations (Cenzer, 2016; Thawley et al., 2019). Second, invasive species can provide novel prey to native species, in which native species may adapt to utilize this novel resource. A native checkerspot butterfly in Nevada, USA incorporated the invasive European weed *Plantago lanceolata* into its diet, and breeding studies indicated a genetic basis to the butterfly's feeding preference (Singer et al., 1993). In some cases, utilizing novel resources requires further adaptation, and a native Australian soapberry bug has evolved longer mouthparts in order to feed on an invasive vine (Carroll et al., 2005). On the other hand, native species may evolve to avoid unfavorable novel introduced prey. As an example, Phillips and Shine (2006) suggested that native black snakes in Australia have evolved increased resistance to cane toad toxin and decreased prey preference for the toads after less than 23 generations. Similarly, the endangered carnivorous marsupial, the northern quoll, has evolved to avoid cane toads as prey, a behavior that was shown to be both heritable and learned (Kelly and Phillips, 2019). Third, invasive species can drive adaptation of native species via facilitation, such as when a novel invasive species acts as a mutualistic partner (Kiers et al., 2010). Traveset et al. (2019) found that the introduction of pine martens (a mammal) led to an increase in seed size of the Mediterranean shrub (*Cneorum tricoccon*), increasing seed dispersal (yet also disrupting native lizard mutualists which selectively consume smaller seeds).

Given that invasive species are similarly able to adapt in response to native species, this may lead to coevolution, whereby adaptation in one species leads to subsequent adaptation in the other interacting species (Leger and Espeland, 2010; Thompson, 1994). For example, Lankau (2012) found that invasive garlic mustard rapidly evolved enhanced production of an allelochemical within native dominated communities, leading to increased tolerance in a native clearweed when sourced from areas with high levels of invasion. Lastly, hybridization between invasive and native species appears to be widespread across various taxa such as fish (Kovach et al., 2015), birds (Stephens et al., 2020), plants (Grosholz, 2002), insects (Havill et al., 2012), and reptiles (Bock et al., 2021; Mooney and Cleland, 2001). Invasive species can even promote hybridization between two native species by providing a novel resource, leading to novel niche overlap between native species that would otherwise not meet nor reproduce (Schwarz et al., 2005).

Invasive species can also drive native species evolution via indirect mechanisms. Through their establishment, invasive species may disrupt abiotic conditions or the native community, shifting the local conditions. An example is seen in responses of an herbivorous zooplankton (*Daphnia*) to the invasion of predatory water fleas in lakes in Wisconsin, USA: instead of decreasing in size, as would be expected to allow them to avoid the new predators, *Daphnia* exhibited a 40% increase in body size due to higher phytoplankton availability from increased top-down control (Gillis and Walsh, 2017). In another example, invasive species that provide an ecological service (see the pine marten example above) can displace native mutualists, which may change the evolutionary trajectory of both native species originally involved in the mutualism. Furthermore, the ability of native species to adapt in the face of invasive species (whether as novel prey or predators) may be dependent on context, including the multi-trophic community they are embedded within (Bezemer et al., 2014; Harvey et al., 2010; Stireman and Singer, 2018). In one tri-trophic system, top-down control by an invasive parasitoid wasp and bottom-up control by an invasive garlic mustard led to a decline in a native North America butterfly. However, following a release in top-down control by the parasitoid, in the subsequent enemy-free space the native butterfly physiologically adapted, attaining the ability to utilize the invasive garlic mustard as a host plant (Keeler and Chew, 2008; Morton et al., 2015; van Driesche, 2008). Despite evidence that invasive species drive evolution of native species via indirect and multi-trophic dynamics, many studies focus only on direct, pairwise interactions. Expanding studies to consider a suite of interacting species is crucial for understanding both how native species are evolving in response to invasive species and for predicting and managing the impacts of invasive species.

Implications for the Future: Applying an Evolutionary Perspective to Invasive Species Management

Invasive species are contributing to the homogenization of both species and genetic material on a global scale, including driving extinctions of native species and diversification of invasive species in their introduced ranges. Invasions are an ecological, economic, and evolutionary threat of our own making. For example, trends in societal popularity and economic value can dictate future propagule pressure as we intentionally import species from other areas (Lockwood et al., 2019). However, even as we facilitate invasions for our gain or by accident, we now spend billions of dollars on their prevention and management. In doing so, we are driving adaptation of characteristics that allow invasive species to avoid control and persist in their invaded range (Lee, 2002), including mimicry of the crops they invade and resistance to herbicides and pesticides (Vigueira et al., 2013). Even with successful extirpation through management practices, an invasive species can still fundamentally alter native ecosystems and obstruct functioning, leaving lasting "legacy effects" that persist into the future (Corbin and D'Antonio, 2012). With some invasive species exhibiting permanence in invaded ecosystems, we are also increasing tension and human conflict over their management, as humans can adjust to invasive species' presence economically, aesthetically, and culturally (Howard, 2019; Pejchar and Mooney, 2009) and oppose the cost and justification of their removal (Crowley et al., 2017). For example, game fish, such as salmonids in the western USA, have been known to disrupt native ecosystems (Knapp et al., 2001), but their reduction is often controversial as they provide economic and recreational benefits to society (Rahel, 2000). Furthermore, we are indirectly contributing to the shifting of native species' ranges through our role in driving global climate change, which likely favors native species with characteristics of invasive species (Sorte et al., 2010b, 2013). Current management practices and biosecurity policies are insufficient in curbing current invasion rates (Pyšek et al., 2020; Seebens et al., 2017).

Future attempts to prevent, control, and eradicate invasive species could benefit from the incorporation of an evolutionary perspective (Whitney and Gabler, 2008). Although protocols are increasingly being implemented to prevent unintentional introductions of non-native species, intentional imports continue, including through the horticultural and pet trades (Bradley et al., 2012; Lockwood et al., 2019). Importation suitability should be informed by Weed Risk Assessments, which, in a version developed by the Australian government, includes population biology characteristics such as hybridization potential and reproductive strategies (Roberts et al., 2011). Many invasive species start out as seemingly innocuous species introductions, and eradication efforts would ideally start during the establishment and lag phases. As an evolutionary method of detection and surveillance of invasive species, genetic diversity has been successful in tracking invasive spread (Chown et al., 2015). Comparably, maintaining genetic diversity of native species' populations, such as managed targeted gene flow, has the potential to combat local species loss within the expanding ranges of invasive species (Kelly and Phillips, 2019). Efforts to prioritize non-native species for control and eradication could be aided by an understanding of population genetics and ecological interactions in order to identify species that are likely to become invasive, causing ecological and evolutionary damage (i.e., hybridization, extinctions, etc.), and evolve resistance to control methods (Allendorf and Lundquist, 2003).

Understanding what makes locations vulnerable to invaders and supporting conditions for rapid adaptation will benefit invasion control and management. For example, disturbed areas, like human-made reservoirs, can harbor invasive species and promote invasion by providing access to uninvaded watersheds and establishing a steady source of propagule pressure (Johnson et al., 2008; Havel et al., 2015) and increasing rapid evolution via habitat alterations (Früh et al., 2012). In such habitats, invasive species with the ability to withstand disturbance and novel conditions are more successful and likely to persist than sensitive native species (Bates et al., 2013). Cities are particularly susceptible to human-mediated species introduction and offer ecological opportunities of novel habitats, resources, and conditions that potentially benefit invaders and their traits associated with establishment, dispersal, and competitive ability (Borden and Flory, 2021). Urban areas also have environmental conditions that are increasingly novel under global climate change, such as higher temperatures than rural areas nearby (Lahr et al., 2018); thus, species adapted to regions with higher human populations have the evolutionary potential to better cope and spread under future climate conditions (Borden and Flory, 2021). Understanding rapid evolution in cities and urban-evolved traits could be beneficial for those working to reduce invasion under expanding urbanization. Moreover, issues of invasive species developing evolved resistance should be carefully considered, with control practices incorporating fluctuation of multiple herbicides, pesticides, and/or biological control agents, and potentially assisted spread of non-resistant genotypes (Stockwell et al., 2003). Finally, continued research on the role of genetic variation, demographic traits, and selection pressures in increasing invasions will shed light on what we might expect in the future under continuing global change (Moran and Alexander, 2014). In summary, a multi-pronged approach to invasive species management that incorporates an evolutionary perspective will help us to meet future challenges as invasion rates continue to increase (Millennium Ecosystem Assessment, 2005; Simberloff et al., 2013).

Conclusion

The number of invasive species worldwide is increasing with continuing globalization, and rates of introductions are not expected to slow down. This increase in species invasions is a global concern, as invasions pose a threat to ecosystems and the services they provide to human communities globally. To date, we have learned that while introductions often involve bottlenecks and reductions in genetic diversity, rapid evolution can often occur in invasive populations, and that invasive species can act as important selective pressures driving evolution in native species including those that do not directly interact with the invasive species. Understanding these processes meets with challenges including distinguishing adaptive, genetic changes from plastic, acclimation responses (Keller and Taylor, 2008; Moran and Alexander, 2014). To determine whether phenotypic variation is driven by genetic differences versus plasticity, researchers can employ "common garden" experiments in which individuals with different characteristics are raised in a similar environment (e.g., Colautti and Barrett, 2013; Colomer-Ventura et al., 2015; Graebner et al., 2012; Santi et al., 2020). Overall, genetic information provides insight into the invasion process. The use of genomics, which expands beyond the use of a few genetic loci, is still in its infancy with a need for more reference genomes of invasive species (Matheson and McGaughran, 2022). But genomics can provide broader insights such as reconstruction of invasion routes through space and time (North et al., 2021; Puckett et al., 2020). Given that invasion will continue to be a major global threat, we need new, multi-pronged management practices if we are to curb ever-increasing invasion rates. An evolutionary perspective is important for understanding, predicting, and managing invasive species.

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