Biological Invasions: An Overview

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Introduction 667
What are Biological Invasions and Why do We Care About Them? 667
The Evolution of Invasion Biology and Insights Into Biological Invasions 669
Important Invasion Concepts 669
The Ten's Rule – Not all Invaders are Alike 669
Invasiveness 669
Invasibility 670
Propagule Pressure 670
Invasion Time Lags 671
Invasion Biogeography 671
Invasion Hypotheses 672
Invasion Frameworks 672
Invasion Outcomes: From Native Subsidies to Devastating Impacts 673
A Range of Invasion Outcomes 673
High-Impact Invaders 674
Anthropogenic Change Facilitates Invasion Outcomes 674
Can Community Assembly Theory Explain Anthropogenic Influences on Invasion Outcomes? 675
Invader Impacts Decomposed 675
Management and Mitigation of Biological Invasions 676
Summary 677
References 677

Abstract

Biological invasions arise when humans intentionally or unintentionally transport biological organisms to new regions of the world where many establish and become serious pest species. Globally, biological invasions represent a leading cause of anthropogenic change by reducing biological diversity, altering ecosystem functions, and disrupting ecosystem services to humans. This article outlines the causes, consequences, and management of biological invasions and overviews the current state of the science of invasion biology.

Key Points

- Why are biological invasions important?
- The nascent field of invasion biology.
- An introduction to key concepts in invasion biology.
- Invasion hypotheses and conceptual frameworks.
- The nature of invader impacts on ecological systems.
- Invasive species management and mitigation.
- Summary.

Introduction

What are Biological Invasions and Why do We Care About Them?

Biological invasions are an unfortunate side-effect of human transportation networks interconnecting the globe via trains, planes, automobiles, and ships. These transportation networks, developed to overcome the great natural barriers to movement presented by oceans, deserts, and mountain ranges, have facilitated the interconnectivity of all manner of organisms from around the globe, with some very serious consequences (Mack *et al.*, 2000). Of course, not all introduced species are problematic and many intentional introductions have greatly benefitted humanity. For example, many of our

Fig. 1 Human introductions of plants and animals into new regions of the world can create serious pests with severe ecological and economic impacts. Invasion biology emerged as a science to understand how introduced species become pests and how to mitigate their impacts. Clockwise from upper left: zebra mussels fouling a boat, with inset closeup of zebra mussel; brown tree snake which depredates endemic birds and lizards on the island of Guam; gypsy moths attacking trees in Ontario, Canada; kudzu blanketing trees and shrubs in the southeastern United States; and feral hogs wreaking havoc on vegetation in Northern Territory, Australia.

most valued agricultural crops like rice from Asia, corn from central America, and wheat from the Middle East are now grown around the world to provide humans with essential local food sources (Crosby, 2003). However, many other organisms intentionally introduced as ornamental plants like kudzu or for animal husbandry like pigs become remarkably problematic pests when they take on feral roles in new lands (**Fig. 1**). Additionally, many organisms arrive as uninvited hitchhikers such as mosquitoes boarding airplanes, weed seeds stowed away among agricultural seed, and earth worms embedded in horticultural imports. While most newly arriving species fail to establish due to harsh environments or resistance from native biota (Williamson and Fitter, 1996), others become peridomestic species restricted to cities and human-altered environments, and yet others become naturalized species that establish wild populations with little effect beyond adding to local biodiversity (Sax and Gaines, 2003). However, a subset of species like kudzu, feral pigs, and zebra mussels become so successful that they overrun their new environments causing tremendous economic, societal, and ecological impacts that ultimately threaten biological diversity. It is this latter group that makes understanding and addressing biological invasions so important.

Understanding biological invasions requires that we resolve a paradox: how do some introduced species, presumably naïve to their new environments, outcompete locally adapted natives (Wallace, 1881; Sax and Brown, 2000). This phenomenon seems to defy a basic tenet of evolution – natural selection is presumed to hone species' traits to maximize their performance under local environmental conditions. For example, a classic study in plant ecology demonstrated that local adaptation can be so important even within species that when individuals are taken from populations living at different elevations (i.e., different environmental conditions) and grown together in common gardens within each elevation zone, the individuals matched to their original environments outperform the newcomers (Clausen *et al.*, 1940). If adaptation to local biotic and abiotic conditions is so important, then how do species from different continents dramatically outperform their native counterparts? The quest to answer this question has given rise to the burgeoning young field of Invasion Biology.

The Evolution of Invasion Biology and Insights Into Biological Invasions

Among the first scientists to recognize biological invasions as significant ecological phenomena was Charles Darwin (Darwin, 1859). In fact, Darwin used case studies of biological invasions to both establish the basis for and limits of the theory of evolution. He presented examples of invaders flourishing in new environments to demonstrate the capacity of biological organisms to increase exponentially and thereby exceed the capacity of their local environments – an underlying premise for the processes of natural selection and evolution (Darwin, 1859). Reciprocally, Darwin (1859) used case studies of invasions to illustrate the limits of evolution for maximizing local adaptation, noting that the capacity of introduced species to rapidly outperform natives is evidence that natives are not necessarily always maximally adapted to their local environments (a result attributed to the constraint that selection can only act on the limited materials provided). With these observations, Darwin simultaneously shed light on the significance of biological invasions as ecologically important phenomena and also provided a crucial hint for resolving the invasion paradox. Despite this early start, invasion biology did not begin to blossom as a science until Charles Elton (1958) wrote the first extensive monograph on this topic 100 years later. In the decades since Elton, the ever-increasing arrivals of new invaders and the undeniable and growing impacts of invaders old and new has driven an exponential increase in invasion research and the ontogeny of invasion biology (Richardson and Pyšek, 2008). Hence, developing an overview of biological invasions requires viewing this topic through the dynamic lens of this nascent and rapidly evolving field to understand what is currently known about the causes, consequences, and management of this global problem.

Catalyzed by the prescience of Elton's monograph, the science of invasion biology emerged from a variety of initially disparate concepts and explanatory hypotheses (reviewed below). Soon after, conceptual frameworks began to arise to collate these ideas and better integrate the field in a process that itself continues to evolve. These discordant beginnings have contributed to a deep-seated and ongoing debate about whether exotic invasive species are actually different from native species at all (Davis *et al.*, 2011; Simberloff, 2011). The existence of this debate harkens back to the invasion paradox itself and the mandate for this field to explain how some introduced species differentiate themselves from the natives in such profound ways that they are able to overwhelm and severely impact native systems. The culmination of research to date paints a complex and incomplete collage suggesting that there may be truth on both sides of this debate – most invaders are not so different from natives, but the differences that distinguish some are profound and may help to resolve the invasion paradox. An overview of key concepts provides a starting point for integrating these ideas and understanding invasion biology.

Important Invasion Concepts

The Ten's Rule – Not all Invaders are Alike

In his monograph, Elton lamented over the fact that the number of well-documented invasion cases was so limited that he was restricted to anecdotal depictions. However, the accumulation of new invasions since and increased documentation of case studies eventually allowed for quantification of general invasion patterns, including the verification of patterns originally postulated by Elton such as the "Ten's Rule". For example, Williamson and Fitter (1996) used early developing databases of introduced plants and animals to show that of all arriving species only about 10% are able to survive in new regions as incidental or casual species, only about 10% of those establish sustaining populations to become naturalized, and only about 10% of those become invasive pests (although Jeschke and Strayer (2005) later found invader success of 50% at each step for vertebrates). Hence, invasive pests appear to represent a limited though extremely important subset of all invaders. The Ten's Rule established a fundamental line of inquiry for invasion ecology: What factors limit most species from establishing or becoming pests? How do invading species transition through these invasion stages from arrival to pest stature? And, most importantly, what factors allow some species to become so problematic in their new range? While this distinction between invasion outcomes seems profound, many earlier studies addressing important invasion questions simply pooled all invaders together failing to acknowledge the important distinction between weak invaders that merely naturalize and strong invaders that become serious pests (*sensu* Ortega and Pearson, 2005). As studies began to explicitly address this distinction, new insights began to emerge as to which factors might differentiate pest species from less problematic invaders (Mitchell and Power, 2003; Van Kleunen *et al.*, 2010), an important point addressed further below.

Invasiveness

One of the earliest and longest lines of inquiry in invasion ecology has been the effort to identify key traits that may allow invasive species to become so successful. This effort, dating back to Baker's attempt to identify those traits defining an "ideal weed" (Baker, 1965), has emphasized the concept of invasiveness or the inherent capacity of a species to invade recipient communities. Implicit in this approach was the assumption that an invader's traits alone could explain invasion outcomes independent of attributes of the recipient community. This line of research has found that some traits such as seed size can help explain the broad success of certain invasive plant groups (Rejmanek and Richardson, 1996) and a subset of traits have been linked to the success of numerous invaders, but no single trait or trait syndrome seems to globally explain invasiveness (Richardson and Pyšek, 2006). Hence, the ideal weed concept has largely been abandoned as efforts since have evolved toward examining invader traits less in isolation and

more with an eye toward the invasion context (Richardson and Pyšek, 2006; Moles *et al.*, 2008). For example, invader traits are increasingly evaluated by comparing strong invaders with weak invaders and natives to identify general differences that might broadly explain the success of highly invasive species (Van Kleunen *et al.*, 2010). Recent efforts have taken an even more context specific approach that evaluates invader traits relative to the local abiotic and biotic filters that define the recipient community (Pearson *et al.*, 2018a). Results from this progression of research suggest that while a few traits may generally favor invader success, context dependence plays an important role in invasion outcomes, and invader success may be understood best by evaluating traits in the context of recipient communities.

Invasibility

Darwin and Elton both noted that the most important barriers for invaders were biotic resistance from established natives and environmental constraints or abiotic resistance. Of the two factors, biotic resistance has received by far the most attention, but collectively these components define the susceptibility of a community to invasion or its invasibility. Obviously, the arctic is no place for a tropical species lacking adaptations for the cold. However, given appropriate abiotic conditions, an invader will encounter established natives that in theory hold a priory advantage over new arrivals. Hence, invaders with traits most similar to the natives will likely encounter strong biotic resistance because their niche is already filled by well-established natives, whereas an invader bearing traits that are sufficiently different from the natives may find reduced biotic resistance or even an empty niche. In combination these observations suggest that successful invaders should have traits sufficiently different from the natives to evade biotic resistance ("Darwin's Naturalization hypothesis"), yet they must have traits sufficiently similar to the natives to align with local abiotic conditions ("Darwin's Naturalization paradox"; see Thuiller *et al.*, 2010). In general, research has supported these hypothesized patterns for plants showing that at larger spatial scales invaders tend to be more related to natives, but that at local scales relatedness and traits tend to diverge (Diez *et al.*, 2008).

Given this important role of biotic resistance, it is not surprising that Elton emphasized both natural disturbances and Anthropogenic disturbances as mediators of invasions because disturbance can weaken biotic resistance by removing prospective competitors, predators, and pathogens while also freeing up resources and creating environments more suitable for invasion. It is well-documented that increasing frequency and intensity of natural and Anthropogenic disturbances facilitates invasions (Davis *et al.*, 2000). More generally, the susceptibility of recipient communities to invasions is recognized as an emergent property of natural systems reflecting inherent community-level attributes such as diversity, productivity, and resilience to natural and anthropogenic perturbations. Progress in understanding invasibility has been challenged by the fact that it is extremely difficult to study emergent properties because, by definition, they arise through synergistic effects of multiple processes. Therefore, traditional reductionist approaches of isolating factors to determine their effect on outcomes disrupts the synergism and impedes understandings of the cumulative effects. Yet, early research necessarily did just this to isolate effects of diversity and productivity on invasibility (Fridley *et al.*, 2007). Adding to this challenge is the fact that scale can also affect each of these processes such that patterns may differ at different scales. For example, studies of the relationship between community diversity and invasibility have generated extensive debate because opposite relationships can be observed at different scales (in general diversity is negatively associated with invasibility at fine spatial scales and positively at large scales). Importantly, in plants, competition which is a primary mechanism for biotic resistance to invasion acts at local neighborhood scales, suggesting that this is the scale at which biotic resistance plays out (Levine and D'Antonio, 1999). In contrast, positive relationships at larger scales are presumably driven by abiotic conditions such as higher productivity accommodating more species - both native and exotic (Stohlgren *et al.*, 1999). Recent work examining the combined effects of diversity, productivity, and resilience on invasibility at local scales highlights that diversity and productivity can play different roles in affecting invasibility depending on ecological context (Pearson *et al.*, 2018b). This research suggests that ecological resilience which is an emergent community property reflecting multiple processes including diversity and productivity may provide a better single metric for understanding community invasibility than either of these metrics alone.

Propagule Pressure

The number of propagules (e.g., seeds, spores, individuals) introduced in any single introduction event, propagule size, as well as the number of introduction events, propagule number, can profoundly influence the establishment success of introduced species across all manner of taxa because higher propagule pressure can overcome stochastic, demographic, and genetic obstacles facing incipient populations (Lockwood *et al.*, 2005; Colautti *et al.*, 2006). Similarly, at the community level, the number of species that are introduced, "colonization pressure", will influence the number of species that establish (Lockwood *et al.*, 2009). Propagule pressure is so influential over initial invader establishment that it can swamp out other ecological processes such as biotic resistance to invasion linked to higher native diversity (Colautti *et al.*, 2006). Moreover, because propagule pressure can be confounded with other ecological factors that might influence invasion (e.g., more species might be introduced in more or less diverse sites), it is important to control for propagule inputs, when possible, in order to tease out the independent effects of other processes. For these reasons, it has been proposed that propagule pressure should provide a null model for biological invasions (Colautti *et al.*, 2006). However, it is important to distinguish anthropogenic propagule pressure created by human vectoring of propagules ("introduction effort") from propagule effects arising from inherent species fecundity, referred to as "propagule rain"

(see Box 1 in Lockwood *et al.*, 2005, 2009) because these are fundamentally different processes. Propagule pressure is an extrinsic process driven by anthropogenic factors, whereas propagule rain or fecundity is an intrinsic process linked explicitly to inherent species traits. Hence, these factors differ in the roles they play in the invasion outcomes and the structuring of communities.

Considering introduction effort and propagule rain in the context of community assembly theory (*sensu* Pearson *et al.*, 2018a) helps to differentiate their roles in determining invasion outcomes. Anthropogenic propagule pressure or introduction effort affects the input rates and identities of organisms entering regional and local species pools and can influence establishment success in the local community by usurping local filters. In contrast, a species' fecundity or propagule rain determines its ability to persist in a community in the absence of such propagule pressure. For example, an introduced plant may experience competition that is strong enough to resist its invasion at ambient propagule inputs equivalent to the natural fecundity of the species, but anthropogenically elevated propagule pressure may allow it to bypass this process by ensuring that enough individuals find safe sites in the community to ensure establishment. Mechanistically, this effect equates to extrinsic anthropogenic factors artificially exaggerating fitness effects in the context of coexistence theory. According to coexistence theory, a species must be able to increase at low abundance in order to successfully invade a community as a function of fitness vs niche differences between the invader and the established community (Chesson, 2000; MacDougall *et al.*, 2009). Therefore, an invader inherently lacking in the fitness capability to invade could successfully establish given artificially inflated propagule inputs. However, if the propagule faucet is turned off or the invader attempts to spread from the source population into areas where its propagules are not artificially elevated, it will be unable to maintain itself in the community unless it has the inherent fitness properties necessary to balance the coexistence equation (*sensu* Chesson, 2000). Therefore, differentiating the discrete roles of these factors is key to determining which invaders establish purely as a function of propagule pressure and which invaders may be initially subsidized by propagule pressure but can persist and invade beyond their initial establishment zones as a function of their inherent species traits. Obviously, differentiating these processes has important ramifications for management. In the former scenario, the species can be effectively managed by turning off the propagule faucet and letting biotic processes play out, but in the latter scenario the species' ability to become problematic derives from its inherent traits as they relate to fitness and niche parameters relative to the native community, rending control more complex.

Invasion Time Lags

While most problematic invaders experience rapid, or even exponential, population growth, the time lag from arrival to achieving such explosive growth can vary greatly among invaders (Crooks, 2005). Some invaders may become naturalized for many decades with little apparent effect only to later explode into problematic pests (Aikio *et al.*, 2010). Since eradication and control are most effective before invaders become widely established, understanding this time lag is critical for effective management. There are several factors that may contribute to these invasion times lags (Crooks, 2005). The foremost may be the fact that exponential growth itself is a threshold phenomenon. Early in the growth phase population doubling is not very notable because doubling of very small numbers still generates very small numbers. However, once the inflection point in the growth curve is reached, the doubling effect becomes dramatic. Add to this phenomenon the fact that generation times and fecundity can vary dramatically across organisms and the biology of this process alone can explain much of the variation in time lags across invaders. Nonetheless, other factors may create additional lags. For example, population growth may be greatly slowed when organisms are at low abundance due to Allee effects such as mates having difficulty finding one another. Evolution is an important factor mediating invasions that may also generate time lags (Whitney and Gabler, 2008). For example, if initial invader populations are not well adapted to their new environment, time may be required for natural selection to hone phenotypes. When invaders arrive from multiple source populations, expanded gene pools may accelerate local adaptation, and, in some cases, invader hybridization with natives can create Frankensteinian pests as with hybrid spartina cordgrass (Aïnouche *et al.*, 2009). An important problem with time lags is that they imply an invasion debt (Duncan, 2021), i.e., even if new invasions are halted, new invaders will likely continue to arise from previously introduced species as they emerge from their lag phases.

Invasion Biogeography

Elton was quite explicit about the fact that many of his case studies involved species that were neither abundant nor necessarily problematic in their native range but became extremely abundant and problematic in their introduced ranges. This pattern suggests that there is an important biogeographic component to biological invasions that may help explain the invasion paradox. In fact, this pattern has led to a "release paradigm" in invasion ecology wherein it is widely assumed that invaders increase in abundance in their new ranges due to release from population controls present in the native range. As intuitive and widely embraced as this idea is today, most invasion studies prior to 2005 tended to focus only on the introduced range with a few studying the invader in the native range but remarkably few conducting paired biogeographic studies in both ranges (Hierro *et al.*, 2005). Yet, if invaders are more abundant in their introduced ranges due to release from population controls in their native ranges, and this increased abundance is the mechanism underlying their impact where introduced, then biogeographic studies are essential to identify the mechanisms underlying invasion outcomes. Today, such biogeographic studies are increasing for plants but only slowly due to the tremendous logistical challenges associated with conducting parallel studies in disparate ranges. As

discussed below, such studies are both challenging the idea of the ubiquity of the release paradigm and providing valuable insights into the invasion paradox.

Invasion Hypotheses

Many hypotheses have posited mechanisms to explain invasion outcomes (see Mitchell *et al.*, 2006). Among the earliest and most popular of these is the enemy release hypothesis which can be traced back to Darwin (1859) and Elton (1958) but was perhaps most fully explicated by Keane and Crawley (2002). The enemy release hypothesis states that introduced organisms benefit when they arrive in a new range because they leave behind their specialist natural enemies which presumably controlled their populations at home. There is substantial evidence that introduced species have lower parasite loads and may experience generally reduced specialist natural enemies in the introduced range (Torchin *et al.*, 2003; Mitchell and Power, 2003), but few studies have definitively linked this process to increased invader abundance or success in the new vs native range (but see DeWalt *et al.*, 2004). Numerous other hypotheses like the evolution of increased competitive ability hypothesis (EICA; Blossey and Nötzold, 1995) and the resource-enemy release hypothesis (Blumenthal, 2005) provide derivations of the enemy release hypothesis that incorporate evolutionary, resource-based, or other mechanisms to explain enemy release (Latombe *et al.*, 2021). The empty niche and biotic resistance hypotheses advocated by Elton both place the emphasis in explaining invader success on recipient community invasibility. The fluctuating resource hypothesis builds on the biotic resistance idea to pose that invasions are driven by disturbances that reduce resistance and increase resource availability for invaders to establish (Davis *et al.*, 2000). The invasional meltdown hypothesis (Simberloff and Von Holle, 1999) incorporates invader feedbacks, postulating that once invasive species get into a new system, they can facilitate other invaders by breaking down biotic resistance and/or creating mutualistic interactions among invaders (see also Parker *et al.*, 2006 for linkages to enemy release). Perhaps most distinct among these is the novel weapons hypothesis which postulates that introduced species may gain advantage over natives because the natives have no experience in dealing with certain invader traits like plant exudation of toxic compounds (Callaway and Ridenour, 2004).

Common to these invasion hypotheses is the idea underlying the release paradigm - that introduced organisms become problematic in their new ranges because they become more abundant there than in the native range. However, biogeographic studies of plants have begun to demonstrate that many introduced species are not more abundant (or larger as predicted by EICA) in the introduced range (Firn *et al.*, 2011; Parker *et al.*, 2013; Pearson *et al.*, 2017). Yet, some of those that do experience population release are among the more problematic pests (Pearson *et al.*, 2017). These results support the idea that the release paradigm does not apply to all invaders, at least for plants. It is notable, however, that most of Elton's examples illustrating biogeographic release involved animals (both vertebrates and invertebrates). It is unclear whether animals are more commonly released, but if so, this might suggest that different processes influence plant vs animal invasions. One invasion hypothesis that may help explain why some high impact invaders are not more abundant in the introduced range is the Neolithic plant invasion hypothesis (MacDougall *et al.*, 2018). This hypothesis postulates that many plant invaders may arise from long-standing relationships with humans who have cultured these organisms over the centuries through agriculture and pastoralism and then paved the way for their success in new ranges by spreading those same practices around the world. This hypothesis predicts that such invaders will have similar success in the old and new worlds but will have a relative advantage in new regions where natives naïve to such practices decline. These ideas have been extended from agriculture to urbanization for both plants and animals under the notion that many organisms may arrive and thrive in urban settings where they can evolve adaptations that allow them to then invade their surroundings (Borden and Flory, 2021).

Collectively, no single invasion hypothesis likely explains all invasion outcomes. In reality, each may offer a valid explanation for a subset of invasions. The question then becomes how can these hypotheses be integrated into comprehensive understanding of biological invasions, and which hypotheses explain the majority of invasion outcomes. Invasion frameworks have emerged as a means for integrating invasion hypotheses and their underlying mechanisms into a more cohesive understanding of invasion biology.

Invasion Frameworks

Early on in invasion ecology, it was recognized that all invaders must travel a similar path to success that requires them to overcome a series of barriers as they arrive, establish, and ultimately flourish in a new environment (Williamson and Fitter, 1996). These concepts have provided the basis for frameworks for both plant (Richardson *et al.*, 2000) and animal invaders (Williamson and Fitter, 1996), but they generally explain the same processes and were eventually merged into a hybrid model accounting for all invader taxa (Blackburn *et al.*, 2011). Such frameworks illustrate that each invader must overcome environmental challenges, competitors, consumers or predators, and population and genetic bottlenecks to establish and expand their populations. Numerous other frameworks offer derivations of this theme with others emphasizing the integration of concepts of invasiveness and invasibility (reviewed in Pearson *et al.*, 2018a). While this general approach has served well for delineating the invasion process and considering how invaders move through invasion stages, it has not focused attention on resolving the invasion paradox to elucidate why some invaders do so much better than the natives.

Two factors fundamental to understanding invasion outcomes that have not been historically integrated into invasion frameworks are context dependency (the conditionality of ecological outcomes) and biogeography. A recent approach incorporates

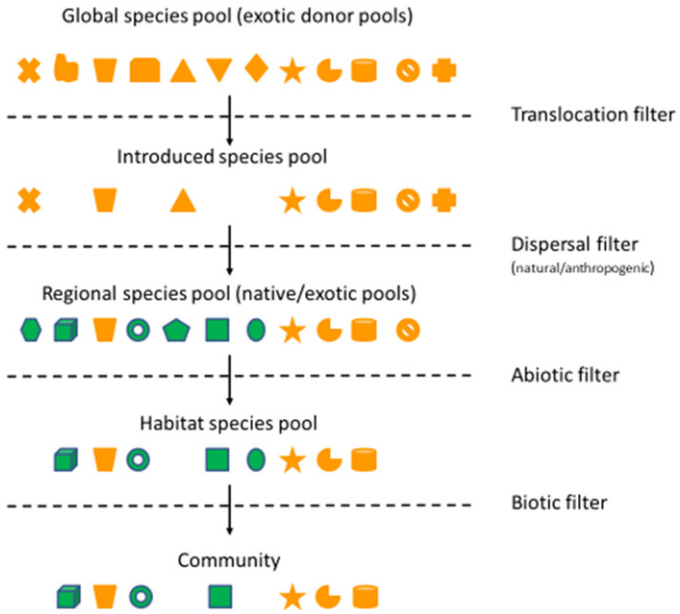

Fig. 2 Community assembly theory applied to biological invasions. In community assembly theory, the composition and relative abundance of species within a community is determined by a series of hierarchical and interactive filters that allow or impede the passage of each prospective community member based on its functional traits (each shape represents a distinct species and trait set; orange indicates exotics, green indicates natives). Applying these concepts to understand biological invasions requires accounting for initial trait sets within global species pools and how they are filtered by human-facilitated dispersal processes to determine which exotic traits reach introduced and regional species pools. The exotic and native trait sets in the regional species pools then pass through local abiotic and biotic filters (these can be hierarchical and interactive) to determine the composition and relative abundance of species within the community. (a) The anthropogenic factors affecting the regional species pools can cause differences in trait sets between exotic and native species within regional species pools that can introduce provenance biases even though local processes act on species traits without regard to species' origins (here trait similarity is spatially correlated, with traits linked to rapid growth and resource exploitation to the right grading toward slower, more stress tolerant traits to the left). (b) Note, that local filtering processes can also be influenced by anthropogenic factors like nutrification and altered disturbance regimes which can favor exotic traits. Figure modified from Pearson, D.E., Ortega, Y.K., Eren, Ö. and Hierro, J.L. (2018a) Community assembly theory as a conceptual framework for invasions. Trends in Ecology and Evolution 33, 313–325.

these concepts into an invasion framework based on community assembly theory – a fundamental ecological theory developed for explaining the structure of natural communities (Pearson *et al.*, 2018a; **Fig. 2**). This framework shows promise for explaining the relative success of weak vs strong invaders as well as identifying biogeographic factors influencing some invasion outcomes by evaluating how invader traits interact with local processes believed to structure natural communities. Applying this approach to empirical studies at the community scale shows that the abundance or success of many weak and some strong invaders may be explained based on how their traits interact with local ecological filters – the same as for the natives. That is to say, the same abiotic and biotic processes (e.g., drought or competition) that determine the abundance of natives may also predict the abundance of many invaders, with outcomes determined by the interaction between each species' traits and these ecological filtering processes. Importantly, this approach may also identify which invaders seem to cheat the rules by having novel traits derived from their original communities that allow them to bypass local assembly rules to dominate the natives. While this approach shows promise for generating broader understandings of invasion outcomes and resolving the invasion paradox, it has not yet experienced extensive testing.

Invasion Outcomes: From Native Subsidies to Devastating Impacts

A Range of Invasion Outcomes

While all invaders may travel similar ecological pathways to enter new systems, different species stop at varying points along the way. These endpoints largely distinguish the status and ultimate impact of different classes of invaders in their recipient ranges, so it is important to understand who stops where and why. Due to the nature of global transport routs, most invaders initially arrive in airports and shipping ports located in larger cities. From these ports, many species continue on hopping from city to city via internal transport routs like roadways, railways, waterways, and domestic flights. Of these, a subset of species that are highly adapted to urban settings may flourish within the cites without penetrating much further. In fact, a global traveler will find familiar cosmopolitan species such as a lamb's quarters, rock pigeons, house sparrows, and house mice greeting them in many cities

around the world. Other invaders make their way beyond the city walls into surrounding agricultural landscapes where they thrive, facilitated by anthropogenic subsidies from wells, fertilizers, and food resources including many rodents, agricultural weeds, and insect pests. Collectively, these peridomestic invaders, whether city mice or country mice, are largely dependent on human actions to maintain their populations. While they may venture into surrounding native habitats, these invaders fail to persist in these less hospitable environments in any substantive way. Some of these organisms have been linked to human civilizations and travel for so long that it is difficult to determine their origins.

Other invaders penetrate beyond the boundary of direct human influence into natural environments where they become naturalized species that establish self-sustaining populations within native communities with relatively minimal effect on community structure and function. In fact, most introduced species that establish wild populations may show little or no detectable evidence of impacting native species (Williamson and Fitter, 1996; Sax and Gaines, 2003). In contrast, a subset of these more feral exotics achieves the status of high-impact invaders with obvious impacts on ecological systems (Mack *et al.*, 2000). Importantly, the division between naturalized and high impact invaders is more a continuum than a discrete boundary. All introduced organisms will interact to some degree with other components of the system. Determining the strengths of these interactions between introduced and native species and what drives the strong interactions, including context dependency, is essential to understand invader impacts.

While historical research has focused on high-impact invaders for obvious reasons, it is important to recognize that introduced species can have a range of interactions in recipient communities that vary from negative to positive, transmitting through a variety of ecological interactions. For example, many naturalized species may provide novel food resources or new habitats that are beneficial to native species (Valentine *et al.*, 2020). These novel resources can generate effects ranging from minor bonuses to strong subsidies that greatly elevate native species populations via increased food (Pearson and Callaway, 2006) or altered habitat (Pearson, 2009). However, strong positive direct effects of invaders on some natives can generate strong negative indirect effects on others. Moreover, if the invader providing the new resource replaces the natives that previously served these resource needs, the natives can become dependent on the introduced species. This situation creates a unique management conundrum wherein controlling the invader can threaten the livelihood of native species. For example, the introduced shrub, saltcedar, has invaded large regions of riparian habitat in the arid southwestern United States where it has displaced native willows. Many native bird species readily nest in saltcedar including the endangered southwestern willow flycatcher, a situation that has created considerable debate over saltcedar control in areas where it now provides the primary nesting habitat (Paxton *et al.*, 2011). In the extreme, some invader-generated resources, which on the surface appear to be beneficial, can create ecological traps (Robertson and Hutto, 2006). This happens when invader traits offer proximal cues suggestive of fitness rewards that beckon to naïve natives but ultimately backfire and reduce fitness - an ecological play on Homer's siren's song. For example, nesting birds may be drawn to invasive shrubs by foliage or architectural cues normally indicative of good nesting habitat only to experience greater nest predation because the novel nest substrates are less protected by thorns or otherwise facilitate nest predators (e.g., Schmidt and Whelan, 1999).

High-Impact Invaders

In contrast to the above examples illustrating how invader interactions can range from beneficial to cryptic impacts, many high-impact invaders have obvious and devastating effects across native species and ecosystems. For example, introduced predators arriving on islands devoid of predators may have severe impacts, encountering a veritable smorgasbord of naïve native prey species that they may decimate in remarkably short time frames. Herbivores can also have serious impacts as demonstrated by the widespread introductions of pigs from Eurasia and North Africa to other regions where they voraciously consume native plants and facilitate introduced weeds by rooting behaviors (Barrios-Garcia and Ballari, 2012). Although small in size and individual or per capita effects, the numbers attained by some invasive invertebrates and pathogens can generate interaction strengths sufficient to transform ecosystems by taking out large community dominants such as the America chestnut of the northeastern United States (Schlarbaum *et al.*, 1998). Other invertebrates like crop pests and mosquitos directly impact human populations by reducing food production and increasing disease transmission. In aquatic systems, which tend to have stronger interaction linkages than terrestrial systems (Strong, 1992), introduced microbes, invertebrates, plants, and predators have all repeatedly proven capable of restructuring food chains and altering ecosystem functions, with some like zebra mussels costing billions in fouling damage to hydroelectric and other facilities (Connelly *et al.*, 2007). Some terrestrial plants can also restructure ecosystems as demonstrated by cheatgrass invasion of large regions of the American West where this species not only directly competes with native plants but has transformed these systems by dramatically increasing fire in communities not historically adapted to fire (D'Antonio and Vitousek, 1992). Given the severity of these outcomes, the driving question is, how does this particular group of strong invaders have such profound impacts in recipient communities when most invaders either fail to establish, remain peridomestic, or simply become mild-mannered, naturalized species?

Anthropogenic Change Facilitates Invasion Outcomes

As noted by Elton long before climate change had achieved the momentum that it has today, humans are changing global environmental conditions in ways that may greatly benefit introduced species, suggesting one fairly simple explanation for biological invasions – humans are shifting the advantage from the home team to the visitors. Since the emergence of the industrial age, the human footprint has grown to dominate the planet in such a way that the current epoch is now recognized as the

Anthropocene, marked by the unprecedented global dominance achieved by a single species (Lewis and Maslin, 2015). The Anthropocene is characterized by five major human-mediated impacts: (1) climate change, (2) habitat transformation/fragmentation (3) extractive uses (mining, over-harvesting), (4) pollutants (including eutrophication), and (5) biological invasions (Sih *et al.*, 2011). In many cases, biological invaders are undoubtedly facilitated by other key drivers like human disturbances, eutrophication, and climate change and may simply be passengers following these anthropogenic sources of change (MacDougall and Turkington, 2005). This is an important concept, because if invaders are simply passengers following other anthropogenic drivers, then managing invaders without addressing the underlying causes is unlikely to succeed. Importantly, because biological invasions and other causes of change commonly interact, it is not always clear when invaders are passengers or drivers. However, from the perspective of system impacts this distinction may be a nuance. For example, nutrient inputs in the absence of invaders may generate modest increases in productivity and shifts in community composition, but the same inputs in the presence of key invaders can transform the system. Hence, even if invaders are passengers following another driver of change, their additive or synergistic effects can be profound. While these anthropogenic factors highlight the role that changing environmental conditions play in facilitating many biological invasions, they do not explain why such changes favor introduced over native species. In short, what is so important about being exotic?

Can Community Assembly Theory Explain Anthropogenic Influences on Invasion Outcomes?

In theory, within a native plant community that is closed to exotics, experimentally simulating anthropogenic change by adding limiting nutrients, altering disturbance timing or intensity, or increasing temperature/CO_2 inputs (i.e., simulating climate change) should shift community composition to favor those native species best adapted to the new conditions. Experimentally increasing disturbance should favor species bearing more ruderal traits, whereas increasing nutrients should favor more competitive species (Grime, 1977). If such experiments are repeated with the same community now opened to exotics, the null expectation would be that the communities should shift in the same manner as described above with the exotic to native representation reflecting the proportion of exotics now added to the source pool, i.e., the null expectation is that the trait representation in the native and exotic pools are similar. However, if global donor pools have a different representation of traits/strategies than the native pools, for example, if they contain a greater proportion of competitive or ruderal species, then we might expect to see a shift in community composition toward exotic ruderals or exotic competitors, linked to increased disturbances or nutrient inputs, respectively (Pearson *et al.*, 2018a; **Fig. 2**). Global species pools could be biased in their trait representation for two reasons. First, they may reflect different evolutionary histories or trajectories wherein natural or anthropogenic processes may have selected for some trait sets/strategies over others as postulated by the Neolithic plant invasion hypothesis (MacDougall *et al.*, 2018). Second, the process of human introductions via anthropogenic means may tend to introduce species bearing certain traits more than others (Colautti *et al.*, 2006), thereby directing the trait sets in the invader pool more toward plastic, ruderal, or other traits potentially favorable under anthropogenic change. Placing biological invasions in the context of community assembly theory in this manner provides a means for interpreting the effect of global species pools and global transport pathways on invasion outcomes.

Invader Impacts Decomposed

Fully understanding invasion outcomes requires deciphering the mechanistic pathways by which invaders impact recipient community components. In the first article of *Invasion Biology*, the founding journal for the study of biological invasions, Parker *et al.* (1999) laid out the basic biology underlying invader impacts. Parker *et al.*'s equation defined invader impact as $I = R \times A \times E$; where I = invader impact, R = the range or area occupied by the invader, A = the invader's average local abundance (individuals, biomass, or equivalent per unit area), and E = the invader's per capita effect or per unit effect on a native species or recipient community component. This equation effectively encapsulates the fundamental components describing the ability of one species to affect another as a function of its density and interaction strength or per capita effect, concepts fundamental to species interactions and community ecology (Wootton, 1994), while also accounting for the spatial extent of the invader. Accordingly, there are two fundamental pathways by which an invader can impact a native species: (1) via abundance or density effects, or (2) via the species' interaction strength or per capita effects (also known as trait effects because such interactions are driven by morphologically, physiologically, or behaviorally based traits). Hence, an invader with relatively weak per capita effects can have strong impacts if it can achieve inordinately high abundance (e.g., many invertebrates). In contrast, an invader with very strong per capita effects could have substantial impacts at modest densities (e.g., predators in the presence of naïve prey). Of course, a strongly interacting invader that also achieves very high abundance can attain higher impacts yet by the multiplicative effects of these two processes (assuming linearity as in the Parker equation). Despite the importance placed on differentiating these interaction pathways in community ecology in recent decades, remarkably little attention has been paid to explicitly decomposing the density vs per capita effects of invaders. Determining the degree to which these two pathways contribute to overall invader impacts is essential for understanding and mitigating biological invasions.

Most invasion hypotheses overtly focus on density effects consistent with the release paradigm and the idea that it is the increased abundance of an invader in its new range that catalyzes its impacts. In contrast, the novel weapons hypothesis focuses on the idea that the per capita effect of an invasive plant on its neighbors increases in the new range because the new neighbors are poorly adapted to root exudates which have little effect on old neighbors (Callaway and Ridenour, 2004). Although this

hypothesis focuses on root exudates as the novel weapon, a biogeographic increase in per capita interaction strength could arise through various mechanisms across different taxa. For example, a predator arriving in a system where there were no previous predators (as on many islands), can be far more lethal to its new naïve prey vs those in its native range. This effect is not restricted to islands, as many predators introduced to systems with extant native predators may employ predation strategies that are novel in the recipient system and hence function as "novel weapons" to native prey species (Sih *et al.*, 2010). While other invasion hypotheses tend to emphasize density effects, the idea of elevated interaction strength in the new range is present in other hypotheses like EICA, which poses that being released from natural enemies allows for plants to reallocate resources from defense to increase competitive abilities, for example by growing larger. Such effects would translate to increased interaction strength or per capita effects, whether via short-term plasticity or longer-term evolution. In sum, any invader might exhibit increased density and/or increased interaction strength in the new range. The question is to what extent do these different pathways contribute to invader success and invader impacts on recipient communities?

This question of the balance of impacts between density and trait effects has not been well addressed in biogeographic studies, but there is some relevant work in the plant literature that begins to speak to this issue. Although most biogeographic studies have focused on comparing invader density or size between native and introduced ranges, studies quantifying invader impacts on their neighbors in both ranges suggest that numerous plant invaders do exhibit higher per capita impacts on their new neighbors via novel plant chemistry (e.g., Callaway *et al.*, 2012). Such studies are collectively establishing that novel interactions between the invader and its neighbors may commonly contribute to invader impacts, at least in plants, suggesting an important role of biogeographic novelty and trait effects in biological invasion outcomes. However, to date these studies have not isolated and manipulated both density and trait effects in a manner necessary to partition the relative influence of these pathways on overall invader impact.

One study applying the Parker *et al.* equation to quantify impacts of many invasive plant species in a grassland system suggests that density effects may dominate over per capita effects due to the way that plants partition resources and the greater capacity for variance in density vs trait effects (Pearson *et al.*, 2016a). For example, in plants, size is often correlated with competitive strength so that larger plants tend to have stronger per capita effects on their neighbors. However, because plants must partition a largely two-dimensional space while competing for the same resources (e.g., N, P, K, water, light), smaller plants can achieve comparable impact to larger plants if they can increase density enough to achieve the same biomass per unit area as larger plants, at least in herbaceous plants. Extending these ideas to the Parker *et al.* equation, even if an invader exhibits higher per capita effects in the new range (higher E), the ability of so many invaders to achieve high local density (A) and range (R) where introduced (whether more abundant than in the native range or not) is likely to drive their overall impact (I). In sum, the capacity for an increased numerical response affecting both A and R will generally exceed the capacity for a per capita effect E in influencing overall invader impact in plants. This should also apply to animals that exhibit aggregating behaviors. Exceptions might include predators on islands that attain dramatic increases in per capita effects over naïve prey but exhibit strong territoriality that suppresses their density effects. If high invader density, as implied by the release paradigm, drives invader impacts, then understanding how invaders overcome the negative density-dependent feedback mechanisms presumed to suppress natives (e.g., the Janzen-Connell Hypothesis; Janzen, 1970) would be key to understanding and managing invader impacts. If density effects most strongly drive invader impacts, this would be welcome news as it is generally more feasible to manage invader abundance than invader per capita effects. This is a critical area requiring further exploration in invasion biology.

Management and Mitigation of Biological Invasions

In line with early conceptual frameworks describing the invasion process, invasive species management frameworks tend to link different management strategies to the specific stages of invasion: arrival, establishment, and spread (Blackburn *et al.*, 2011). Accordingly, management generally prioritizes preventing species from arriving as this is by far the most effective approach. As invaders arrive and begin to establish, management targets early detection and rapid eradication of the invaders before they can become well-established and widespread. Once invaders become widespread, the emphasis becomes control and mitigation of impacts as much as possible because it is rarely possible to extirpate well-established invaders except on islands. However, control is often a very expensive endeavor with highly variable outcomes. Finally, restoration may be advocated in priority areas where attempts are made to remove established invaders and reestablish native communities (Gann *et al.*, 2019), but this is also a difficult and costly endeavor with variable success. A variety of tools are used for achieving these objectives depending on the taxa targeted. These include pesticides (e.g., herbicides, insecticides, fungicides, and piscicides), mechanical controls (e.g., sawing trees/shrubs, mowing herbaceous plants, dredging aquatic plants), the directed use of fire and water (e.g., controlled burning), soil amendments (e.g., nutrient or carbon additions), and classical biological control (the introduction of exotic organisms generally from the native range of the pest that serve as natural enemies of the pest where introduced). Ideally, these tools are implemented in the context of integrated pest management where multiple tools are used synergistically to optimize management outcomes (Flint and Van den Bosch, 2012). While on the surface, it might seem that management would be as simple as applying the right tool(s) to eradicate or control the offending invader, history has demonstrated that invasive species management is more complicated.

Invasive species management is as complex as human medicine (see Pearson and Ortega, 2009). In fact, human medicine provides an analogous framework that could help guide and advance invasive species management. In human medicine a variety of physical and chemical treatments are used to alleviate ailments within complex biological organisms. While these treatments can be extremely effective, virtually every medical treatment has side effects, which may range in severity from minor to severe due

to the complexity of the human body and limited precision of the treatments used (Evans and McLeod, 2003). Successfully managing human health requires the weighing of potential treatment side effects against the intended treatment outcome given a specific diagnosis and condition of the patient. The same is true in invasive species management. Invasive species management tools have side effects due to the complexity of natural systems and the limited specificity of the tools employed. Management side effects can vary from innocuous to rather severe, and, as with human medicine, the severity of the situation determines the level of acceptable risk of side effects. Hence, developing surgical precision in invasive species management requires understanding the ecology of the systems (the patient) and the nature of the invader and the impacts that must be mitigated (nature of the ailment) in order to balance management side effects against the intended outcome for a given management scenario.

Complicating matters further, anthropogenic forces like climate change, nutrification, and biological invasions are fundamentally altering ecological systems in ways that create moving targets for conservation. Processes like rising temperatures and/or increasing N inputs differ from historical pulsed perturbations in that they are directional and so push systems out of historic equilibrium dynamics and launch them onto trajectories. While ecological theory suggests that these systems will eventually stabilize into new equilibrium states (Beisner *et al.*, 2003), this could take tens to thousands of years. Likewise, biological invasions tend to be directional as introduced species are rarely extirpated from continental systems once widely established, and, as invasions accumulate, they can create novel ecosystems dominated by mixes of species with no common evolutionary history (Hobbs *et al.*, 2006). Hence, it is essential to recognize that these anthropogenic forces create moving targets for management, in many cases making it impossible to fully conserve systems in or restore them to their "original" state. This profound influence of anthropogenic drivers has forced dramatic changes in the thinking and strategies behind much conservation. Historically, conservation has focused on returning conditions to some paradigm historic state. However, such goals are increasingly implausible in today's Anthropocene (Hobbs *et al.*, 2006). More realistic approaches require acknowledging how systems are changing and working within those parameters to conserve species and ecological functions. Within this context, prioritization of invasive species management objectives will ideally range from (1) preserving intact systems where feasible, (2) managing for historic species composition, form and/or function where possible (where systems still function within historic equilibrium dynamics), and (3) directing systems toward the best possible outcomes in the case of altered ecological trajectories and novel ecosystems.

Recent global literature reviews addressing the efficacy of invasive species management suggest that management efforts are increasingly successful at controlling targeted invasive plant species and even vertebrates in island systems, however, these successes do not always result in system recovery (Pearson *et al.*, 2016b; Prior *et al.*, 2018). In invasive plant management, control of targeted weeds is increasingly successful, but a big problem is "secondary invaders" (Pearson *et al.*, 2016b). Far too often, when the target plant is controlled, it is replaced by another invader that is equally or more problematic. These findings indicate that simply controlling the target weed is not always sufficient and in many cases reestablishment of natives via reseeding or replanting may be necessary following weed suppression in order to recover the community. On islands, vertebrate eradication can profoundly benefit native species, especially naïve prey of introduced predators. However, these actions can also result in deleterious unintended consequences. For example, on Macquarie Island eradication of introduced cats benefited native seabirds depredated by the cats but it allowed introduced rat populations (also suppressed by the cats) to surge and decimate native plants (Bergstrom *et al.*, 2009). New tools are being developed for evaluating potential community-level outcomes prior to such management actions that show promise for better vetting proposed management actions and improving invasive species management (e.g., Baker and Bode, 2021). In sum, invasive species management is advancing, but it has much further to go to reach the type of surgical precision now seen in some aspects of human medicine. Applying adaptive management approaches to quantify and document both successes and failures of management actions as is done in human medicine will facilitate further advancement.

Summary

Biological invasions present one of the greatest threats to the diversity of natural systems and the ecosystem services they provide to humans. Addressing this problem requires better understandings of the mechanisms that allow introduced organisms to outperform locally adapted native species to solve the invasion paradox. Invasion biology is a nascent but rapidly advancing field. Work at the forefront of this field suggests that invaders may outperform natives by (1) simply expressing more strongly the same traits that are beneficial to natives within the recipient community (pre-adaptations) or (2) by expressing novel traits that allow the invaders to break community rules to outperform the natives (including exaptations). In terms of impact, the ability of invaders to reach high densities in the new range may be more important than increased per capita effects in driving overall invader impacts in many cases. If this is true, mitigating invader impacts will require better understandings of how invaders overcome negative density dependent feedback mechanisms to achieve high abundance. Addressing these issues will be key to advancing invasion biology and mitigating biological invasions.

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