The relationship between invader abundance and impact

HELEN R. SOFAER*,† CATHERINE S. JARNEVICH*, AND IAN S. PEARSE*

U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado 80526 USA

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Abstract. The impacts of invasive species generally increase with their abundance, but the form of invader abundance–impact relationships remain poorly described. We highlight the utility of abundance–impact curves for three questions. First, abundance–impact relationships can clarify whether prevention and management should focus on the species likely to become abundant or those likely to cause large impacts per individual. Second, comparing abundance–impact relationships between native and exotic species can reveal any systematic differences in their effects on ecological systems. Third, identifying any thresholds in the relationship between invader impact and abundance can be used to select management targets and design invasive species control strategies. With increasing extent and resolution of datasets of invasive organisms worldwide, we now have the opportunity to explore in detail the form and context dependence of the abundance–impact relationship. Doing so provides opportunities to improve the prediction of invader impact, to better understand the differences between exotic and resident organisms, and to scale the impacts of invasive species from localities to ranges.

Key words: community assembly; invader impact; invasibility; invasive species management; nonlinear averaging; scale dependence.

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† E-mail: hsofaer@usgs.gov

INTRODUCTION

For nearly two centuries, biologists have used exotic and invasive species as models to test dynamic processes in ecology and evolution that may be hard to observe in native ecosystems (Sax 2007). Exotic species richness, novel range sizes, and rates of invasive species spread have been analyzed to tackle ecological theory relating to community saturation, dispersal limitation, and environmental filtering (Shea and Chesson 2002, Sax 2007). The need for risk assessment and management prioritization has led to sustained interest in quantifying and ultimately predicting the impacts of particular exotic species, a task that has proven to be formidable (Vilà et al. 2011, Pyšek et al. 2012, Simberloff 2013, Blackburn 2014). Despite the challenges, rigorous evaluations of the impacts of exotic species are important because the costs and benefits of established, emerging, and potential invaders will determine how we manage invasive species (Thiele et al. 2010, Barney et al. 2013, Kumschick 2015).

Understanding and predicting invasive species impacts require both clear definitions and robust measurement of impacts. Invasive species are defined as the subset of exotic (i.e., non-native) species with a propensity to spread (Richardson et al. 2000). Rates of spread are independent of “impact,” broadly defined as any response of the
recipient system. Both the value (good or bad) and severity (how good; how bad) of a species’ total impact are subject to human valuation (Tassin et al. 2017). As with all aspects of environmental stewardship, it is necessary to continuously take stock of the goals and intentions of exotic species management.

At its core, the impact of an exotic species depends on the abundance and per capita effects of individuals of that species (Parker 1999, Yokomizo et al. 2009, Thiele et al. 2010, Ricciardi et al. 2013). Notably, these same terms emerge in theories that predict the coexistence of species within the same trophic level (MacDougall et al. 2009) and that quantify the importance (i.e., impact) of a species within a multi-trophic food web (Woottton and Emmerson 2005). The relationship between a species’ abundance and its impact depends on how per capita effects vary with abundance. Quantifying this relationship is useful for decomposing the impacts of an invader into those that arise from high abundance and those that arise from high per capita effects. Here, we define abundance–impact curves and highlight how understanding their patterns of variation across space and time and among invaders can provide insight into three outstanding questions in invasion biology: predicting invasions, comparing native and exotic species, and guiding management strategies across spatiotemporal scales.

**Abundance, Per Capita Effects, and Impact: Defining Abundance–Impact Curves**

The intuitive link between an invasive species’ abundance and impact was most prominently summarized via the Parker equation (Parker 1999), which specifies impact (I) as a linear function of abundance (A), invaded range size (R), and per capita effect (E): $I = A \times R \times E$. Studies have used this type of framework to consider impacts to populations, communities, ecosystem processes, and economics (Pimentel 2011, Ricciardi et al. 2013, Latzka et al. 2016, Pearson et al. 2016). While this equation provides a useful heuristic, unpacking its assumptions in light of ecological theory can guide our understanding of how and why exotic species vary in both the level of abundance that they achieve and in their per capita effects on recipient communities and ecosystems. In particular, the Parker equation summarized range-wide impact by assuming invader abundance and per capita effects are both independent and constant over an invader’s novel range. These assumptions were clearly highlighted by Parker (1999), who referred to their linear equation as a “gross simplification,” as well as by subsequent authors who have refined this framework (Thiele et al. 2010, Barney et al. 2013). Relaxing these assumptions implies that per capita effects can vary as a function of abundance, and that both abundance and per capita effects can vary in response to abiotic and biotic conditions in the recipient community. We largely focus on this heterogeneity within an invaded range and use the term “impact” to denote the total local impacts ($A \times E$).

One way to visualize the relationship between abundance and per capita effects is by plotting the impact (I) of an invader as a function of its abundance (A; Fig. 1). For comparisons among organisms that vary in size, metrics such as biomass or cover can be used to represent abundance. Empirical studies have found support for different forms of abundance–impact relationships and therefore for a different additional impact of each individual at a given level of abundance. An outstanding question is whether there are consistent patterns in the type of abundance–impact relationship observed for different impacts or attributes of the invader and recipient system. For example, are linear relationships more likely in constrained situations, such as in the relationship between invasive and native plant cover? Are impacts on measures of richness and diversity often nonlinear, with invaders excluding native individuals and species primarily at high densities? These patterns have been borne out when multiple impacts are studied for a single invader; Japanese stiltgrass (*Microstegium vimineum*) cover showed a negative linear relationship with native cover but a nonlinear relationship with native richness (Tekiela and Barney 2015). However, the form of relationships can differ even for the same invader and impact. Both the per capita effects (i.e., slope) and the form of abundance–impact relationships have been shown to vary among habitat types and with disturbance (Thiele et al. 2010). Understanding the sources of this context dependence
Fig. 1. The impact of an invader is expected to be an increasing function of abundance. Following Yokomizo et al. (2009), we illustrate four types of abundance–impact relationships, which affect the optimal allocation of management resources aimed at control (see also Vander Zanden et al. 2017). In each case, the derivative of the function describes how per capita effects vary with abundance (dashed lines). Note that relationships can be increasing or decreasing depending on the type of impact, and linear relationships may be observed when nonlinear relationships are truncated. (A) With a linear relationship, the slope of the impact line defines the constant per capita effect of each additional individual. Linear abundance–impact relationships are frequently documented. For example, reed canary grass (*Phalaris arundinacea* L.) cover showed a negative linear relationship with native richness and indices of native botanical integrity, as well as with arthropod abundance and richness (Spyrreas et al. 2010). In horizontal surveys, Chinese privet (*Ligustrum sinense*) was negatively linearly related to herbaceous cover and density and to native richness, effects supported experimentally by negative effects on native seedling survival and growth (Greene and Blossey 2012). (B) Under an asymptotic relationship, initial invaders have high per capita effects, but subsequent individuals have increasingly smaller additional effects. Richness and other diversity indices decreased with increasing dominance of purple loosestrife (*Lythrum salicaria*) or reed canary grass (Schooler et al. 2006). Chinese privet can also show a negative asymptotic relationship to indices of diversity (Hart and Holmes 2013); note that reed canary grass and Chinese privet are highlighted because studies have documented both linear and nonlinear relationships. In another example, the abundance of invasive round gobies (*Neogobius melanostomus*) showed a negative asymptotic relationship with abundance of their invertebrate prey, including invasive dreissenid mussels, in a horizontal comparison supported by experimental rock transfers (Lederer et al. 2006). (C) Under a sigmoidal relationship, the impact function shows a threshold, with large effects of each individual when the invader’s population size is near the inflection point. Invading individuals
is a major challenge that would yield clear benefits for invasive species management and control. The abundance–impact graphical or statistical approach has been used to assess impacts of exotic species (Pearson et al. 2016), but to date most studies have compared impacts between invaded and uninvaded areas rather than along a gradient of invader abundance (Vila/C18 et al. 2011, Gallardo et al. 2016). The relationship between abundance and impacts can be measured empirically in experiments that manipulate the abundance of an invader, longitudinal studies that observe changing abundance of an invader over time, and horizontal studies that compare sites with different abundances of the invader (Fig. 2). Combinations of these approaches are particularly powerful, such as when long-term monitoring is conducted at many sites across space, or when mechanistic relationships detected in experiments can be compared to patterns of abundance and impacts in observations collected across broad spatial scales.

There are two primary benefits of studying abundance–impact relationships. First, it will be useful to estimate whether most variation in impacts among species arises from variation in their abundance or in their per capita effects. Second, partitioning the contributions to total impact depends on understanding nonlinearities in the abundance–impact curve. While examples exist for many possible nonlinear forms (Fig. 1), there is a major need to identify consistent patterns in how abundance–impact relationships vary depending on the type of impact, the invasive taxa, and the abiotic and biotic characteristics of the recipient system. Optimization models demonstrate that nonlinear abundance–impact curves with inflection points at either low or high abundance can result in either a severe over- or underestimation of the impacts imposed by an invader, and hence of the optimal management effort (Yokomizo et al. 2009). Quantifying nonlinearities will help to overcome the pitfalls of the fallacy of averages by making available the tools of nonlinear averaging to understand how variation in invader abundance scales to impact (Denny 2017).

Neither abundance nor per capita effect is a unique property of a species, and each varies over a species’ range. Even problematic invaders are rare or innocuous somewhere and usually in most places (Hansen 2013). Spatial variation in abundance can be used to approximate spatial variation in impact; for example, models of common carp (Cyprinus carpio) abundance were found to have sufficient predictive ability to be useful for guiding management, even when extrapolating to an adjacent area (Kulhanek et al. 2011a). Cheatgrass (Bromus tectorum) occurs across North America, but only achieves high abundance (and thereby high impact) in parts of the Intermountain West. Even within the region where high abundance is reached, habitat models of occurrence overestimate this species’ potential impact and could misdirect control efforts (Bradley 2013). Disturbance plays a key role in mediating the abundance–impact relationship in this system, as cheatgrass promotes fire, which in turn reduces sagebrush abundance (Fig. 3). The positive feedback between cheatgrass abundance and fire can cause a regime shift that fundamentally alters the abundance–impact relationship (Fig. 3).

Just as abundance varies over space, so too do per capita effects. For example, black rat (Rattus rattus) has been introduced to regions throughout the world and persists in a broad range of climates where it depletes bird nests. However, the impacts (presumably arising from both high per capita effects and high abundance) of black rats are greatest on islands that lack native ground-dwelling mammals and are lower in...
cooler mainland climates where the black rat is quickly outcompeted by its invasive congener the brown rat (*Rattus norvegicus*; Jones et al. 2008). Similarly, the per capita competitive effects of diffuse knapweed (*Centaurea diffusa*) on grass species in the North American invaded range are higher than on related grasses in the native range (Callaway and Aschehoug 2000). Finally, per capita effects can be mechanistically linked to an invader’s abundance; for example, invasive crustacean species with greater consumption of native prey, for a given prey density, tend to become more abundant and result in greater impact on the recipient community (Dick 2017).

**Why Estimate Abundance–Impact Curves? Three Examples**

**Predicting invader impacts**

Anticipating the impact of potential invaders has been one of the most elusive challenges of invasion biology. Studies have attempted to retrospectively predict impact based on species traits (Castro-Diez et al. 2011), impacts in other invaded locations (Kulhanek et al. 2011b), phylogenetic relationships (Alcaraz et al. 2005, Cadotte et al. 2009), and measured aspects of their ecological interactions such as functional response (Dick 2017). While each of these
approaches have had some success in finding correlates of invasiveness or impact, those correlates are often inadequate to accurately predict novel problematic invaders (Pyšek et al. 2012). Abundance–impact relationships can clarify whether problematic invaders—those with large impacts—are simply the most abundant exotic species, or whether they often have large per capita effects. In other words, should risk assessments focus on identifying species with the potential to become abundant, or focus on species with large per capita effects at low densities? This is a key question because the traits that facilitate high abundance can differ from those associated with large per capita effects, as well as from traits that promote other dimensions of invasiveness such as spread rates and range size (Catford et al. 2016).

In community ecology, methods for predicting both potential abundance and per capita effects often center on species traits, and trait similarity between an invader and species in the recipient community. Abundance–impact curves may be particularly important in assessing the role of species similarity on impact because theory predicts that, at least in some cases, similarity may have opposing effects on abundance and per capita effects (MacDougall et al. 2009). Coexistence theory shows how niche differences between an invader and a resident species can facilitate successful establishment when these differences make intraspecific competition stronger than interspecific competition, so that each species can increase when it is rare (Chesson 2000). However, establishment of an invader does not imply strong impacts, which in coexistence theory are instead associated with niche similarity combined with a fitness advantage that allows the invader to increase in abundance (MacDougall et al. 2009). In other words, coexistence theory predicts that similarity between the traits of a potential invader and species in the recipient community can have opposing effects on establishment success of the invader and population-level impacts on resident species. This process has received some support in plant communities where native plants that are close relatives of invasive species are more likely to be displaced (Li et al. 2015, Case et al. 2016). A similar tension is captured by “Darwin’s naturalization conundrum,” hereafter DNC, which describes opposing predictions for how similarity affects establishment (Thuiller et al. 2010). Specifically, exotic species that are similar to those represented in the recipient community should be more likely to persist in that environment (pass through an abiotic filter), yet those that are dissimilar should be more likely to escape competition and other negative interactions with members of the recipient community (pass through the biotic filter).

A key question is whether niche-based processes invoked by coexistence theory and DNC can predict abundance in addition to establishment. If an exotic species is able to colonize a given environment, its abundance might be expected to be greater if it is more dissimilar from members of the recipient community because of low niche overlap and competition with the recipient community. Compared to
exotic species that are similar to members of the recipient community, dissimilar exotic species tend to use novel resources (Violle et al. 2011) and can escape local enemies such as predators, herbivores, or pathogens (Keane and Crawley 2002), which may promote abundance. Meta-analysis has shown that biotic resistance is more likely to reduce abundance than to prevent establishment (Levine et al. 2004), supporting a role for niche differences in shaping abundance. Trait-based community assembly theory encompasses opposing effects of functional similarity on species’ abundances that are conceptually similar to those in DNC, and these models have made meaningful progress in anticipating which species are most abundant in a community (Laughlin et al. 2012).

For ecosystem-level impacts, traits and trait dissimilarity between an invader and the recipient community are also expected to differentially affect abundance and per capita effects. Research on functional traits differentiates between “response traits,” which allow an organism to thrive (i.e., become abundant) in a novel environment, and “effect traits,” which cause changes (i.e., per capita effects) to that environment (Suding et al. 2008). Direct ecosystem-level impacts, and indirect impacts at other scales of organization, often arise from cases where novel functional roles underlie strong per capita effects (Levine et al. 2003, Simberloff 2011a). Prominent examples of ecosystem-level impacts driven by invasive species include changes to nutrient flows by novel nitrogen fixers (Allison and Vitousek 2004), alteration of trophic structure and energy flows by suspension-feeding dreissenid mussels (Dreissena sp.; Higgins and Vander Zanden 2010), shifts in disturbance regimes by novel fire-adapted plants (Mack and D’Antonio 1998), and changes in physical structure of vegetation by novel engineers (Anderson et al. 2006). State changes in ecosystem properties such as these may require both novel functional roles and high abundance. Furthermore, the magnitude of dissimilarity in any given trait needed to cause an ecosystem-level impact remains unknown, even for well-studied traits in terrestrial plants, such as leaf chemistry, resource acquisition, biomass accumulation, and phenology (Ehrenfeld 2010).

Trait-based perspectives offer the potential to derive hypothesized patterns of invader abundance and impact, but also highlight the challenges and contingencies associated with generating predictions across space. If dissimilarity between exotic species and their recipient communities plays an important role in shaping abundance and/or per capita effects, this would allow for predictions of impact across landscapes. Recent work has integrated spatial variation in abundance with spatially invariant abundance–impact relationships to derive summaries and spatial predictions of impact (Vander Zanden et al. 2017). Extending this framework to consider spatial variation in abundance–impact relationships will require both rich datasets and an understanding of the mechanisms of invader impact, and hence the key mediating traits; although challenging, such work is in line with the recognition that per capita effects are likely to vary across habitat types (Thiele et al. 2010). In addition, characterizing the conditions under which functional dissimilarity indeed affects invader abundance and per capita effects in an opposing manner will have important implications for management, as such a pattern would alter local and landscape-scale impacts, compared with a scenario in which abundance and per capita effects are independent or positively related.

**Are abundance–impact relationships different between native and exotic species?**

In the field of invasion biology, a heated discussion has arisen as to whether exotic species are fundamentally different from native species (Simberloff 2011b, Davis 2011). The stakes of this argument are large because it bears on how we invest in the detection, quarantine, and control of exotic species. The argument has at least partially revolved around qualitative assessments of management goals. However, parts of this debate may be addressed empirically by formulating the question as whether the function (i.e., effect and impact) of invaders on a community or ecosystem fundamentally differs from native species (Meiners et al. 2002). From a community or ecosystem ecology perspective, we are able to ask quantitatively whether invasive species alter fundamental processes and patterns in ways that comparable native species do not. At a coarse level, the mechanisms via which invasive species cause impacts fall within mechanisms seen in uninvaded systems: competition, predation,
allelopathy, nutrient cycling, etc., but the magnitude and context dependence can differ (Levine et al. 2003, Ehrenfeld 2010).

The question here could be expressed as “does the change in the abundance of an exotic organism perturb the system more than the change in abundance of a native organism?” Any such differences in the abundance–impact relationship can be quantified by fitting functions relating abundance to impact for both native and exotic species. This approach can explicitly estimate the form of abundance–impact relationships for each impact of interest (Fig. 1), while quantifying any differences between native and exotic species (Fig. 4). We outline three ways in which the abundance–impact curves of exotic and native species might differ, using a decline in recipient community diversity as an example impact (Fig. 4). In panels A and B, we illustrate an exotic species whose threshold of impact is lower (A) and per capita effects are higher than a native species. These scenarios might be expected if eco-evolutionary novelty introduced by the exotic species cause greater impacts; for example, novel allelopathic weapons cause greater interference competition; novel attack traits allow a greater functional response to naïve prey (Saul and Jeschke 2015). In Panel C, we illustrate an exotic species whose per capita effects are identical to a native species, but the exotic achieves higher abundance. This scenario might be expected if density-dependent mortality factors are lost for an exotic species, such as with enemy release (Keane and Crawley 2002). In each of these cases, we imagine ways in which an exotic species may cause greater impacts than a comparable native species; however, abundance and per capita effects of exotic species may often be lower or equivalent to those of local native species.

Scaling the impact of invaders and managing invasions with A–I curves

Summarizing the impact of exotic species is necessary to answer fundamental questions for management. Which exotic species have the

![Diagram](image-url)

Fig. 4. Do abundance–impact curves differ when considering the abundance of native and exotic organisms? Here, we imagine relationships between the plot-level abundance of a focal organism (either native or exotic) and diversity within the plot. We illustrate three testable differences in this relationship that might occur between native and exotic species. In all cases, we imagine that plot-level diversity decreases with increasing abundance of the focal organisms due to competition for space or resources. In relationship (A), we imagine a threshold-type response of diversity to focal species abundance, where the threshold is at a lower abundance for the exotic species. In relationship (B), we imagine a linear response of plot diversity to the abundance of the focal species, where the exotic species has a higher per capita effect than the native species. In relationship (C), we imagine identical per capita effects; however, the exotic species is able to achieve higher average abundance than the native species.
greatest impact? Is it worthwhile to actively treat invasive species through various control measures, and to what target level of abundance? The Parker equation was designed to summarize impact across the invaded range (Parker 1999). Substantial work has been done since that time to add sophistication to modeling abundance and per capita effects over a species’ geography (Thiele et al. 2010, Thomsen et al. 2011, Barney et al. 2013, Vander Zanden et al. 2017). The majority of these approaches utilize some form of abundance–impact curves. In each of these cases, nonlinearities in the abundance–impact relationship play an important role in accurately estimating impact and making decisions about management strategies (Yokomizo et al. 2009, Thiele et al. 2010).

An accurate representation of nonlinearities in the abundance–impact relationship becomes particularly important when considering variation in the abundance of an invader across space or over time. For example, zebra mussels (Dreissena polymorpha) and Eurasian watermilfoil (Myriophyllum spicatum) are rare in most locations, and under hypothesized abundance–impact relationships, the relatively few sites predicted to experience large impacts can be prioritized for management (Latzka et al. 2016). This work illustrated how both the shape of the abundance distribution and different abundance–impact curves for different measures of impact shape the distribution of impact and the total estimated impact across the landscape. Because of the properties of nonlinear averaging (Denny 2017), at high invader abundance ignorance of the abundance–impact relationship will cause an underestimation of impact when the abundance–impact curve is accelerating (e.g., Fig. 1D), and it will overestimate impact when the abundance–impact curve is decelerating (e.g., Fig. 1B).

Accounting for nonlinear relationships is important when making decisions on the management of invasive species. The question of when the ecological benefits of management outweigh its costs can draw from the body of work on economic injury levels and economic thresholds (i.e., management triggers) in pest and weed management (Higley and Pedigo 1996). The economic injury level is the abundance of a pest at which yield loss exceeds treatment costs. Economic injury levels are determined by estimating how yield loss (the impact), treatment efficacy, and cost per unit treatment each vary with pest abundance. Economic thresholds then take into account the dynamics of the system by estimating the abundance of pests at which treatment should be applied in order to maintain the population below the economic injury level. Yokomizo et al. (2009) use a similar framework to demonstrate that the assumed abundance–impact relationship is a sensitive component of optimal decision-making in managing invasive species. More rigorous knowledge of abundance–impact relationships could be integrated into bioeconomic models, which can guide the development of management strategies that account for trade-offs among different types of management activities, such as survey and control (Epanchin-Niell 2017). For example, models could evaluate trade-offs in the amount of control effort allocated toward sites already experiencing high impacts versus sites where impacts are low but that may contribute disproportionately to future spread (e.g., outlying populations).

Because eradication of invasive species is rarely feasible and management efforts are aimed at lowering invader abundance and rates of spread, there is clear need for studies of abundance–impact relationships that estimate per capita effects across a range of densities and for a suite of impacts. Empirical studies have highlighted cases where low invader abundance is associated with community and ecosystem-level impacts (as in Fig. 1B); in these cases, management aimed at reducing that impact would invest too little in control if it assumed a linear abundance–impact relationship. For example, manipulation of Pacific red lionfish (Pterois volitans) densities found that prey abundance declined steeply from zero to one lionfish per m² (Benkwitt 2015). Similarly, low proportions of Japanese barberry (Berberis thunbergii) in litter composition led to shifts in microbial community structure (Elgersma and Ehrenfeld 2011). In both these cases, as well as in other systems (Matsuoka et al. 2009), other ecological responses showed different abundance–impact relationships. Most studies tend to measure one or a few ecosystem properties rather than assessing impact on a suite of metrics (Hulme et al. 2013). Ideally, known relationships could be used to...
translate across impacts at different levels of biological organization. For example, if plant traits largely determine processes such as nutrient cycling, water dynamics, and energy flows, it may be possible to scale-up from invader abundance to impacts on plant communities, and in turn to impacts on key ecosystem-level processes (Suding and Goldstein 2008). Alternatively, if management activities focus on mitigating impact as a whole, the responses of multiple population, community, and ecosystem-level metrics to invader abundance can be integrated into a single multivariate estimate of impact (Barney et al. 2013).

CONCLUSIONS AND APPLICATIONS

Abundance–impact relationships lie at the intersection of community assembly theory, invasion ecology, and invasive species management. Understanding how increases in the abundance of one organism shape community and ecosystem dynamics is an area where advances in basic ecology can inform management, and where ongoing invasions can act as large-scale natural experiments that provide empirical tests of ecological theory. The resource management reality of multiple disturbances and invaders often requires triage, and a common objective is to maximize impact reduction per dollar spent. Information about the abundance–impact relationship can help prioritize management activities and avoid inefficient treatments in a way that is directly analogous to management triggers in agroecosystems (Higley and Pedigo 1996, Yokomizo et al. 2009, Barney 2016). The value of the economic threshold in agricultural systems has been a reduction in costly applications of control measures such as pesticide and herbicide treatments. As invasion biology continues to embrace quantitative methods of ranking impact, we can save expenses, focus our efforts on the largest problems, and reduce the negative side effects caused by ineffective or unnecessary control measures.

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