

# REVIEWS

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## Progress toward understanding the ecological impacts of nonnative species

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**Abstract.** A predictive understanding of the ecological impacts of nonnative species has been slow to develop, owing largely to an apparent dearth of clearly defined hypotheses and the lack of a broad theoretical framework. The context dependency of impact has fueled the perception that meaningful generalizations are nonexistent. Here, we identified and reviewed 19 testable hypotheses that explain temporal and spatial variation in impact. Despite poor validation of most hypotheses to date, evidence suggests that each can explain at least some impacts in some situations. Several hypotheses are broad in scope (applying to plants and animals in virtually all contexts) and some of them, intriguingly, link processes of colonization and impact. Collectively, these hypotheses highlight the importance of the functional ecology of the nonnative species and the structure, diversity, and evolutionary experience of the recipient community as general determinants of impact; thus, they could provide the foundation for a theoretical framework for understanding and predicting impact. Further substantive progress toward this goal requires explicit consideration of within-taxon and across-taxa variation in the per capita effect of invaders, and analyses of complex interactions between invaders and their biotic and abiotic environments.

**Key words:** *biological invasion; context dependence; ecological impact; invasive species; niche theory; prediction; risk assessment.*

### INTRODUCTION

Under human influence, species are being transferred between regions faster and farther than at any other time in Earth's history (Ricciardi 2007) and, in some cases, have caused enormous changes to recipient ecosystems (Asner and Vitousek 2005, Ehrenfeld 2011, Simberloff 2011). Despite considerable advances in our understanding of how nonnative species spread and establish self-sustaining populations (Catford et al. 2009, Davis 2009, Lockwood et al. 2013), our ability to forecast when and where they will exert strong ecological impacts remains weak (NRC 2002, Hulme et al. 2013). Given that the consequences of nonnative species invasions provide the impetus for management (Byers et al. 2002, Lockwood et al. 2013) and effective prioritization of management resources depends on accurate forecasts of the potential damage of an invasion (NRC 2002), a predictive

understanding of impact should be a central goal of invasion ecology (Pyšek and Richardson 2010). However, review articles that aim to synthesize invasion theory (e.g., Catford et al. 2009, Blackburn et al. 2011) have focused primarily on the process of colonization rather than the effects of invaders. Although there exist some conceptual frameworks for measuring and studying impact (Parker et al. 1999, Ricciardi 2003, Thomsen et al. 2011), there has been no attempted synthesis of mechanistic hypotheses, which we believe is essential for guiding future research toward an improved understanding of impact. In this paper, we review approaches to quantifying impacts and discuss the challenges of predicting them. We then identify mechanistic hypotheses from the invasion biology literature that explain variation in ecological impact among different invaders across temporal and spatial scales. We organize these hypotheses into conceptual categories and evaluate empirical evidence to determine the extent to which they are supported and may contribute to a broad theoretical framework.

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*What is impact?*

From a societal perspective, impacts are often measured in terms of economic costs and benefits, but such evaluations are strongly dependent on stakeholder perceptions (García-Llorente et al. 2008, Pyšek and Richardson 2010) and may fail to capture the broad range of environmental effects caused by a species invasion (Lockwood et al. 2013). Here we focus on *ecological impact*, which we define as a measurable change to the properties of an ecosystem by a nonnative species. The logical implications of this definition are that (1) every nonnative species has an impact simply by becoming integrated into the system, (2) such impacts may be positive or negative and vary in magnitude on a continuous scale, and (3) impacts can be compared through time and across space. This definition contrasts with existing conceptions that dichotomize impact (e.g., Williamson and Fitter 1996, Kolar and Lodge 2002), as well as those that rely on human perceptions of which species have significant effects (e.g., “pest” species; Pimentel et al. 2001) and thereby conflate ecological effects with non-ecological metrics. Although perceptions of impact may be altered by changing societal values (Pyšek et al. 2012), a focus on ecological effects avoids some of these sociologically induced changes and allows better comparisons across time and space.

Impact is sometimes treated as a discrete stage within a series of stages in the invasion process, e.g., transport → introduction → establishment → spread → impact (Catford et al. 2009, Lockwood et al. 2013), but in reality, a nonnative species may have ecological effects at any point after its introduction. Impact can be measured at the level of an organism (e.g., effects on individual mortality and growth), a population (abundance, genetics), a community (species richness, evenness, composition, trophic structure), an ecosystem (physical habitat, nutrient cycling, contaminant cycling, energy flow), or a region (species richness, beta diversity). Among these, individual-level and population-level impacts are most commonly studied, whereas ecosystem-level impacts are less frequently reported and rarely quantified (Parker et al. 1999), probably because they require detailed technical study (e.g., Asner and Vitousek 2005). For the vast majority of invasions, no impact studies have been performed at all (Parker et al. 1999). Experimental, even correlational, studies of impact are scarce for many highly invasive species (Parker et al. 1999, Ricciardi and Cohen 2007, Kulhanek et al. 2010a, Hulme et al. 2013). Despite a recent global assessment of invasive plant impacts (Pyšek et al. 2012), most impact studies are isolated local assessments (Hulme et al. 2013). Nevertheless, myriad case studies suggest that subtle and indirect effects of nonnative species, despite being easily overlooked, are common and often significant to the structure and function of ecosystems (Simberloff 2011, Vilà et al. 2011). This growing empirical evidence casts doubt on the conven-

tional notion that all but a small percentage of nonnative species are benign (Davis et al. 2011).

Where quantitative studies exist, comparisons and generalizations are hampered by the lack of common metrics. Parker et al. (1999) proposed a simple integrative equation based on the total area occupied by the nonnative species in its novel range ( $R$ ), its abundance ( $A$ , in numbers or biomass per square meter), and its per capita effect ( $E$ ). Thus, the overall ecological impact ( $I$ ) is given by

$$I = R \times A \times E$$

which yields a standardized metric that can be compared across species or across sites for a given species. The per capita effect  $E$  must be defined explicitly because the same nonnative species can have multiple effects (e.g., zebra mussels alter energy pathways through filtration and biodeposition of nutrients, and alter habitat space by the formation of attached clusters of shells; Ricciardi 2003). Given the potential variety of ecological interactions involving a single species, different measured effects can yield a different magnitude and direction of the overall impact metric (Ward and Ricciardi 2007).

Because data on per capita effects are relatively scarce, most inferences about impact are derived from what is known about the abundance and range size of a nonnative species. These surrogate variables can confuse differences between invasiveness and impacts. Invasiveness has two competing definitions: The first is that an invasive is any nonnative organism that enters a novel environment with human assistance, establishes a self-sustaining population, and spreads rapidly; a second definition requires that the spreading nonnative organism also have impacts on native populations, communities, or ecosystems (Daehler 2001). While policy advocates favor the latter definition, scientists are split with significant portions of the invasion ecology research community siding with each definition (Young and Larson 2011). We have no intention of resolving this debate here, because it is not fundamentally important to defining, measuring, or responding to impacts. Instead, we focused on information relevant to increasing our predictive understanding of impacts. To that end, we considered only hypotheses that address abundance and spread as they relate to events after the establishment of a nonnative species; events that lead to establishment have already been well covered in several other reviews (e.g., Catford et al. 2009, Blackburn et al. 2011). If we follow the Parker et al. (1999) definition of impact, then the critical factor in any hypothesis that also addresses invader abundance and spread is how the mechanism might modify per capita effects, or lead to nonlinearities in the per capita effect. A recent meta-analysis by Thomsen et al. (2011) suggested that the abundance of a nonnative species was a universal modifier of its impact in aquatic systems. Unfortunately, the relationship between abundance and impact is

generally unknown (Yokomizo et al. 2009), even for species having well-documented invasion histories (Kulhanek et al. 2010a). Positive linear relationships between density and impact have been identified for some nonnative species (Ricciardi 2003, Kulhanek et al. 2010b) and might be common in nature. However, nonlinear impacts may result from interactions between the per capita effect and the abundance of a species (Gonzalez et al. 2008), or from interactions among multiple nonnative species; e.g., via interference (Vance-Chalcraft and Soluk 2005) or facilitation (Simberloff and Von Holle 1999, Ricciardi 2001).

Those nonnatives that rapidly attain high abundance or large geographic ranges are presumed to have high impacts and are often labeled “invasive,” whereas those that are localized and rare are presumed to have few or no impacts and are considered “noninvasive” (D’Antonio and Kark 2002); this definition of impact has made the leap into nontechnical literature (e.g., see Convention on Biological Diversity and IUCN, both *available online*).<sup>6,7</sup> However, beyond the trivial expectation that the impacts of an invading species accumulate as it occupies more territory, there is surprisingly little correlation between the invasion success of a species (i.e., its rate of establishment or spread) and the magnitude of its impact (Ricciardi and Cohen 2007). Even sparsely distributed nonnative species can have strong local impacts (e.g., the Asian clam *Potamocorbula amurensis* and Atlantic salmon *Salmo salar*), whereas widespread and abundant nonnatives do not necessarily disrupt ecosystems (e.g., freshwater jellyfish *Craspedacusta sowerbyi* and dandelion *Taraxacum officinale*). Nevertheless, some of the mechanisms that control the abundance and range size of a nonnative species likely also control its impacts within a community (Maron and Marler 2008, Ricciardi et al. 2011a).

*Variation and complexity in impact:  
implications for prediction*

One pattern that has emerged from invasion studies is that larger impacts occur much less frequently than smaller ones (Williamson and Fitter 1996). Indeed, impacts have an inverse magnitude–frequency relationship remarkably similar to natural hazards such as earthquakes (Ricciardi et al. 2011b); for example, although a substantial proportion of global animal extinctions have been linked to nonnative species (Clavero and García-Berthou 2005), relatively few invasions appear to cause extinctions (Simberloff 1981, Sax et al. 2002). Another observation is that the impacts of the same nonnative species can vary greatly across space and time (Parker et al. 1999, Strayer et al. 2006, Jokela and Ricciardi 2008, Ricciardi and Kipp 2008, Hulme et al. 2013). Some of this observed variation must result from differences in detection or from inadequate

study, which would account for many apparently benign cases (NRC 2002). Local biotic and abiotic variables affect the abundance and performance of the nonnative species such that the magnitude, and even the direction, of impacts of the same species may differ across heterogeneous sites (D’Antonio et al. 2000, Neira et al. 2005, Jokela and Ricciardi 2008, Kestrup and Ricciardi 2009). The invasion history of the recipient community is an additional factor; impacts by previous invasions can remove sensitive species and create a harder community that is resistant to the effects of subsequent, functionally similar invaders (Balmford 1996, Rodriguez 2001).

Impacts vary significantly over time, typically accruing rapidly in the early stages of establishment as the incipient population grows (Ricciardi 2003), but then often leveling off or even attenuating in the long term (Strayer et al. 2006). There can also be lengthy lag times between establishment and peak impact (Crooks 2005). Probable causes of temporal variation in impact include the population dynamics of the nonnative species, adaptations by the nonnative species and the recipient community, interactions within a dynamic pool of resident species (new arrivals, loss of resident enemies), and a changing abiotic environment (Simberloff and Von Holle 1999, Crooks 2005, Strayer et al. 2006). Impacts attenuate for multiple reasons, including inter- or intraspecific regulation of the nonnative species (e.g., adaptation by native enemies, abiotic constraints on population growth) and other adjustments by the recipient community (Strayer et al. 2006). The temporal scale on which we expect to see such attenuation may vary enormously.

Finally, another source of spatial and temporal variation is the synergistic effect of overlapping stressors such as climate change, nitrogen deposition, and disturbance associated with land use, which can modify the tempo and magnitude of invasive species’ impacts (Byers 2002, Didham et al. 2007). In spite of substantial evidence that invasions can be the sole cause of major ecological disruptions (e.g., Clavero and García-Berthou 2005), each new observed impact begs the question of whether the nonnative species is a driver or merely a “passenger” of the ecological change (Didham et al. 2005, King and Tschinkel 2008). This uncertainty is exemplified by the interaction between climate change and plant invasions. There is no doubt that the success of some nonnative plants is being driven by shifting thermal barriers and changes in atmospheric CO<sub>2</sub> concentration (Weltzin et al. 2003), and, on a regional scale, nonnative plants are likely also contributing to climate change. Sixteen years ago, it was estimated that at least 3% of the planet’s ice-free land surface area was covered by nonnative plants, even excluding areas under agricultural cultivation (Mack 1997). Increasingly large areas of tropical forest in Central and South America are converted to grassland dominated by African species (Mack and Lonsdale 2001), with potentially strong

<sup>6</sup> <http://www.cbd.int/invasive/>

<sup>7</sup> [http://www.iucn.org/about/union/secretariat/offices/iucnmed/iucn\\_med\\_programme/species/invasive\\_species/](http://www.iucn.org/about/union/secretariat/offices/iucnmed/iucn_med_programme/species/invasive_species/)

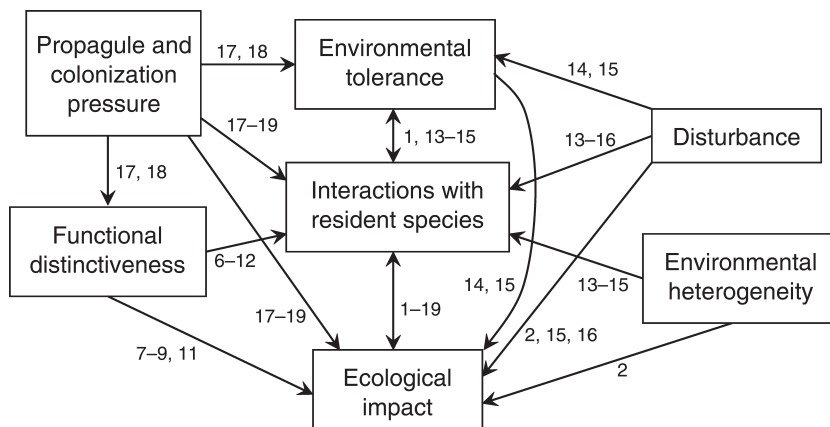


FIG. 1. Potential pathways of community-level and ecosystem-level impacts. Numbers refer to the hypotheses described in Table 1.

effects on carbon cycling, albedo, and hydrology in these regions (Williams and Baruch 2000, Jackson et al. 2002, Ehrenfeld 2011). Understanding the respective roles of invasion and other anthropogenic stressors in causing ecological impacts is a key challenge for invasion ecology.

The complexity and idiosyncrasy of impact is now well recognized. Studies have revealed that community- and ecosystem-level impacts are driven by myriad indirect, often subtle, sometimes cascading effects (Jones et al. 1998, White et al. 2006, Simberloff 2011), which can yield counterintuitive results. For example, nonnative herbivorous insects released to control European spotted knapweed (*Centaurea maculosa*) in North America occasionally exacerbate knapweed's negative effects on neighboring native plants (Callaway et al. 1999). Yet, although impacts are highly context dependent and potentially complex, they are not entirely unpredictable. The type and direction (but usually not the magnitude) of many impacts can be forecasted from the invasion history of a species if it is sufficiently broad and well documented (Grosholz and Ruiz 1996, Ricciardi 2003, Kulhanek et al. 2010a, b). Data from multiple invaded sites across environmental gradients can be used to predict particular types of impact, although this has been done for only a few invaders to date (Ricciardi 2003, Kulhanek et al. 2010b). A number of studies have attempted to use ecological traits to predict which nonnative species will have negative impacts, based on expected relationships between the per capita effect of the species and features of its biology and life history (McIntyre et al. 2005, Keller et al. 2007, Nentwig et al. 2009, Shirley and Kark 2009). Trait-based approaches have had limited success thus far (NRC 2002), perhaps because the *interactions* between the traits of a nonnative species and the recipient environment are ultimately important but have hardly been explored. Impacts have been related to functional differences between the traits of the nonnative and of the recipient community (Vitousek 1990, Ricciardi and Atkinson 2004), but few

studies have examined traits of highly invaded communities that differ in their resistance to invasion-mediated change (Levine et al. 2003).

#### *What generalizations exist?*

Given the complexity of the mechanisms and mediators of ecological impact (Fig. 1), it is perhaps not surprising that there are no general models for predicting the consequences of invasions (Parker et al. 1999, Williamson 1999, Lockwood et al. 2013). As such, there are few reliable methods available to managers to guide decisions regarding which species introductions are relatively safe and which ones should be prioritized for prevention or control (Byers et al. 2002, NRC 2002). Nevertheless, the burgeoning number of empirical and experimental studies of a broad array of taxa and ecosystem types (e.g., reviewed by Ricciardi and MacIsaac 2011, Simberloff 2011, Vilà et al. 2011, Pyšek et al. 2012) has revealed insights into why some nonnative species have greater impacts than others and why some ecosystems are more vulnerable to being altered by such species. As a fundamental step toward synthesis, we review testable hypotheses that have been developed from these studies and organize them into categories reflecting their conceptual linkages (Table 1).

#### HYPOTHESES BASED ON TRAITS OF SPECIES OR ECOSYSTEMS

A large proportion of the literature in invasion ecology has examined either the traits of nonnative species or those of recipient communities to explain particularly damaging invasions. Species traits have been demonstrably linked to invasiveness (Kolar and Lodge 2002, van Kleunen et al. 2010), but less so to impact (Byers et al. 2002, NRC 2002, Ricciardi 2003, Pyšek et al. 2012, Lockwood et al. 2013). Some physiological, behavioral, and life history correlates of impact have been identified for terrestrial plants (McIntyre et al. 2005, Pyšek et al. 2012) and mammals (Nentwig et al. 2009). For example, the rapid exploitation of resources (e.g., a high predation rate) is

commonly observed among high-impact invaders (Strayer et al. 1999, Johnson et al. 2008, Morrison and Hay 2011, Dick et al. 2013), although its generality has not been tested.

Elevated fecundity can allow nonnative species to dominate a landscape, according to spatial models (e.g., mass effects in meta-community models; Leibold et al. 2004). The classic competition/colonization trade-off, which allows a superior competitor and superior disperser or offspring-producer to coexist, recognizes fecundity and dispersal as the counterbalance to niche exploitation (Tilman 1997, Chesson 2000b, Mouquet et al. 2005). An empirically based risk assessment of freshwater mollusks identified fecundity as a predictor of pest status (Keller et al. 2007), but such studies remain rare. Fecundity has not received as much empirical or theoretical consideration as propagule pressure in the invasion literature, but models suggest that fecundity can influence the dominance of nonnative plants (Richardson and Rejmanek 2004) and that it interacts with environmental conditions to influence the impacts of nonnative species (Jacquelyn et al. 2005, Shea et al. 2005).

All such traits must be considered in context with the traits of the affected system, where productivity, disturbance regime, insularity, and area interact with nonnative species to determine the magnitude and direction of system disruptions (Li and Moyle 1981, Tilman 1999, Levine et al. 2003, Simon and Townsend 2003, Thomsen et al. 2011, Pyšek et al. 2012; see also *Uncontrolled consumers/enemy release hypothesis*). Rather than enumerating hypotheses based on each possible trait, we have organized all the other hypotheses based on community structure, niche components, propagule influx, changing environments, and synergistic effects.

#### HYPOTHESES BASED ON COMMUNITY STRUCTURE

##### *Trophic position*

A nonnative species' trophic position has long been thought to have a strong bearing on its community- and ecosystem-level impacts (Elton 1958, Li and Moyle 1981, Ehrlich 1989, Lodge 1993, Moyle and Light 1996, Strayer 2010). A few highly visible and well-publicized cases have led to the perception that nonnative predators (particularly apex predators) can generate profound impacts on native ecosystems, including the extinction of native prey. The most notable examples are the loss of dozens of species of native birds, reptiles, and bats after the introduction of the brown tree snake (*Boiga irregularis*) to Guam and the disappearance of hundreds of haplochromine cichlid fishes following the proliferation of the Nile perch (*Lates niloticus*) in Lake Victoria. An analysis of IUCN-documented extinctions concluded that nonnative species, particularly predators, were a leading cause of biodiversity loss (Clavero and García-Berthou 2005). However, several studies of native bird and fish assemblages found little evidence that trophic position is a strong predictor of community-

level impact (e.g., Marchetti et al. 2004a, Blackburn et al. 2005).

Trophic hypotheses also implicate nonnative herbivores (Nunez et al. 2010, Strayer 2010) and omnivores (Ehrlich 1989) as being disruptive to particular communities. Intense grazing by zebra mussels (*Dreissena polymorpha*) in North American lakes and rivers (Ricciardi 2003, Ward and Ricciardi 2007, Higgins and Vander Zanden 2010) and by goats on islands (Courchamp et al. 2003) has created enormous ecological impacts. Disruptive nonnative omnivores include the rusty crayfish (*Orconectes rusticus*) in the North American Great Lakes (Bobeldyk and Lamberti 2010), the king crab (*Paralithodes camtschaticus*) in the Barents Sea (Falk-Petersen et al. 2011), and Eurasian rats (*Rattus rattus* and *R. norvegicus*) introduced to islands worldwide (Jones et al. 2008, St. Clair 2011). On the other hand, Moyle and Light (1996) argued that, although omnivorous fishes may alter ecosystem properties, they generally have had little effect on the composition of invaded assemblages.

In multivariate categorical analyses (e.g., multiple logistic regression, regression trees, information theoretic analyses) searching for repeated traits among a suite of similar or related organisms, trophic position has demonstrated little or no importance (Marchetti et al. 2004a, b, Blackburn et al. 2005). Marchetti and colleagues examined eight variables to predict the impacts of successfully established nonnative fish in California and found no support for trophic position's importance in one analysis (Marchetti et al. 2004a) and only a slight effect in a study that used an alternative statistical technique (Marchetti et al. 2004b). In related work, Blackburn et al. (2005) tested the effect of different nonnative mammalian diet strategies (e.g., omnivory, vertebrate flesh eating, egg eating, herbivory) on native bird extinctions on oceanic islands and found that each mammal species had unique impacts on the native avian fauna regardless of its trophic position.

The lack of a clear effect of trophic position may be due to the simplified, semi-arbitrary categorization necessary to parse organisms into discrete classes, particularly given the varying degree of omnivory found in a majority of animal taxa (Polis 1998, Moyle and Marchetti 2006). In addition, many of these analyses focus on extinction data, which may not be rich enough to distinguish multiple interacting factors. Early theory posited that omnivory destabilized food webs (Pimm and Lawton 1978), but recent theoretical work suggests that weak omnivory can stabilize complex food webs and reduce extinction probabilities (e.g., McCann and Hastings 1997, Vandermeer 2006). Thus, nonnative omnivores might stabilize systems while having strong effects on some individual species, if their trophic interactions are weak (Ingram et al. 2009). Finally, large community-level impacts tend to be caused by nonnative species that can create food web links, redirect energy, or cause trophic cascades (Vander Zanden et al.

TABLE 1. Published hypotheses regarding the ecological impact of nonnative species.

Theme/hypothesis	Reference for hypothesis	Prediction
I) Hypotheses based on traits of species or ecosystems		
1) Species traits	Baker (1965), Ehrlich (1989)	Behavioral and life history traits (e.g., fecundity, body size, aggression) determine which nonnative species alter communities; e.g., stronger impacts are caused by species with higher reproductive potential and/or greater rates of resource consumption.
2) Ecosystem traits (apart from diversity)	Li and Moyle (1981), Moyle and Light (1996)	Ecosystem characteristics (e.g., productivity, disturbance regime, insularity, area) determine which systems are more vulnerable to disruption by a nonnative species.
II) Hypotheses based on community structure		
3) Trophic position	Elton (1958), Davis (2003), Clavero and Garcia-Berthou (2005)	Greater impacts are expected from predatory (rather than competitive) interactions. Top predators are the most disruptive.
4) Uncontrolled consumer/enemy release	Pimm (1987, 1991)	The greatest impacts are caused by generalist consumers that are uncontrolled by predators.
5) Biotic resistance	Elton (1958), Moyle and Light (1996)	Diverse communities are more resistant to being altered by nonnative species. Impacts are buffered in complex food webs.
III) Niche-based hypotheses		
6) Niche replacement/limiting similarity	Elton (1958)	Nonnative species that have niche overlap with natives and are superior competitors have larger impacts.
7) Novel resource use/trait distinctiveness	Vitousek (1990), Cleland (2011)	Nonnative species that use key resources differently from natives will have larger impacts.
8) Novel weapons	Callaway and Ridenour (2004)	Stronger impacts are exerted by nonnative species that release novel allelopathic, defensive, or antimicrobial chemicals.
9) Ecosystem engineering	Crooks (2002), Cuddington and Hastings (2004), Wright and Jones (2004)	Nonnative ecosystem engineers that modify habitat in unique ways have larger impacts.
10) Evolutionary naïveté	Diamond and Case (1986), Cox and Lima (2006)	The impact of nonnative species depends on the recipient community's evolutionary experience with functionally similar species.
11) Phylogenetic distinctiveness	Ricciardi and Atkinson (2004)	Larger impacts are caused by nonnative species that add novel taxa to the community.
12) Evolution of increased competitive ability (EICA)	Blossey and Nötzold (1995)	In the absence of enemies, nonnative plants can reallocate resources from defense mechanisms into growth and reproduction, and thus dominate native competitors.
IV) Hypotheses related to a changing abiotic environment		
13) Environmental heterogeneity	Levine and Rees (2004), Melbourne et al. (2007)	Spatial or temporal heterogeneity creates refugia against the impacts of nonnatives on native populations, and vice versa, thereby allowing coexistence.
14) Environmental matching	Kestrup and Ricciardi (2009)	The impact of a nonnative is inversely correlated with the distance of the novel habitat conditions from the species' environmental optimum.
15) Disturbance/directional change	MacDougall and Turkington (2005)	Disturbance and directional changes in the environment create conditions that disfavor some native species and favor nonnative species, thereby magnifying the impacts of the latter.
16) Dynamic equilibrium model	Huston (1979, 2004)	Disturbance, productivity, and competitive ability determine rates of competitive displacement. Larger impacts occur in systems with high productivity and high disturbance.
V) Organismal influx		
17) Propagule pressure	Ricciardi et al. (2011a)	Impacts are a function of the number, composition and frequency of introduced propagules.
18) Colonization pressure	Alpert (2006), Lockwood et al. (2009)	A higher rate of species introductions increases the probability of a nonnative species that has large impacts.
VI) Synergistic effects		
19) Invasional meltdown	Simberloff and Von Holle (1999), Ricciardi (2005)	As more nonnative species are added to a system, some nonnatives will facilitate others, thereby resulting in an accumulation of nonnatives and their synergistic impacts.

TABLE 1. Extended.

Similar concepts	Considered important for establishment?	Tested for impact?
uncontrolled generalist consumer, phylogenetic distinctiveness, novel resource use	yes	yes, for some taxa (e.g., Keller et al. [2007], Morrison and Hay [2011])
biotic resistance	yes	yes, with mixed results; (e.g., islands vs. mainlands; Ebenhard [1988], Vilà et al. [2011], Pyšek et al. [2012])
uncontrolled consumer	no	yes, but no significant effect found (Marchetti et al. [2004a, b], Blackburn et al. [2005])
species traits hypotheses, EICA	explains post-establishment success	no
limiting similarity	yes	yes (Robinson and Wellborn [1988], Levine et al. [2004], Maron and Marler [2008], Carey and Wahl [2010])
biotic resistance	yes	yes, with mixed results (Simberloff [1981], Forsy and Allen [1999], Hoopes and Hall [2002])
species traits, phylogenetic distinctiveness	yes	yes, for some taxa (e.g., Morrison and Hay [2011])
ecological naïveté, phylogenetic distinctiveness	explains post-establishment success	yes, mostly for terrestrial plants (Wardle et al. [1998], Callaway et al. [2008], Letnic et al. [2008])
novel resource use	explains post-establishment success	yes (Vitousek et al. [1987], Crooks [2002], Gonzalez et al. [2008])
novel resource use, novel weapons, phylogenetic distinctiveness	no	see novel weapons and phylogenetic distinctiveness
evolutionary naïveté	yes	yes (Ricciardi and Atkinson [2004], Strauss et al. [2006])
enemy release, novel weapons	explains post-establishment success	not directly, and supporting evidence is weak (reviewed by Blumenthal et al. [2009])
environmental matching	yes	yes, for spatial heterogeneity (e.g., Kestrup and Ricciardi [2009]) and, more rarely, for temporal heterogeneity (e.g., Levine and Rees [2004], Strayer et al. [2006])
environmental heterogeneity, disturbance/directional change	yes	yes, for aquatic animals (e.g., Taniguchi et al. [1998], Jokela and Ricciardi [2008], Alcaraz et al. [2008], Kestrup and Ricciardi [2009])
environmental matching	yes	yes, primarily for terrestrial plants (e.g., D'Antonio and Vitousek [1992], Byers et al. [2002])
ecosystem traits	yes	yes, for terrestrial plants (Brewer [2011])
colonization pressure	yes	not directly
propagule pressure, invasional meltdown	yes	not directly (see Ricciardi and Kipp [2008])
colonization pressure	yes	yes (e.g., Ricciardi [2001, 2005], Levin et al. [2002], O'Dowd et al. [2003])

1999, Simon and Townsend 2003, Baxter et al. 2004, Carlsson et al. 2004, Kurle et al. 2008, Kimbro et al. 2009). This effect has never been formalized into a testable hypothesis, partly because it has been unclear how to quantitatively differentiate a disrupted food web from one with a newly added species. More recently, however, it has become feasible to quantify some impacts at the community or ecosystem level (i.e., trophic cascades or alterations to energy flow) using stable isotope analysis (Vander Zanden et al. 1999, 2003, Maron et al. 2006).

#### *Uncontrolled consumers/enemy release hypothesis*

A special subset of the trophic position hypothesis posits that an uncontrolled predator will have strong effects, particularly in insular systems where communities are naïve (see ecological naïveté hypothesis), native populations are small or limited in extent, and refugia are scarce (e.g., Herbold and Moyle 1986, Pimm 1987, Ebenhard 1988). The largest community-level impacts are caused by generalist consumers introduced to simple communities, in which they are likely to attain high densities and drive some resident species to extinction. Pimm (1991) draws a parallel between cascading food web effects caused by the loss of predators and those caused by the introduction of consumers into places where higher predators are lacking; this equivalency links food web theory, species-removal experiments, and the trophic position hypothesis for invasion impacts. Indeed, insular habitats such as lakes and oceanic islands appear to be disproportionately vulnerable to the impacts of nonnative generalist predators and herbivores (Ebenhard 1988, Cox and Lima 2006, Ricciardi and MacIsaac 2011).

Pimm (1991) discusses “uncontrolled consumers” and “release from enemies” simultaneously because both hypotheses suggest that a lack of top-down control leads to an expanding nonnative population and, hence, greater impact. Evidence for the enemy release hypothesis (Keane and Crawley 2002) is contradictory. There is a distinct difference in results between biogeographic studies that compare numbers of enemies in native vs. nonnative ranges and community studies that examine the effect of enemies on native and nonnative species (Colautti et al. 2004). Biogeographic studies appear to show consistent, but insufficient, evidence in favor of enemy release, whereas community studies suggest that nonnative species are no less affected by enemies than native species within the same local community. This discrepancy is important when considering impacts; exposure to fewer enemies may allow nonnative species to shift resources toward growth and reproduction in ways that improve competitive ability and thus increase their impacts, but the relationship between enemy release and impact is complicated by context dependence (Colautti et al. 2004, Zangerl and Berenbaum 2005). For plants, the release from enemies is hypothesized to lead to additional resources available for allocation to

growth or reproduction (Blossey and Nötzold 1995; see subsection *Evolution of increased competitive ability [EICA]*), which, in turn, improves the competitive ability of the nonnative and its potential for impacts on natives.

#### *Biotic resistance*

The biotic resistance hypothesis predicts that a diverse community is more likely to limit the establishment, population growth, and impact of nonnative species (Elton 1958, Levine and D’Antonio 1999, Levine et al. 2004), based on the premise that a richer assemblage should have a greater number of filled niches (thus fewer opportunities for colonization) and an elevated probability of occurrence of strong competitors and predators (Huston 1997, Crawley et al. 1999). As an explanation for establishment success, this hypothesis has received perhaps more attention than any other topic in invasion ecology, but its relevance to impact is under-studied. Biotic resistance may play a greater role in reducing impact than in preventing the establishment of an invader (Levine et al. 2004). In spite of some empirical support for biotic resistance to impact (Robinson and Wellborn 1988, Levine et al. 2004, Maron and Marler 2008, Carey and Wahl 2010), several studies suggest that species-rich environments are prone to invasion with community composition impacts and that some species-poor environments can resist invasion and impacts particularly well (Baltz and Moyle 1993, Stohlgren et al. 1999). For example, a diverse and abundant community of planktivores did not prevent a nonnative planktonic predator from extirpating native species in Canadian Shield lakes (Boudreau and Yan 2003). Contrary to the popular view that simple communities are more easily disrupted (Elton 1958), Baltz and Moyle (1993) observed that a species-poor fish assemblage in an unregulated stream resisted the establishment of nonnative fishes, despite opportunities for incursion by several species inhabiting other parts of the drainage basin. The authors instead concluded that abiotic factors (principally environmental suitability) and the presence of native predators were more important determinants of community integrity than species diversity per se. Moreover, in some cases, the nonnative species’ vulnerability to resident predators may indirectly harm native species through apparent competition: The additional prey subsidy offered by the nonnative species may enhance the predator’s population and, thus, its impact on native prey (Short et al. 2002) to the point where this impact is greater than resource competition from the nonnative species (Noonburg and Byers 2005).

#### NICHE-BASED HYPOTHESES

Many hypotheses for establishment success focus on niche differences between native and nonnative members of the community, with the assumption that the exploitation of unused resources (empty niches) or more competitive ways of accessing resources (niche replace-



ment) will allow the nonnative species to integrate into the community. These two approaches to niche differences have contrasting implications for impacts. A nonnative species that uses novel resources is unlikely to have direct competitive effects, but may have indirect effects on the native community (e.g., via alteration of ecosystem properties), whereas a nonnative species that accesses limited resources in novel ways may competitively exclude native species. Both routes can lead to significant community-level impacts.

Evolution is another obvious driver of change in the spread dynamics and impacts of nonnative species over time, and is frequently invoked to explain time lags between establishment and range expansion (see also *Environmental heterogeneity*). Evolutionary mechanisms may also combine with other mechanisms to generate impacts (e.g., the evolution of increased competitive ability during release from specialist enemies).

#### *Niche replacement/limiting similarity*

Simberloff (1981) examined limiting similarity between natives and nonnatives and found little evidence of extinction and minimal community-level impacts resulting from invasions. While this is suggestive of a predominance of empty niches (unexploited resources), Simberloff noted that there was no way to tell how many nonnative species were negatively affected by competition from residents. Herbold and Moyle (1986) used California fish assemblages to argue a very different story: Nonnatives that established into natural environments commonly led to impacts on native species. They pointed out that extinction may occur over a long time frame, and hence, a low extinction rate in a short period did not necessarily imply low impact. They also took issue with Simberloff's focus on human-dominated or disturbed landscapes (in which they expected lower impacts) and his pooling of island and mainland invasions (with the expectation that islands experience higher impacts). In fact, Simberloff's (1981) results did suggest higher impacts on islands. A number of recent articles have reinvigorated this debate by drawing attention to the apparent lack of native extinctions following the introduction of nonnative species (e.g., Sax et al. 2002, Davis 2003, Sax and Gaines 2003, Gurevitch and Padilla 2004). The rejoinders (e.g., Olden and Poff 2003) offer similar arguments as Herbold and Moyle (1986). Meta-analyses have found no significant difference between ecosystem-level impacts of nonnative nitrogen-fixing plant species on islands and mainlands (Vilà et al. 2011), but nonnative plants in general are far more likely to cause reduced plant and animal richness on islands (Pyšek et al. 2012).

The more important distinction may be the role of available resources (Davis et al. 2000). Shea and Chesson (2002) build on community ecology theory and limiting similarity to revive the key idea that available resources are equivalent to an empty niche and, therefore, increase the potential for successful

establishment by nonnative species. Extending the available resource argument to impacts takes us back to the hypothesis that nonnative species with limited niche overlap with natives should have limited direct impacts. We might expect to see strong impacts from niche overlap with a superior nonnative competitor; for example, Bryce et al. (2002) examined niche overlap in red and grey squirrels to explain areas of coexistence and areas of exclusion by the nonnative greys. Hoopes and Hall (2002) consider niche overlap by arguing that a nonnative plant that excludes a native plant from a portion of its potential habitat probably has smaller regional effects than a nonnative that impacts a native over its entire range of habitat types. This expectation can be extended further to contrast niche and fitness differences between natives and nonnatives, with the idea that niche differences should increase coexistence, whereas fitness differences should lead to negative impacts and potential exclusion (Melbourne et al. 2007, MacDougall et al. 2009). Hejda et al. (2009) found that plants that could create substantially denser stands than native species were likely to have the strongest impacts; here, the difference between the native and invasive fitness was more important than absolute fitness. One exception to the niche/fitness dichotomy may lie with rare species that may leave gaps in resource use that can be exploited by nonnative species (Forys and Allen 1999); here, we would expect that the reduced abundance of the native would aid establishment of the nonnative species, whose presence would potentially accelerate the local extinction of the native.

#### *Novel resources/novel weapons/novel behavior*

Substantive impacts have been shown to occur when a nonnative species transforms key resources or uses them differently from resident species (Vitousek 1990; see also *Ecosystem engineering*). For example, nonnative nitrogen-fixing plants alter nutrient availability and dynamics in their new habitats (Allison and Vitousek 2004, Caldwell 2006, Cipollini et al. 2008) in ways that create wholesale changes to community structure (Carino and Daehler 2002, Lorenzo et al. 2010) and ecosystem development (Vitousek et al. 1987). It has been suggested that successfully established nonnatives with traits that diverge from those among natives in the invaded community are most likely to cause strong impacts, because they may fundamentally alter ecosystem processes (Vitousek 1990, Cleland 2011; but see Vilà et al. 2011).

Novel weapons (unique biochemical, physical, or behavioral attributes that repel enemies) have surprisingly widespread effects ranging from changes in nutrients to changes in trophic structure. The most common examples come from plant allelopathy (Callaway and Ridenour 2004, Stinson et al. 2006, Callaway et al. 2008). Allelopathic compounds can disrupt native mutualisms in such a way as to reduce the performance

of native plants (Stinson et al. 2006, Callaway et al. 2008), and improve nutrient availability for the nonnative species (Chen et al. 2009, Tharayil et al. 2009). Through such intimate interactions, allelopathy can profoundly alter ecosystem function (Wardle et al. 1998). Although some invasive animals (e.g., cane toads *Bufo marinus*) can produce toxic secretions that can damage predator populations (Letnic et al. 2008), the novel weapons hypothesis has been studied exclusively for terrestrial plants to date (Jeschke et al. 2012).

The novel weapons concept could be extended to include new behaviors that alter species interactions and can thus compound some of the trophic effects. The displacement of native animals has often been attributed to heightened interspecific aggression by a nonnative species (Dubs and Corkum 1996, Holway et al. 1999, Pintor et al. 2009). On oceanic islands, prey species often have not evolved with a full complement of predator archetypes and, therefore, may have lost a suite of anti-predator behaviors through time, especially those that are in some way evolutionarily costly to maintain (Lahti et al. 2009). From this perspective, it is not the foraging preference or aggression of the nonnative predators that necessarily drives large impacts, but rather the weak or nonexistent anti-predator behaviors of the native prey themselves (Banks and Dickman 2007; see ecological naïveté hypothesis). Sih et al. (2010) note that predatory impacts arise even from nonconsumptive interactions between predator and prey; in consumptive interactions, the impact or cost to the prey population is the loss of individuals through ingestion, but there also exist nonconsumptive costs of anti-predator behaviors, such as maintaining vigilance for predators instead of foraging. The two costs have been shown to be nearly identical in terms of their effects on prey population size (Preisser and Bolnick 2008).

#### *Ecosystem engineering*

Ecosystem engineering, as applied to the impacts of nonnative species, is a concept closely allied to the novel resource use hypothesis. Nonnative ecosystem engineers can modify their habitat to create more favorable conditions for themselves and, at the same time, impact native communities. Although this concept is similar to changes in species richness and community structure that accompany succession, nonnative ecosystem engineers tend to alter environments on shorter time scales than successional change. Some theoretical work suggests that nonnative engineers in suboptimal habitats can have accelerating rates of spread as they alter habitats toward their own optimum (Cuddington and Hastings 2004, Cuddington et al. 2009). For example, beavers can alter habitat to the point where it no longer supports them and then must disperse to a new area. In highly stressful environments, ecosystem engineers may facilitate a range of native and nonnative species by ameliorating stressful conditions (Crain and Bertness 2006), but they can lower species richness by reducing system complexity (Crooks

2002) or by shifting ecosystem productivity away from intermediate levels (Wright and Jones 2004). Even when they do not successfully establish, nonnative ecosystem engineers may still initiate a process of habitat alteration in which successive introductions produce cumulative changes that both facilitate the engineer's eventual establishment and produce impacts, even before its population increases appreciably (Gonzalez et al. 2008). Nonnative engineers also complicate restoration efforts; even if they can be eradicated, the altered habitat may remain unsuitable to the original native community for an extended period of time (Byers et al. 2006, Buckley et al. 2007, Gonzalez et al. 2008).

#### *Evolutionary naïveté/phylogenetic distinctiveness*

The disproportionate effects of nonnative predators and herbivores introduced to islands, lakes, and other insular ecosystems have been attributed to prey naïveté: a lack of evolutionary exposure to functionally similar organisms (Diamond and Case 1986, Short et al. 2002, Cox and Lima 2006, Berglund et al. 2009). This explains why nonnative predators and herbivores appear to have stronger effects on native prey populations than do native predators (Parker et al. 2006, Salo et al. 2007). Naïveté can also explain variation in the impacts of nonnative competitors. For example, the zebra mussel, a dominant biofouling mollusk, has contributed to severe population declines of North American freshwater mussels, which evolved in the absence of such organisms. By contrast, European mussels that had been exposed to the zebra mussel prior to the last glaciation generally did not suffer comparable impacts (Ricciardi et al. 1998). Other examples suggest that naïveté can be devastating even for continental biota: (1) the replacement of native red squirrels by nonnative grey squirrels in Europe is mediated by the natives' lack of immunity to a virus carried by the greys (Tompkins et al. 2003), (2) a fungal pathogen carried by nonnative North American crayfish has decimated native crayfish populations throughout Europe (Reynolds 1988), and (3) a fungus introduced with Chinese chestnut trees has driven the American chestnut to near extinction (Anagnostakis 1987). Note that these are counterexamples to the enemy release hypothesis, in which there is a net positive effect of natural enemies on the nonnative species (the "enemy of my enemy is my friend" hypothesis; Colautti et al. 2004). Such net effects arise when the introduction of an enemy differentially impacts a naïve resident competitor.

A logical corollary of this hypothesis is that recipient communities are most likely to be disrupted by novel invaders: those that have no ecological analogue in the community. This concept is reflected in the previous discussion of novel resource use (Vitousek 1990) and the novel weapons hypothesis (Callaway and Ridenour 2004), but the effect may be more general. The generality of the naïveté hypothesis has been tested using phylogeny as a proxy for ecological novelty (Ricciardi and Atkinson 2004, Strauss et al. 2006), based on the

premise that ecological similarity diminishes with decreasing phylogenetic relatedness (Burns and Strauss 2011). Indeed, nonnative species belonging to novel genera in the recipient community have stronger impacts on native species in aquatic systems (Ricciardi and Atkinson 2004), and nonnative grass “pest” species are more distantly related to native grasses than are nonnative “non-pest” species in California (Strauss et al. 2006). A paradox that remains to be resolved is that novelty can also render the nonnative species naïve to the effects of resident enemies (Ricciardi and Ward 2006, Verhoeven et al. 2009, Sih et al. 2010), and thus, perhaps limit its impact within some recipient communities.

#### *Evolution of increased competitive ability (EICA)*

Given that it is expected that nonnative species perform better in the absence of their specialist predators or parasites (see *Enemy release hypothesis*), if they arrive in their new range without these enemies, they may divert available energy and resources (previously allocated to defenses) to growth and reproduction (Coley et al. 1985). This hypothesis helps explain increased competitive ability and the potential for increased invasion success as well as increased impacts, although the latter aspect has not been tested explicitly. Blossey and Nötzold (1995) suggested that, in the absence of specialist herbivores, nonnative plants reallocate defense resources in ways that enhance their competitive ability (e.g., through increased growth and reproduction, or the production of allelopathic chemicals). Although EICA is intuitively appealing, particularly for explaining sudden increases in dominance and impacts from long-established nonnatives, empirical evidence for it is mixed (DeWalt et al. 2004, Rogers and Siemann 2004, Franks et al. 2008), potentially because escape from enemies and evolution of increased competitive ability may take place in the context of resource availability (Blumenthal 2006). Blumenthal et al. (2009) found that plants from resource-rich environments indeed had more enemies in their native environment and lost more enemies in the invasion of a novel environment, but they did not find evidence of such plants having higher impacts.

#### HYPOTHESES RELATED TO A CHANGING ABIOTIC ENVIRONMENT

One issue with niche hypotheses is that they rely to some extent on equilibrium outcomes and neglect the dynamic nature of ecological systems. Hypotheses that ignore environmental change may be rendered irrelevant by temporal heterogeneity. Spatial heterogeneity is another cause of context-dependent impacts. Recognizing these aspects, a series of hypotheses combine niche concepts with the effects of spatial or temporal variation.

#### *Environmental heterogeneity*

Spatial and temporal heterogeneity can mitigate the impacts of nonnative species by limiting the nonnative’s

abundance or by creating refugia for natives, thereby allowing coexistence at local and regional meta-community scales (Levine and Rees 2004, Melbourne et al. 2007, Kestrup and Ricciardi 2009). If native and nonnative species differ in their ability to acquire and use resources as the environment varies, then they may coexist when each species can exploit resources during favorable periods in ways that allow them to endure temporarily unfavorable periods (Chesson 2000a, b). Co-occurring species that exploit slight variations differently will lead to greater species richness rather than exclusion (Melbourne et al. 2007), although the nonnative species may still alter community structure and native species abundance. As such, Melbourne et al. (2007) conclude that competitively dominant nonnative species will have a larger impact on native communities in homogeneous, rather than heterogeneous, environments.

Few empirical studies have examined the influence of temporal environmental variation on the impact of an invasion (Strayer et al. 2006, Hawkes 2007, Melbourne et al. 2007, Thomsen et al. 2011), although some research has demonstrated long-term changes in impact that might be linked to fluctuating habitat conditions or to the population dynamics of the nonnative species (Crooks 2005, Strayer et al. 2006, Strayer et al. 2011). Rapid density-dependent population growth can result in short time lags between species introduction and conspicuous impacts, but prolonged lags (up to 100 years or more; e.g., Rilov et al. 2004) may result from habitat shifts, evolutionary adaptation by the nonnative species, or increased vulnerability of native species as a result of changes in food webs, disturbance regimes, or other biotic and abiotic conditions (Byers 2002, Crooks 2005, Hawkes 2007).

#### *Habitat filtering/environmental matching*

Local environmental conditions can limit the survivorship and reproductive success of nonnative species (e.g., Helms and Vinson 2005), an effect termed “habitat filtering” (Weiher and Keddy 1999). Suboptimal conditions may limit the impacts of nonnatives by constraining performance or population size. This constraint is illustrated by spatial variation in competitive interactions between nonnatives and natives along environmental gradients (Taniguchi et al. 1998, Alcaraz et al. 2008, Kestrup and Ricciardi 2009). We would expect peak performance, and thus a stronger per capita effect, from a nonnative species in an environment that closely matches its physiological optimum (Fig. 2). This hypothesis has value in risk assessment models by offering a basis for the selection of environmental predictors of impact (e.g., Jokela and Ricciardi 2008), provided that the nonnative species does not adapt to new conditions such that its physiological optimum changes over time.

#### *Disturbance/directional change*

Disturbance that removes native species or that shifts an environment further from physiological conditions

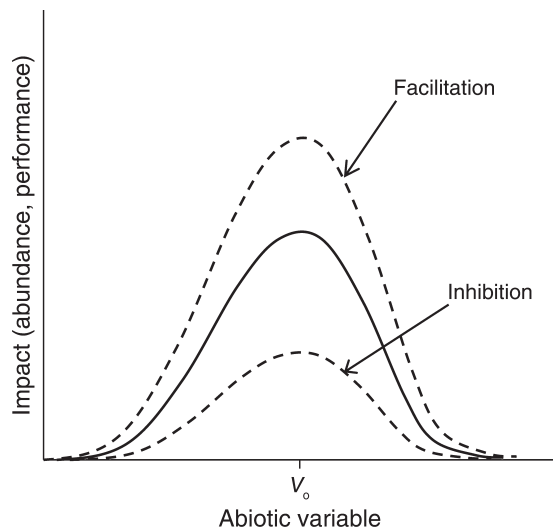


FIG. 2. Variation in impact, as explained by the environmental matching, biotic resistance, and biotic facilitation hypotheses. Ecological impact is correlated with the invader's abundance or performance (e.g., feeding efficiency), which declines with distance between the ambient condition and a physiological optimum,  $V_0$ , along an abiotic gradient (environmental matching hypothesis), and co-varies with resident species interactions; the latter resulting in either inhibition (biotic resistance hypothesis) or facilitation of the invader (invasional meltdown hypothesis).

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favored by the native community will promote the establishment and dominance of nonnative species (Lockwood et al. 2013). In this context, disturbance has two linked components: (1) It is accompanied by the physical removal of resident organisms, and thus may free resources for opportunistic invaders (Davis et al. 2000); and (2) if the disturbance includes directional change (a shift in abiotic conditions), then the environment may become increasingly less hospitable for natives (Stachowicz et al. 2002). Nonnative species could appear to have very large per capita effects arising from impacts that are exacerbated by suboptimal conditions for natives (Byers 2002) or that actually stem directly from the disturbance itself (King and Tschinkel 2008). The generality of disturbance as a moderator of invasion success and impact has not been explored. There is some evidence that disturbance is more important for the establishment and range expansion of introduced plants than for animals (Lozano and MacIsaac 1997). A well-known case in which nonnative dominance is favored by changes in disturbance is when natural fire regimes are altered by introduced plants: For example, by accelerating the frequency of fires from 60–100 years to 3–5 years through a positive feedback, cheatgrass (*Bromus tectorum*) dominates North American prairies (D'Antonio and Vitousek 1992). The role of disturbance in nonnative animal dominance has been demonstrated in shallow marine benthic environments, where the availability of primary colonizable space is limited; but the influence of disturbance on impact in

these environments has not been studied beyond its effect on the ability of nonnative fouling invertebrates to monopolize substrate (Altman and Whitlatch 2007).

#### *Dynamic equilibrium*

The dynamic equilibrium model of species diversity integrates disturbance, productivity, and competitive ability to determine rates of competitive displacement (Huston 1979). This model predicts that, for native and nonnative species alike, disturbance will cause diversity to increase in highly productive environments (by removing dominant species and allowing inferior competitors to survive) and decline in unproductive environments (where competition is limited) (Huston 1979, 1994). Huston (2004) adapted this theory to address plant invasions and predicted that, although we might expect a higher probability of establishment in either unproductive/undisturbed environments or disturbed/productive environments, the highest impacts from nonnative species should be in systems with high productivity and, possibly, with high disturbance. Whilst the establishment prediction of the model has some empirical support (e.g., Renne et al. 2006), the impact prediction has hardly been tested. Brewer (2011) has recently found that the effects of Japanese stilt grass (*Microstegium vimineum*) are greater in shady forests than in open floodplain forests, owing to lower species diversity in the floodplain gaps. By contrast, one study suggests that impacts of introduced aquatic predators are highest in unproductive lakes (Li and Moyle 1981).

#### HYPOTHESES RELATED TO ORGANISMAL INFLUX

##### *Propagule pressure*

Propagule pressure describes the number of nonnative individuals released in a single event or in several events spread through time. The higher the propagule pressure, the more likely a species is to establish a self-sustaining population (Simberloff 2009). Although the relationship to establishment success has been demonstrated numerous times across a variety of species, the influence of propagule pressure on impact is still poorly elucidated. One mechanism by which propagule pressure can influence impact is by enhancing post-establishment population growth (Ricciardi et al. 2011a). Large numbers of initial colonists could increase the rate of population growth by allowing the incipient population to overcome a suite of factors associated with small population size (e.g., Allee effects, stochastic events), and this rapid growth could have concomitant effects on other members of the community. However, few researchers have tested the key premise that higher propagule pressure leads to higher population growth rates.

An additional aspect of propagule pressure is that a higher influx of individuals may also include more genotypes of the nonnative species, each having potentially different per capita effects (see also *Colonization pressure*). As a large number of individuals are

released by various transport vectors into an area, there is an increasing probability of introduction of harmful genotypes or individuals capable of hybridizing with natives (reviewed in Ricciardi et al. 2011a). In addition, the novel genetic admixtures that are produced under such circumstances can lead to higher impacts if they allow a nonnative species to evolve quickly to local conditions, acquire a key trait to expand its niche, or evolve novel resource use. It is not clear how often high propagule pressure is associated with an increase in the diversity of genotypes introduced, but this could be a powerful mechanism for generating strong impacts and for causing the impacts of an established species to change over time.

#### *Colonization pressure*

Colonization pressure refers to the number of nonnative species, subspecies, or genotypes released; it is a taxon-level equivalent to propagule pressure (Lockwood et al. 2009). Higher colonization pressure leads to higher nonnative species establishment simply by chance (Colautti et al. 2006, Lockwood et al. 2009), and thus increases the probability that a harmful taxon will be added to the recipient community (Alpert 2006). In aquatic systems, for example, the number of nonnative species that are implicated in severe declines of native populations is a simple linear function of the total number of nonnative species present, indicating a sampling effect (Ricciardi and Kipp 2008). Colonization pressure also increases the number of nonnative species that can interact with each other, as well as the likelihood of the re-assembly of coevolved species complexes, potentially leading to synergistic effects.

#### HYPOTHESES ADDRESSING SYNERGISTIC EFFECTS

##### *Invasional meltdown/biotic facilitation*

Over the past decade there has been increasing recognition of the importance of facilitative interactions and coevolved adaptations in determining the consequences of species introductions. The invasional meltdown hypothesis predicts that increasing colonization causes ecosystems to become progressively more invaded and disrupted, resulting in a rapid accumulation of nonnative species and their impacts (Simberloff and Von Holle 1999). It stems from the observation that facilitations are at least as common as antagonistic interactions among nonnative species (Simberloff and Von Holle 1999, Ricciardi 2001, Bruno et al. 2003). Although most studies citing this hypothesis focus predominantly on cases in which one nonnative species promotes the establishment of another, the hypothesis also encompasses the consequences arising from nonnative species that enhance one another's population growth or per capita effect. Such positive interactions can produce synergistic impacts in which the joint effect of two or more interacting species is greater than the sum of the effects of the species acting alone; evidence of this phenomenon is found among various taxa in

terrestrial, freshwater, and marine systems (Simberloff and Von Holle 1999, Ricciardi 2001, 2005, Levin et al. 2002, O'Dowd et al. 2003).

Because facilitations may be most frequent and strongest among coadapted nonnative species, combinations of such species are more likely to generate synergistic impacts (Ricciardi 2005). In particular, nonnative mutualisms that improve the fitness of each species can magnify their respective impacts (Rudgers and Clay 2008); even nonnative predator-prey and parasite-host species combinations can produce magnified impacts on native species (Tompkins et al. 2003, Hay et al. 2004, Dick et al. 2010). For example, the predatory impact of the brown tree snake (*Boiga irregularis*) in Guam was exacerbated in the presence of its coevolved prey, which subsidized the snake's diet as the snake drove several endemic species of birds, bats, and reptiles to extinction (Fritts and Rodda 1998). Similarly, in Australia, European rabbits (*Oryctolagus cuniculus*) subsidize the European fox (*Vulpes vulpes*), promoting its surplus killing of naïve native prey (Short et al. 2002). In the Great Lakes, the combined activities of Eurasian dreissenid mussels and their natural predator, the round goby (*Neogobius melanostomus*), may have facilitated the proliferation and transfer of a rare strain of *Clostridium* bacteria through the food web, resulting in recurring outbreaks of avian botulism that kill tens of thousands of native fish and waterfowl annually (Yule et al. 2006). The invasional meltdown hypothesis further predicts that synergistic disruptions will become more frequent as ecosystems become more invaded. Experimental studies of the impacts of particular combinations of nonnative species have begun to emerge (Adams et al. 2003, Johnson et al. 2009, Young et al. 2009, Relva et al. 2010), but the general relationship between impact and colonization pressure remains to be explored.

#### SYNTHESIS AND FUTURE RESEARCH

At present, our theoretical understanding of the dispersal and establishment of nonnative species is far more advanced than that of impact (Catford et al. 2009, Davis 2009, Lockwood et al. 2013). Nevertheless, in spite of the lack of explicit consideration of impact in most syntheses and conceptual frameworks of invasion (e.g., Catford et al. 2009, Blackburn et al. 2011), at least 19 hypotheses can elucidate, to some degree, why some nonnative species have greater impacts and why some ecosystems are more vulnerable to alteration by such species—research questions that are of central importance to invasion ecology (Byers et al. 2002, Levine et al. 2003, Lockwood et al. 2013). The majority of these hypotheses were constructed to understand invasiveness (establishment and spread) originally, but they can be extended to understand the impact of nonnative species by explaining variation in abundance and range size ( $A$  and  $R$ , respectively, in the Parker equation; Parker et al. 1999). The nature of the relationship between abun-

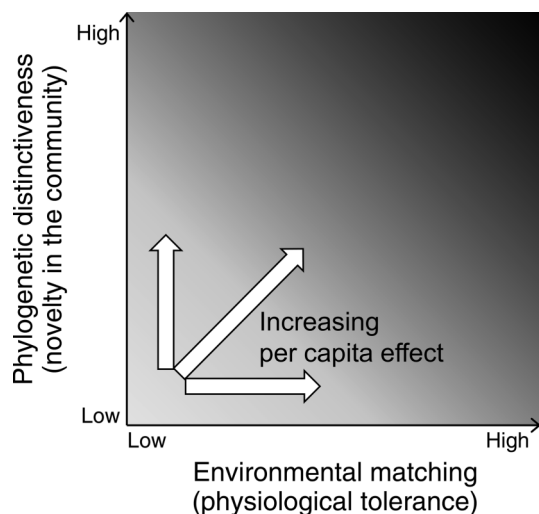


FIG. 3. Impact is a function of the interactions between traits of the invader and of the biotic and abiotic environment. The per capita effect of the invader is predicted to increase in habitats in which it is more phylogenetically distinct among resident species (phylogenetic distinctiveness hypothesis) and more physiologically matched to abiotic conditions (environmental matching hypothesis).

dance and impact remains to be elucidated; a number of plausible abundance–impact curves may exist, and each of these has important implications for management (Yokomizo et al. 2009, Thiele et al. 2010). Progress toward a theoretical framework for impact would be further enhanced through examination of factors that account for variation (within and across taxa) in the per capita effect ( $E$ ) of nonnative species. The few existing hypotheses that directly address per capita effect apply to a broad range of taxa and biomes, and perhaps could be combined to construct integrative models of impact (e.g., Fig. 3).

Similar to most concepts in invasion ecology (Catford et al. 2009), the current body of theory on impact has much overlap and redundancy, which reflects not only different approaches and histories of study but also the complexity of interacting factors governing impact (Table 1, Fig. 1). Confusion surrounding the definition of “invasive” has likely contributed to some disorganization of theory by conflating invasiveness with impact. A greater encumbrance to developing a theoretical framework is the lack of rigorous analyses and tests of generality for the vast majority of hypotheses to date. Those hypotheses that have received empirical attention tend to suffer from a taxonomic bias; for example, the EICA hypothesis has been explored exclusively for plants, but we know of no reason why it could not play a role in the impacts of nonnative animals. The hypothesized determinants of a nonnative species’ impact for which there appears to be broad empirical support include: (1) the evolutionary experience of the recipient community (ecological naïveté hypothesis); (2) the degree to which the local environment constrains the abundance of the

nonnative species (environmental matching hypothesis); (3) variation in the number, composition and frequency of individuals released (propagule pressure hypothesis), which can influence the magnitude, direction, and scope of impact; and (4) novel traits that may promote changes in availability of key resources, with large-scale consequences for community structure and ecosystem processes (ecological naïveté, novel weapons, novel resource, and trait divergence hypotheses). It is not certain whether each of these four determinants represents an irreducible level of theory; that is, they may not necessarily fit into a single hierarchical or synergistic framework, instead, they could be context dependent, or only a subset may operate in tandem. However, we believe further work will show that these determinants are complementary, and each applies broadly across taxa and biomes, and thus should be integrated into a general theory of impact.

Further research should not be limited to the hypotheses that currently have the broadest support. Although most hypotheses considered in our review (Table 1) have not yet been shown to be generally applicable across species or biomes, each can explain significant impacts in some situations. Empirical tests of generality might be accomplished through meta-analyses that allow for the quantification of probability distributions of different types of impact under different habitat conditions. The chief limitation of such studies is the availability of sufficiently detailed data on a community or ecosystem prior to invasion (NRC 2002). Nevertheless, a diversity of underexploited approaches such as micro- and meso-cosm experiments (e.g., Adams et al. 2003, Maron and Marler 2008, Carey and Wahl 2010), computer simulations (e.g., Gonzalez et al. 2008, Powell et al. 2011), and comparative analyses across geographic regions could yield much insight into the patterns and mechanisms of impact.

Future progress toward a theoretical framework will most profitably result from explicit consideration of the traits and interactions of nonnative species, the recipient community, and the abiotic environment, as well as the evolutionary context of the invasion. There is a need to develop more hypotheses that address the *indirect* effects of invasion, in which the nonnative species’ influence is transmitted through multiple interacting species, both native and nonnative. Despite being rarely studied, such effects are known to have significant consequences for communities and ecosystem function (Baxter et al. 2004, Ricciardi 2005, White et al. 2006, Nelson et al. 2010, Simberloff 2011) and can complicate management actions (Zavaleta et al. 2001). A growing awareness of the importance of multiple interacting stressors (e.g., Hobbs 2001, van der Wal et al. 2008) should provide further impetus for developing a mechanistic understanding of indirect effects and impacts in general. However, the largest challenge to understanding impact is being able to distinguish invasion-mediated effects from other co-occurring anthropogenic stressors (Didham et al. 2005, 2007, King and Tschinkel 2008), which may alter the

effects of both resident and future invaders (Byers et al. 2002), and thus are a major contributor to spatial and temporal variation in impact (Strayer et al. 2006).

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