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Progress Toward Understanding the Ecological Impacts of Non-native Species

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Abstract

A predictive understanding of the ecological impacts of non-native 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 identify and review 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 non-native 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

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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 & Vitousek 2005; Ehrenfeld 2011; Simberloff 2011). Despite considerable advances in our understanding of how non-native species spread and establish self-sustaining populations (Lockwood et al. 2013; Catford et al. 2009; Davis 2009), 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 non-native 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 & Richardson 2010). 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 & 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 non-native species. The logical implications of this definition are that (1) every non-native 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 & Fitter 1996; Kolar & 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 (Lockwood et al. 2013; Catford et al. 2012), but in reality, a non-native 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).

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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 & 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 & Cohen 2007; Kulhanek et al. 2010*a*; 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 non-native 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 conventional notion that all but a small percentage of non-native 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 non-native species in its novel range (R), its abundance (A, in numbers or biomass per m^2), 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 than can be compared across species or across sites for a given species. The per capita effect *E* must be defined explicitly because the same non-native 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

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species, different measured effects can yield a different magnitude and direction of the overall impact metric (Ward & 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 non-native species. These surrogate variables can confuse differences between invasiveness and impacts. We have defined impacts above, but invasiveness has two competing definitions: the first is that an invasive is any non-native organism that enters a novel environment with human assistance, establishes a self-sustaining population, and spreads rapidly; a second definition requires that the spreading non-native 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 & 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 focus on information relevant to increasing our predictive understanding of impacts. To that end, we consider only hypotheses that address abundance and spread as they relate to events after the establishment of a non-native 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 non-linearities in the per capita effect. A recent meta-analysis by Thomsen et al. (2011) suggested that the abundance of a non-native 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

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histories (Kulhanek et al. 2010*a*). Positive linear relationships between density and impact have been identified for some non-native species (Ricciardi 2003; Kulhanek et al. 2010*b*) 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 amongst multiple non-native species – e.g., via interference (Vance-Chalcraft & Soluk 2005) or facilitation (Simberloff & Von Holle 1999; Ricciardi 2001).

Those non-natives 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 'non-invasive' (D'Antonio & Kark 2002); this definition of impact has made the leap into non-technical literature (e.g., CBD 2010; IUCN 2010). 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 & Cohen 2007). Even sparsely distributed non-native species can have strong local impacts (e.g., the Asian clam *Potamocorbula amurensis*; Atlantic salmon *Salmo salar*), whereas widespread and abundant non-natives do not necessarily disrupt ecosystems (e.g., freshwater jellyfish *Craspedacusta sowerbyi*; dandelion *Taraxacum officinale*). Nevertheless, some of the mechanisms that control the abundance and range size of a non-native species likely also control its impacts within a community (Maron & Marler 2008; Ricciardi et al. 2011*a*).

Variation and complexity in impact: implications for prediction

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One pattern that has emerged from invasion studies is that larger impacts occur much less frequently than smaller ones (Williamson & Fitter 1996). Indeed, impacts have an inverse magnitude-frequency relationship remarkably similar to natural hazards such as earthquakes (Ricciardi et al. 2011*b*); for example, although a substantial proportion of global animal extinctions have been linked to non-native species (Clavero & 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 non-native species can vary greatly across space and time (Parker et al. 1999; Strayer et al. 2006; Jokela & Ricciardi 2008; Ricciardi & 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 non-native 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 & Ricciardi 2008; Kestrup & Ricciardi 2009). The invasion history of the recipient community is an additional factor; impacts by previous invasions can remove sensitive species and create a hardier 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 non-native species, adaptations by the non-native species and the recipient community, interactions within a dynamic pool of resident species (new

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arrivals, loss of resident enemies), and a changing abiotic environment (Simberloff & Von Holle 1999; Crooks 2005; Strayer et al. 2006). Impacts attenuate for multiple reasons, including inter- or intra-specific regulation of the non-native 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 & García-Berthou 2005), each new observed impact begs the question of whether the non-native species is a driver or merely a "passenger" of the ecological change (Didham et al. 2005; King & Tschinkel 2008). This uncertainty is exemplified by the interaction between climate change and plant invasions. There is no doubt that the success of some non-native plants is being driven by shifting thermal barriers and changes in atmospheric CO_2 concentration (Weltzin et al. 2003), and, on a regional scale, non-native 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 non-native 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 & Lonsdale 2001), with potentially strong effects on carbon cycling, albedo, and hydrology in these regions (Williams & 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.

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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 counter-intuitive results. For example, non-native 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 & Ruiz 1996; Ricciardi 2003; Kulhanek et al. 2010*a*,*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. 2010*b*). A number of studies have attempted to use ecological traits to predict which non-native 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; Shirley & Kark 2009; Nentwig et al. 2009). Trait-based approaches have had limited success thus far (NRC 2002), perhaps because the *interactions* between the traits of a non-native 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 non-native and of the recipient community (Vitousek 1990; Ricciardi & 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).

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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 Vilà et al. 2011; Simberloff 2011; Ricciardi & MacIsaac 2011; Pyšek et al. 2012) has revealed insights into why some non-native 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).

I. Hypotheses based on traits of species or ecosystems

A large proportion of the literature in invasion ecology has examined either the traits of non-native species or those of recipient communities to explain particularly damaging invasions. As mentioned above, such trait-based approaches have had limited success in explaining or predicting impacts of non-native species. 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; Lockwood et al. 2013; Pyšek et al. 2012). Some physiological, behavioral, and life history correlates of impact have been identified for terrestrial plants (McIntyre et al. 2005; Pyšek et al. 2009) and mammals (Nentwig et al. 2009). For

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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 non-native 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 2000*b*; Mouquet et al. 2005). An empirically-based risk assessment of freshwater molluscs 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 non-native plants (Richardson & Rejmanek 2004) and that it interacts with environmental conditions to influence the impacts of non-native species (Jacquemyn 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 non-native species to determine the magnitude and direction of system disruptions (Li & Moyle 1981; Tilman 1999; Levine et al. 2003; Simon & Townsend 2003; Thomsen et al. 2011; Pyšek et al. 2012; see also discussions of enemy release and island vulnerability, below). 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.

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II. Hypotheses based on community structure

Trophic Position

A non-native species' trophic position has long been thought to have a strong bearing on its community- and ecosystem-level impacts (Elton 1958; Li & Moyle 1981; Ehrlich 1989; Lodge 1993; Moyle & Light 1996; Strayer 2010). A few highly visible and well-publicized cases have led to the perception that non-native 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 non-native species, particularly predators, were a leading cause of biodiversity loss (Clavero & 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; Ribero et al. 2007).

Trophic hypotheses also implicate non-native 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 & Ricciardi 2007; Higgins and Vander Zanden 2010) and by goats on islands (Courchamp et al. 2003) has created enormous ecological impacts. Disruptive non-native omnivores include the rusty crayfish (*Orconectes rusticus*) in the North American Great Lakes (Bobeldyk & 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

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297 islands worldwide (Jones et al. 2008; St. Clair 2011). On the other hand, Moyle and Light
298 (1996) argued that although omnivorous fishes may alter ecosystem properties, they generally
299 have had little effect on the composition of invaded assemblages.

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

311 The lack of a clear effect of trophic position may be due to the simplified, semi-arbitrary
312 categorization necessary to parse organisms into discrete classes, particularly given the varying
313 degree of omnivory found in a majority of animal taxa (Polis 1998; Moyle & Marchetti 2006).
314 In addition, many of these analyses focus on extinction data, which may not be rich enough to
315 distinguish multiple interacting factors. Early theory posited that omnivory destabilized food
316 webs (Pimm & Lawton 1978), but recent theoretical work suggests that weak omnivory can
317 stabilize complex food webs and reduce extinction probabilities (e.g., McCann & Hastings 1997;
318 Vandermeer 2006). Thus, non-native omnivores might stabilize systems while having strong
319 effects on some individual species, if their trophic interactions are weak (Ingram et al. 2009).

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Finally, large community-level impacts tend to be caused by non-native species that can create foodweb links, redirect energy or cause trophic cascades (Vander Zanden et al. 1999; Simon & Townsend 2003; Carlsson et al 2004; Baxter 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; Vander Zanden et al. 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., Herbert & 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 non-native generalist predators and herbivores (Ebenhard 1988, Cox & Lima 2006; Ricciardi & MacIsaac 2011).

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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 non-native population and, hence, greater impact. Evidence for the enemy release hypothesis (Kean & Crawley 2002) is contradictory. There is a distinct difference in results between biogeographic studies that compare numbers of enemies in native versus non-native ranges and community studies that examine the effect of enemies on native and non-native species (Colautti et al. 2004). Biogeographic studies appear to show consistent, but insufficient, evidence in favor of enemy release, whereas community studies suggest that non-native 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 non-native 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 & Berenbaum 2005). For plants, the release from enemies is hypothesized to lead to additional resources available for allocation to growth or reproduction (Blossey and Notzold 1995; see *Evolution of Increased Competitive Ability*), which, in turn, improves the competitive ability of the non-native 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 non-native species (Elton 1958; Levine & 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

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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 of impact (Robinson & Wellborn 1988; Levine at al. 2004; Maron & Marler 2008; Carey & 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 & Moyle 1993; Stohlgren et al. 1999). For example, a diverse and abundant community of planktivores did not prevent a non-native planktonic predator from extirpating native species in Canadian Shield lakes (Boudreau & 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 non-native 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 non-native species' vulnerability to resident predators may indirectly harm native species through apparent competition: the additional prey subsidy offered by the non-native 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 non-native species (Noonburg & Byers 2005).

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III. Niche-based hypotheses

Many hypotheses for establishment success focus on niche differences between native and non-native members of the community, with the assumption that the exploitation of unused resources (empty niches) or more competitive ways of accessing resources (niche replacement) will allow the non-native species to integrate into the community. These two approaches to niche differences have contrasting implications for impacts. A non-native 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 non-native 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 non-native 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 non-natives 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 non-native species were negatively affected by competition from residents. Herbold and Moyle (1986) used California fish assemblages to argue a very different story: non-natives that established into natural environments commonly

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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 non-native species (e.g., Sax et al. 2002; Davis 2003; Sax & Gaines 2003; Gurevitch & Padilla 2004). The rejoinders (e.g., Olden & Poff 2003) offer similar arguments as Herbold and Moyle (1986). Meta-analyses have found no significant difference between ecosystem-level impacts of non-native nitrogen-fixing plant species on islands and mainlands (Vilà et al. 2011), but non-native 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 non-native species. Extending the available resource argument to impacts takes us back to the hypothesis that non-native 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 non-native competitor; for example, Bryce et al. (2002) examine niche overlap in red and grey squirrels to explain areas of coexistence and areas of exclusion by the non-native greys. Hoopes and Hall (2002) consider niche overlap by arguing that a non-native plant that excludes a native plant from a portion of its potential habitat probably

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has smaller regional effects than a non-native 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 non-natives, 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 non-native species (Forys & Allen 1999); here, we would expect that the reduced abundance of the native would aid establishment of the non-native 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 non-native species transforms key resources or uses them differently from resident species (Vitousek 1990; see also *Ecosystem Engineering*). For example, non-native nitrogen-fixing plants alter nutrient availability and dynamics in their new habitats (Allison & 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 non-natives 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).

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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 & 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 non-native 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 discussed previously. The displacement of native animals has often been attributed to heightened interspecific aggression by a non-native species (Dubs & 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 non-native predators that necessarily drives large impacts, but rather the weak or non-existent anti-predator behaviors of the native prey themselves (Banks & Dickman 2007; see *Ecological Naivete Hypothesis*). Sih et al. (2010) note that predatory impacts arise even from non-consumptive interactions between predator and prey; in consumptive interactions, the impact or cost to the prey population is the

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loss of individuals through ingestion, but there also exist non-consumptive 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 (Pressier & Bolnik 2008).

Ecosystem Engineering

Ecological engineering, as applied to the impacts of non-native species, is a concept closely allied to the *Novel Resource Use* hypothesis. Non-native 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, non-native ecosystem engineers tend to alter environments on shorter time scales than successional change. Some theoretical work suggests that non-native engineers in suboptimal habitats can have accelerating rates of spread as they alter habitats toward their own optimum (Cuddington & 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 non-native species by ameliorating stressful conditions (Crain & Bertness 2006), but they can lower species richness by reducing system complexity (Crooks 2002) or by shifting ecosystem productivity away from intermediate levels (Wright & Jones 2004). Even when they do not successfully establish, non-native 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). Non-native engineers also complicate

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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 Naiveté / Phylogenetic Distinctiveness

The disproportionate effects of non-native predators and herbivores introduced to islands, lakes and other insular ecosystems has been attributed to prey naiveté – a lack of evolutionary exposure to functionally similar organisms (Diamond & Case 1986; Short et al. 2002; Cox & Lima 2006; Berglund et al. 2009). This explains why non-native predators and herbivores appear to have stronger effects on native prey populations than do native predators (Parker et al. 2006; Salo et al. 2007). Naiveté can also explain variation in the impacts of non-native 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 naiveté can be devastating even for continental biota: 1) the replacement of native red squirrels by non-native 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 non-native 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 counter-examples to the ERH, in which there is a net positive effect of natural enemies on the non-native species (the 'Enemy of My Enemy is My Friend' hypothesis; Colautti

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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 & Ridenour 2004), but the effect may be more general. The generality of the naiveté hypothesis has been tested using phylogeny as a proxy for ecological novelty (Ricciardi & Atkinson 2004; Strauss et al. 2006), based on the premise that ecological similarity diminishes with decreasing phylogenetic relatedness (Burns & Strauss 2011). Indeed, non-native species belonging to novel genera in the recipient community have stronger impacts on native species in aquatic systems (Ricciardi & Atkinson 2004), and non-native grass 'pest' species are more distantly related to native grasses than are non-native 'non-pest' species in California (Strauss et al. 2006). A paradox that remains to be resolved is that novelty can also render the non-native species naïve to the effects of resident enemies (Ricciardi & 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 non-native 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,

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548 although the latter aspect has not been tested explicitly. Blossey and Nötzold (1995) suggested
549 that, in the absence of specialist herbivores, non-native plants reallocate defense resources in
550 ways that enhance their competitive ability (e.g., through increased growth and reproduction, or
551 the production of allelopathic chemicals). Although EICA is intuitively appealing, particularly
552 for explaining sudden increases in dominance and impacts from long-established non-natives,
553 empirical evidence for it is mixed (DeWalt et al. 2004; Rogers & Siemann 2004; Franks et al.
554 2008), potentially because escape from enemies and evolution of increased competitive ability
555 may take place in the context of resource availability (Blumenthal 2006). Blumenthal et al.
556 (2009) found that plants from resource-rich environments indeed had more enemies in their
557 native environment and lost more enemies in the invasion of a novel environment, but they did
558 not find evidence of such plants having higher impacts.
559

560 ## IV. Hypotheses related to a changing abiotic environment

561 One issue with niche hypotheses is that they rely to some extent on equilibrium outcomes and
562 neglect the dynamic nature of ecological systems. Hypotheses that ignore environmental change
563 may be rendered irrelevant by temporal heterogeneity. Spatial heterogeneity is another cause of
564 context-dependent impacts. Recognizing these aspects, a series of hypotheses combine niche
565 concepts with the effects of spatial or temporal variation.
566

567 **Environmental Heterogeneity**

568 Spatial and temporal heterogeneity can mitigate the impacts of non-native species by limiting the
569 non-native's abundance or by creating refugia for natives, thereby allowing coexistence at local
570 and regional meta-community scales (Levine & Rees 2004; Melbourne et al. 2007; Kestrup &

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Ricciardi 2009). If native and non-native 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 2000*a*,*b*). Co-occurring species that exploit slight variations differently will lead to greater species richness rather than exclusion (Melbourne et al. 2007), although the non-native species may still alter community structure and native species abundance. As such, Melbourne et al. (2007) conclude that competitively dominant non-native 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 non-native 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 non-native 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 non-native species (e.g., Helms & Vinson 2005) – an effect termed ‘habitat filtering’ (Weiher & Keddy 1999). Suboptimal conditions may limit the impacts of non-natives by constraining

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performance or population size. This constraint is illustrated by spatial variation in competitive interactions between non-natives and natives along environmental gradients (Taniguchi et al. 1998; Alcaraz et al. 2008; Kestrup & Ricciardi 2009). We would expect peak performance – and thus a stronger per capita effect – from a non-native 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 & Ricciardi 2008), provided that the non-native 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 favored by the native community will promote the establishment and dominance of non-native 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). Non-native 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 & 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 & MacIsaac 1997). A well-known case in which non-native dominance is favored by changes in disturbance

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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 & Vitousek 1992). The role of disturbance in non-native 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 non-native fouling invertebrates to monopolize substrate (Altman & Whitlach 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 non-native 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 non-native 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

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639 unproductive floodplain gaps. By contrast, one study suggests that impacts of introduced aquatic
640 predators are highest in unproductive lakes (Li & Moyle 1981).
641
642 ## V. Hypotheses related to organismal influx
643 **Propagule Pressure**
644 Propagule pressure describes the number of non-native individuals released in a single event or
645 in several events spread through time. The higher the propagule pressure, the more likely a
646 species is to establish a self-sustaining population (Lockwood et al. 2005; Simberloff 2009).
647 Although the relationship to establishment success has been demonstrated numerous times across
648 a variety of species, the influence of propagule pressure on impact is still poorly elucidated. One
649 mechanism by which propagule pressure can influence impact is by enhancing post-
650 establishment population growth (Ricciardi et al. 2011*a*). Large numbers of initial colonists
651 could increase the rate of population growth by allowing the incipient population to overcome a
652 suite of factors associated with small population size (e.g., Allee effects, stochastic events), and
653 this rapid growth could have concomitant effects on other members of the community.
654 However, few researchers have tested the key premise that higher propagule pressure leads to
655 higher population growth rates.
656 An additional aspect of propagule pressure is that a higher influx of individuals may also
657 include more genotypes of the non-native species, each having potentially different per capita
658 effects (see also *Colonization Pressure*). As a large number of individuals are released by
659 various transport vectors into an area, there is an increasing probability of introduction of
660 harmful genotypes or individuals capable of hybridizing with natives (reviewed in Ricciardi et al.
661 2011*a*). In addition, the novel genetic admixtures that are produced under such circumstances

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662 can lead to higher impacts if they allow a non-native species to evolve quickly to local
663 conditions, acquire a key trait to expand its niche, or evolve novel resource use. It is not clear
664 how often high propagule pressure is associated with an increase in the diversity of genotypes
665 introduced, but this could be a powerful mechanism for generating strong impacts and for
666 causing the impacts of an established species to change over time.
667
668 **Colonization Pressure**
669 Colonization pressure refers to the number of non-native species, subspecies or genotypes
670 released; it is a taxon-level equivalent to propagule pressure (Lockwood et al. 2009). Higher
671 colonization pressure leads to higher non-native species establishment simply by chance
672 (Colautti et al. 2006; Lockwood et al. 2009), and thus increases the probability that a harmful
673 taxon will be added to the recipient community (Alpert 2006). In aquatic systems, for example,
674 the number of non-native species that are implicated in severe declines of native populations is a
675 simple linear function of the total number of non-native species present, indicating a sampling
676 effect (Ricciardi & Kipp 2008). Colonization pressure also increases the number of non-native
677 species that can interact with each other, as well as the likelihood of the re-assembly of co-
678 evolved species complexes, potentially leading to synergistic effects (addressed below).
679
680 ## VI. Hypotheses addressing synergistic effects
681 **Invasional Meltdown / Biotic Facilitation**
682 Over the past decade there has been increasing recognition of the importance of facilitative
683 interactions and co-evolved adaptations in determining the consequences of species
684 introductions. The invasional meltdown hypothesis predicts that increasing colonization causes

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ecosystems to become progressively more invaded and disrupted, resulting in a rapid accumulation of non-native species and their impacts (Simberloff & Von Holle 1999). It stems from the observation that facilitations are at least as common as antagonistic interactions among non-native species (Simberloff & Von Holle 1999; Ricciardi 2001; Bruno et al. 2003). Although most studies citing this hypothesis focus predominantly on cases in which one non-native species promotes the establishment of another, the hypothesis also encompasses the consequences arising from non-native 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 amongst various taxa in terrestrial, freshwater and marine systems (Simberloff & Von Holle 1999; Ricciardi 2001, 2005; Levin et al. 2002; O'Dowd et al. 2003).

Because facilitations may be most frequent and strongest among co-adapted non-native species, combinations of such species are more likely to generate synergistic impacts (Ricciardi 2005). In particular, non-native mutualisms that improve the fitness of each species can magnify their respective impacts (Rudgers & Clay 2008); even non-native 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 co-evolved prey, which subsidized the snake's diet as the snake drove several endemic species of birds, bats and reptiles to extinction (Fritts & 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

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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 non-native 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 non-native species is far more advanced than that of impact (Lockwood et al. 2013; Catford et al. 2009; Davis 2009). 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 non-native 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 non-native 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 abundance and impact remains to be elucidated; a number of plausible abundance-impact curves

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731 may exist, and each of these has important implications for management (Yokomizo et al. 2009;
732 Thiele et al. 2010). Progress toward a theoretical framework for impact would be further
733 enhanced through examination of factors that account for variation (within and across taxa) in
734 the per capita effect (E) of non-native species. The few existing hypotheses that directly address
735 per capita effect apply to a broad range of taxa and biomes, and perhaps could be combined to
736 construct integrative models of impact (e.g., Fig. 3).

737 Similar to most concepts in invasion ecology (Catford et al. 2009), the current body of
738 theory on impact has much overlap and redundancy, which reflects not only different approaches
739 and histories of study but also the complexity of interacting factors governing impact (Table 1;
740 Fig. 1). Confusion surrounding the definition of "invasive" has likely contributed to some
741 disorganization of theory by confusing invasiveness with impact. A greater encumbrance to
742 developing a theoretical framework is the lack of rigorous analyses and tests of generality for the
743 vast majority of hypotheses to date. Those hypotheses that have received empirical attention
744 tend to suffer from a taxonomic bias; for example, the EICA hypothesis has been explored
745 exclusively for plants, but we know of no reason why it could not play a role in the impacts of
746 non-native animals. The hypothesized determinants of a non-native species' impact for which
747 there appears to be broad empirical support include: 1) the evolutionary experience of the
748 recipient community (*Ecological Naïveté Hypothesis*); 2) the degree to which the local
749 environment constrains the abundance of the non-native species (*Environmental Matching*
750 *Hypothesis*); 3) variation in the number, composition and frequency of individuals released
751 (*Propagule Pressure Hypothesis*), which can influence the magnitude, direction and scope of
752 impact; and 4) novel traits that may promote changes in availability of key resources, with large-
753 scale consequences for community structure and ecosystem processes (*Ecological Naivete, Novel*

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754 *Weapons, Novel Resource,* and *Trait Divergence* hypotheses). It is not certain whether each of
755 these four determinants represents an irreducible level of theory – that is they may not necessary
756 fit into a single hierarchical or synergistic framework; instead, they could be context-dependent,
757 or only a subset may operate in tandem. However, we believe further work will show that these
758 determinants are complementary, and each applies broadly across taxa and biomes, and thus
759 should be integrated into a general theory of impact.

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

771 Future progress toward a theoretical framework will most profitably result from explicit
772 consideration of the traits and interactions of non-native species, the recipient community and the
773 abiotic environment, as well as the evolutionary context of the invasion. There is a need to
774 develop more hypotheses that address the *indirect* effects of invasion, in which the non-native
775 species' influence is transmitted through multiple interacting species, both native and non-native.
776 Despite being rarely studied, such effects are known to have significant consequences for

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777 communities and ecosystem function (Baxter et al. 2004; Ricciardi 2005; White et al. 2006;
778 Nelson et al. 2010, Simberloff 2011) and can complicate management actions (Zavaleta et al.
779 2001). A growing awareness of the importance of multiple interacting stressors (e.g., Hobbs
780 2001; van der Wal et al. 2008) should provide further impetus for developing a mechanistic
781 understanding of indirect effects and impacts in general. However, the largest challenge to
782 understanding impact is being able to distinguish invasion-mediated effects from other co-
783 occurring anthropogenic stressors (Didham et al. 2005, 2007; King & Tschinkel 2008), which
784 may alter the effects of both resident and future invaders (Byers et al. 2002) and thus are a major
785 contributor to spatial and temporal variation in impact (Strayer et al. 2006).
786

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790

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Table 1. Published hypotheses regarding the ecological impact of non-native species.

Theme/hypothesis	Reference for hypothesis	Prediction	Similar concepts	Considered important for establishment?	Tested for impact?
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 non-native species alter communities. E.g. Stronger impacts are caused by species with higher reproductive potential and/or greater rates of resource consumption.	*Uncontrolled Generalist Consumer; Phylogenetic Distinctiveness; Novel Resource Use*	Yes	Yes, for some taxa (e.g. Keller et al. 2007; Morrison & Hay 2011)

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2. Ecosystem traits (apart from diversity)	Li & Moyle 1981; Moyle & Light 1996	Ecosystem characteristics (e.g., productivity, disturbance regime, insularity, area) determine which systems are more vulnerable to disruption by a non-native species.	*Biotic Resistance*	Yes	Yes, with mixed results (e.g. islands vs mainlands – Ebenhard 1988; Vilà et al. 2011; Pysek et al. 2012)
II. Hypotheses based on community structure					
3. Trophic position	Elton 1958, Davis 2003, Clavero & García-Berthou 2005	Greater impacts are expected from predatory (rather than competitive) interactions. Top predators are the most disruptive.	*Uncontrolled Consumer*	No	Yes, but no significant effect found (Marchetti et al. 2004a,b; Blackburn et al. 2005)
4. Uncontrolled Consumer / Enemy Release	Pimm 1987, 1991	The greatest impacts are caused by generalist consumers that are uncontrolled by predators.	*Species traits hypotheses; EICA*	Explains post-establishment success	No

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5. Biotic resistance	Elton 1958, Moyle & Light 1996	Diverse communities are more resistant to being altered by non-native species. Impacts are buffered in complex food webs.	*Limiting Similarity*	Yes	Yes (Robinson & Wellborn 1988; Levine et al. 2004; Maron & Marler 2008; Carey & Wahl 2010)
III. Niche-based hypotheses					
6. Niche Replacement / Limiting Similarity	Elton 1958	Non-native species that have niche overlap with natives and are superior competitors have larger impacts.	*Biotic resistance*	Yes	Yes, with mixed results (Simberloff 1981, Forys & Allen 1999, Hoopes & Hall 2002)
7. Novel Resource Use / Trait Distinctiveness	Vitousek 1990, Cleland 2011	Non-native species that use key resources differently from natives will have larger impacts.	*Species Traits; Phylogenetic Distinctiveness*	Yes	Yes, for some taxa (e.g. Morrison & Hay 2011)
8. Novel Weapons	Callaway & Ridenour 2004	Stronger impacts are exerted by non-native species that release novel	*Ecological Naïveté; Phylogenetic*	Explains post-establishment	Yes, mostly for terrestrial plants (Wardle et al. 1998;

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		allelopathic, defensive or antimicrobial chemicals.	*Distinctiveness*	success	Callaway et al. 2008; Letnic et al. 2008)
9. Ecosystem Engineering	Crooks 2002; Cuddington & Hastings 2004; Wright & Jones 2004	Non-native ecosystem engineers that modify habitat in unique ways have larger impacts.	*Novel Resource Use*	Explains post-establishment success	Yes (Vitousek et al. 1987; Crooks 2002; Gonzalez et al. 2008)
10. Evolutionary Naïveté	Diamond & Case 1986; Cox & Lima 2006	The impact of non-native species depends on the recipient community's evolutionary experience with functionally similar species.	*Novel Resource Use; Novel Weapons; Phylogenetic Distinctiveness*	No	See *Novel Weapons* & *Phylogenetic Distinctiveness*.
11. Phylogenetic Distinctiveness	Ricciardi & Atkinson 2004	Larger impacts are caused by non-native species that add novel taxa to the community.	*Evolutionary Naïveté*	Yes	Yes (Ricciardi & Atkinson 2004; Strauss et al. 2006).

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12. Evolution of Increased Competitive Ability (EICA)	Blossey & Nötzold 1995	In the absence of enemies, non-native plants can reallocate resources from defense mechanisms into growth and reproduction, and thus dominate native counterparts.	*Enemy Release; Novel Weapons*	Explains post-establishment success	Not directly, and supporting evidence is weak (reviewed by Blumenthal et al. 2009).
IV. Hypotheses related to a changing abiotic environment					
13. Environmental Heterogeneity	Levine & Rees 2004; Melbourne et al. 2007	Spatial or temporal heterogeneity creates refugia against the impacts of non-natives on native populations, and vice versa, thereby allowing coexistence.	*Environmental Matching*	Yes	Yes, for spatial heterogeneity (e.g. Kestrup & Ricciardi 2009) and, more rarely, for temporal heterogeneity (e.g. Levine & Rees 2004; Strayer et al. 2006).

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14. Environmental Matching	Kestrup & Ricciardi 2009	The impact of a non-native is inversely correlated with the distance of the novel habitat conditions from the species' environmental optimum.	*Environmental Heterogeneity; Disturbance/ Directional Change*	Yes	Yes, for aquatic animals (e.g. Taniguchi et al. 1998; Jokela & Ricciardi 2008; Alcaraz et al. 2008; Kestrup & Ricciardi 2009).
15. Disturbance/ Directional Change	MacDougall & Turkington 2005	Disturbance and directional changes in the environment create conditions that disfavor some native species and favor non-native species, thereby magnifying the impacts of the latter.	*Environmental Matching*	Yes	Yes, primarily for terrestrial plants (e.g. D'Antonio & Vitousek 1992; Byers et al. 2002).
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.	*Ecosystem Traits*	Yes	Yes, for terrestrial plants (Brewer 2011).

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V. Organismal influx

17. Propagule Pressure	Ricciardi et al. 2011*a*	Impacts are a function of the number, composition and frequency of introduced propagules.	*Colonization Pressure*	Yes	Not directly.
18. Colonization Pressure	Alpert 2006; Lockwood et al. 2009	A higher rate of species introductions increases the probability of a non-native species that has large impacts.	*Propagule Pressure; Invasional Meltdown*	Yes	Not directly (see Ricciardi & Kipp 2008).

VI. Synergistic Effects

19. Invasional Meltdown	Simberloff & Von Holle 1999; Ricciardi 2005	As more non-native species are added to a system, some non-natives will facilitate others, thereby resulting in an accumulation of non-natives and their synergistic impacts.	*Colonization Pressure*	Yes	Yes (e.g. Ricciardi 2001, 2005; Levin et al. 2002; O'Dowd et al. 2003).

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FIGURE LEGENDS

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

Figure 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_o , 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*).

Figure 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 amongst resident species (*Phylogenetic Distinctiveness Hypothesis*) and more physiologically matched to abiotic conditions (*Environmental Matching Hypothesis*).

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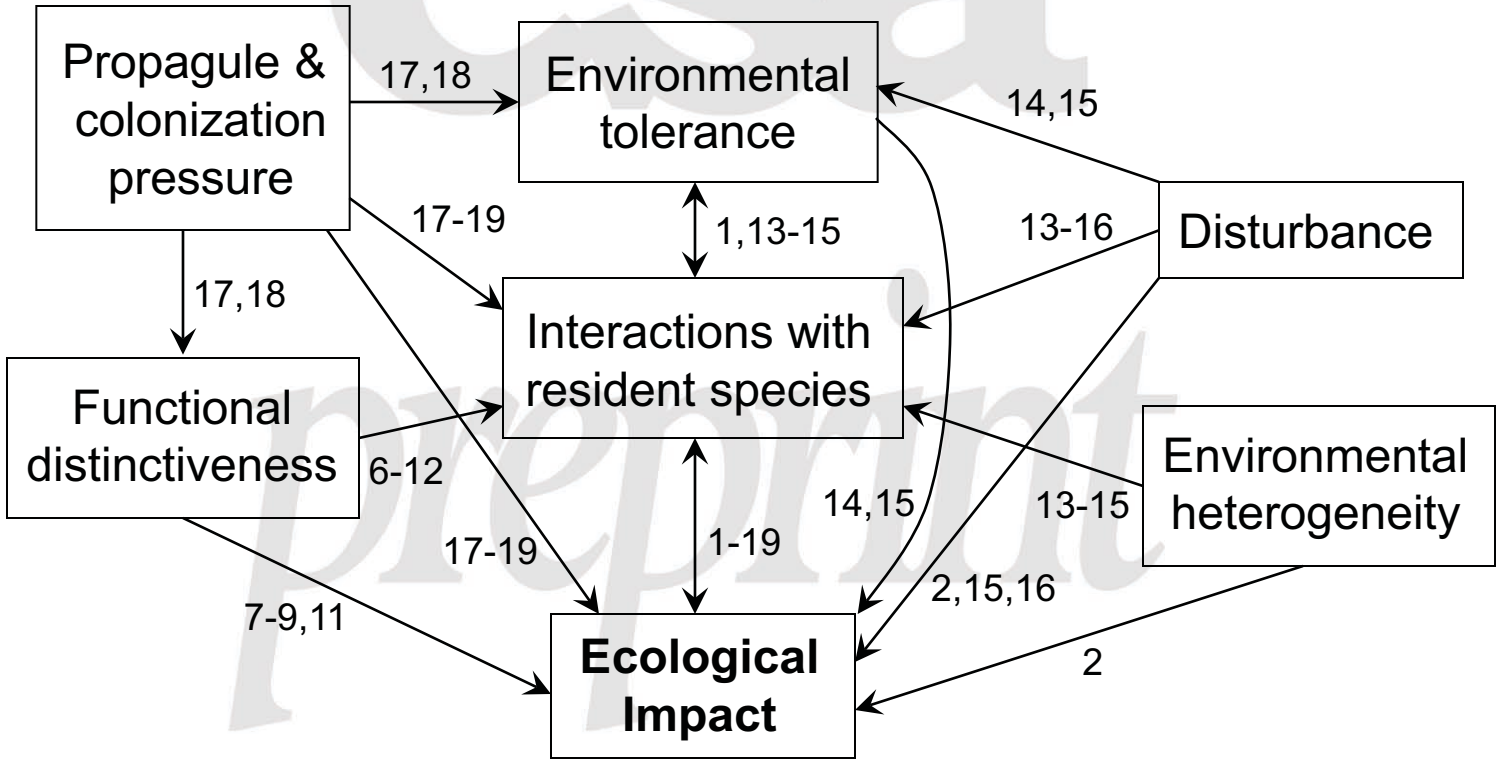

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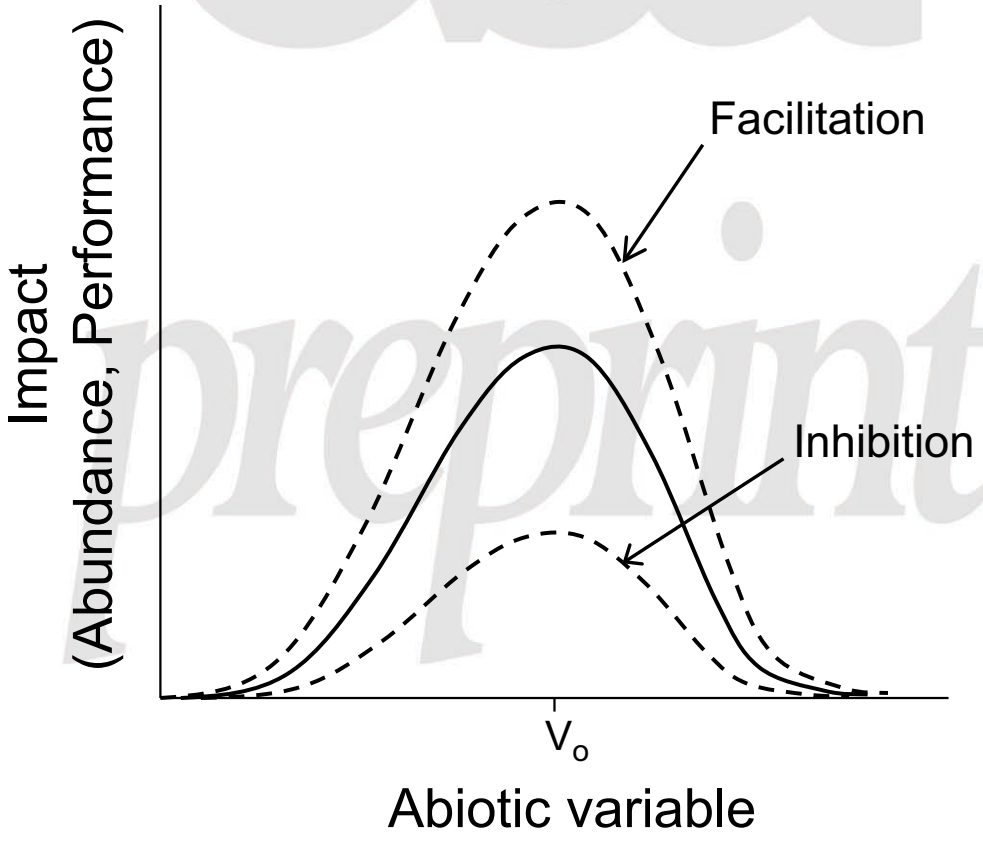

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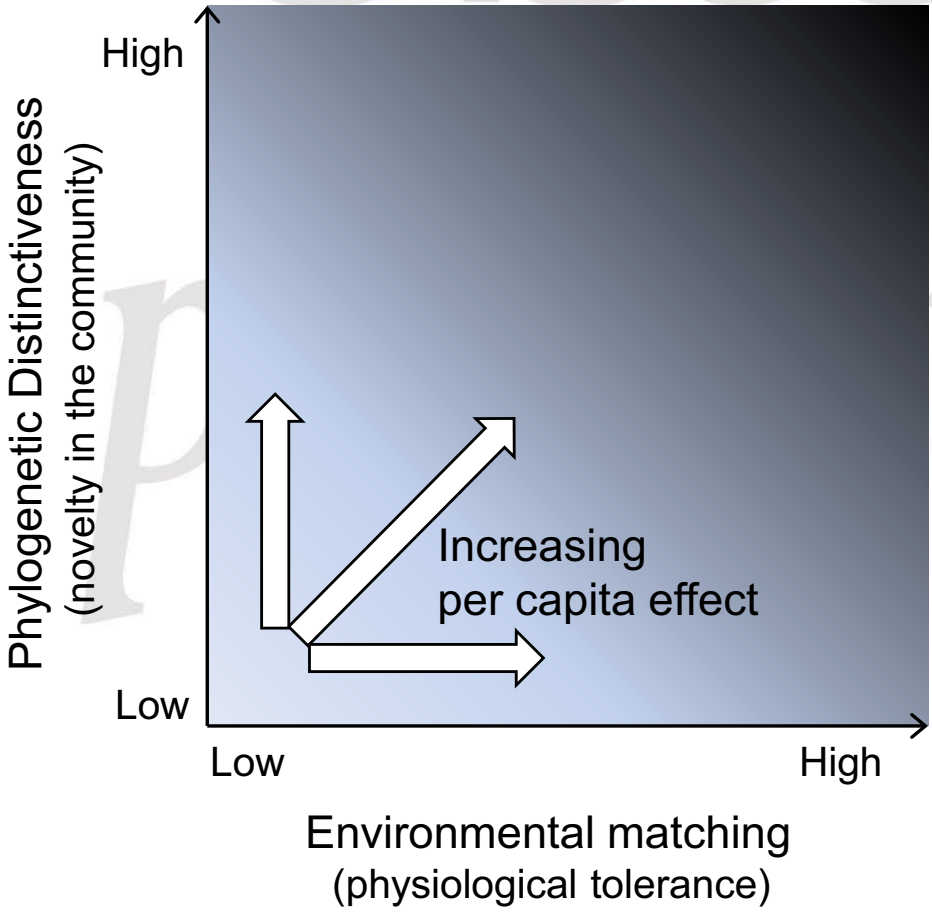

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