

Chapter 17

EXPANDING THE  
PROPAGULE PRESSURE  
CONCEPT TO  
UNDERSTAND  
THE IMPACT OF  
BIOLOGICAL INVASIONS

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### 17.1 INTRODUCTION

Most introduced species fail to establish sustainable populations, and many of those that do become established invaders do not cause strong impacts (Williamson 1996; Parker et al. 1999). Others can displace native species, disrupt ecosystem processes, threaten human and animal health and generate large economic costs. Why some introduced species are more successful or more disruptive than others are central questions of invasion ecology. Exploration of these questions has identified propagule pressure – the quantity, richness, or frequency of individuals or life stages of a species released into an area – as the most important determinant of establishment success (Williamson 1996; Lockwood et al. 2005; Simberloff 2009). The basis for this relationship is the greater risk of extinction that small populations suffer because of intrinsic and extrinsic factors including random changes in birth and death rates, small-scale catastrophes like extreme weather events, inbreeding depression and reduced efficiency in mate location and foraging. Indeed, when individuals are introduced in greater numbers or greater frequency they are more likely to form sustainable populations (Sakai et al. 2001).

Although Elton (1958) and others before him recognized the role of the dispersal of propagules in the global distribution of plants and animals, the concept of propagule pressure did not develop until many years later. As Simberloff (2009) noted, propagule pressure was not considered in the key research questions highlighted in the mid-1980s by the international Scientific Committee on Problems of the Environment, whose agenda spurred the growth of invasion ecology during the subsequent two decades (Richardson & Pyšek 2008; Simberloff, this volume). Research interest in the concept began to grow exponentially only during the past decade (Simberloff 2009).

A burgeoning number of studies (reviewed by Lockwood et al. 2005; Simberloff 2009) have shown propagule pressure to be a consistent predictor of establishment and spread of non-indigenous species. Furthermore, recent research points to an overwhelming influence of the pattern of dispersal and non-random variation in propagule supply on the outcome of an invasion (Colautti et al. 2006; Wilson et al. 2009). However, propagule pressure may play an even greater role in the outcome of an invasion than has

been previously recognized. Although there has been a surge of experimental and modelling studies that explore the intricacies of the relationship between propagule pressure and establishment success, to our knowledge no study has examined the specific links between propagule pressure and the ecological impact of an invasion. There are no hypotheses that explicitly relate these concepts, beyond the obvious expectation that the frequency and diversity of impacts will increase with invasions (Lockwood et al. 2005; Catford et al. 2009). Here, we consider mechanisms by which propagule pressure can modulate impact and how a predictive understanding of this relationship would be valuable to the management and risk assessment of invasions.

### 17.2 PROPAGULE PRESSURE AND IMPACT DEFINED

Propagule pressure encompasses variation in the quantity, composition and rate of supply of non-indigenous organisms resulting from the transport conditions and pathways between source and recipient regions. Therefore, measures of propagule pressure generally involve (i) the number of individuals introduced ('propagule abundance'), (ii) the number of taxa or genotypes introduced ('propagule richness') and (iii) the total number or frequency of introduction events (Table 17.1). Lockwood and colleagues (2009) argue for a distinction between the number of introduced species (which they term 'colonization pressure') and other forms of propagule pressure, to better understand the processes that account for variation in non-indigenous species richness. For our purposes, we consider as a single form of propagule pressure the entire richness of introduced propagules, from genotypes to higher taxa. Thus our definition of propagule pressure incorporates colonization pressure as well as genetic (intraspecific) variation among propagules. The importance of genotypic variation to establishment success and post-establishment spread is becoming increasingly recognized (Sexton et al. 2002; Roman 2006; Lavergne & Molofsky 2007), and here we discuss how it may also play a significant role in impact.

A widely used synonym for propagule abundance is 'propagule size' (see, for example, Forsyth & Duncan 2001), which is also used by plant ecologists to des-

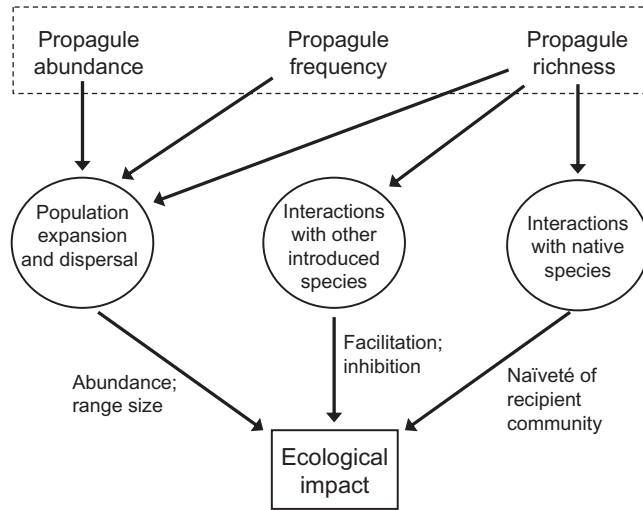
**Table 17.1** Forms of propagule pressure that are commonly studied. Studies have examined either a single form or proxy variable of propagule pressure, or an aggregate measure of multiple forms. The relative importance of each form to the successful establishment and impact of an introduced species varies among recipient systems.

Form	Definition	Proxy variables	Examples of recent studies
Propagule abundance	The number of individuals of a non-indigenous species introduced to an area	Vector activity (e.g. volume of ballast water released)	Forsyth & Duncan 2001; Ahlroth et al. 2003; Colautti 2005; Verling et al. 2005
Propagule richness	The number of non-indigenous taxa (e.g. species, genera, families) or genotypes introduced to an area	Vector richness; Number of pathways or donor regions; Number of source populations	Ahlroth et al. 2003; Verling et al. 2005; Roman & Darling 2007; Chiron et al. 2009
Propagule frequency	The total number, or rate, of discrete introduction events	Vector activity (e.g. number of ship visits; number of tourists)	Forsyth & Duncan 2001; Colautti 2005; Verling et al. 2005; Drake et al. 2005; Drury et al. 2007; Roman & Darling 2007

cribe the physical dimensions of seeds and other plant reproductive structures, regardless of whether the plant is non-indigenous; therefore, we adopt the former term to avoid confusion. Although propagule abundance involves population-level processes and propagule richness involves community-level processes, these forms are correlated: a greater input of propagules increases both the number of individuals and the number of taxa introduced, in a non-linear manner (Lockwood et al. 2009). Two added dimensions are the physiological condition of the propagules upon release and human cultivation of introduced individuals, both of which can influence establishment success (Mack 2000; Verling et al. 2005) but are not considered here. Finally, it should be noted that herein propagule pressure refers exclusively to the introduction of non-indigenous species to an area, rather than the propagule release (fecundity) associated with invaders after they are established in the area.

We define ecological impact as a measurable change to the properties of organisms, populations, communities or ecosystems. Several factors generate variation in impacts (Parker et al. 1999; Ricciardi 2003). Different impacts arise from different functional roles of the invader within the recipient community; for example, the zebra mussel's effects on pelagic food

webs result from its filter-feeding activities, whereas its effects on benthic communities are largely related to its gregarious attachment and structural transformation of submerged surfaces (Ricciardi 2003). An invader's impacts may differ considerably across regions as its abundance and functional role are altered by local abiotic conditions (D'Antonio et al. 2000) and by interactions with resident species (Robinson & Wellborn 1988; Simberloff & Von Holle 1999; Ricciardi 2005). If the invader is a novel organism that uses resources differently than the rest of the community, then resident native species are more likely to be naïve and sensitive to its effects and less likely to offer resistance to its population growth (Ricciardi & Atkinson 2004). Finally, the size of the invaded range determines the absolute scale of the invader's impact; over a larger range, an invader can have a greater impact on biodiversity by affecting a larger number of native species and a greater proportion of the area occupied by those species (Parker et al. 1999). In summary, impact can be described as a function of three principal mediators: the invader's abundance, its functional ecology relative to the recipient community and its range size in the invaded region. Here, we consider how different forms of propagule pressure can influence impact through each of these mediators (Fig. 17.1).



**Fig. 17.1** Interactions between three forms of propagule pressure (propagule abundance, frequency and richness) and population-level and community-level processes that mediate the impact of introduced species. Major processes are circled. Specific mediating factors or processes of importance are indicated beside the arrows leading to impact.

### 17.3 INFLUENCE OF PROPAGULE PRESSURE ON MEDIATORS OF IMPACT

#### The invader's abundance and population growth

Propagule pressure affects the post-establishment abundance of an introduced species (see Blackburn et al. 2001; Marchetti et al. 2004; Drake et al. 2005; Britton-Simmons & Abbott 2008). Logically, a population will establish and grow more rapidly – and cause impacts sooner – if a large number of individuals are introduced at a given time or if there is a high frequency of introduction events. An increase in propagule abundance can accelerate population growth and establishment by supplying colonists with sufficient numbers to overcome Allee effects (Sakai et al. 2001) or sufficient genetic variation to adapt to local conditions (Ahlroth et al. 2003), thereby reducing the time available for native species to adapt to the stresses imposed by the invader (Schlaepfer et al. 2005). Despite these probable outcomes, the data available for testing correlations between impact and propagule pressure are scarce and yield ambiguous results. For non-indigenous ungulate mammals established in New Zealand (see Forsyth & Duncan 2001) there is no relationship between their ecological impact (reviewed by Lever 1985; Long 2003) and the minimum number of

individuals released (logistic regression of ranked high- or low-impact species versus log-transformed propagule abundance,  $P > 0.05$ ; A. Ricciardi, unpublished data), although the most damaging species, red deer, *Cervus elaphus*, had received the greatest introduction effort. In the Great Lakes, invading fishes deemed responsible for native species declines tend to be those that have been introduced frequently through stocking programs (six of nine stocked species versus four of 16 non-stocked species; Fisher's exact test,  $P = 0.053$ ), but this result is confounded by a taxonomic bias: most stocked fishes are salmonids (Crawford 2001).

Frequent introductions over time increase the likelihood that a species will be introduced when abiotic variables are optimal for reaching high abundances (Drake et al. 2006), which ultimately affects the onset and magnitude of impact. Propagule pressure could also restore non-indigenous populations that have suffered a severe decline (Gotelli 1991), and insure that the invader will have an opportunity to recolonize an area after a disturbance. A sufficiently high frequency of releases could allow the non-indigenous species to become established and dominate native species before the latter recover sufficiently to provide resistance (see, for example, Altman & Whitlatch 2007). Moreover, in rare instances, propagule pressure can maintain an unsustainable population of a non-indigenous species at a level of abundance sufficient to exert a significant impact. For example, a frequent supply of propagules

can erode a population of a closely related native species through hybridization or reproductive interference, as shown by the cumulative negative effect of multiple releases of domestic dogs and cats on the genetic integrity of native canids and wildcats, even where the natives are more abundant (Simberloff 1996; Pierpaoli et al. 2003).

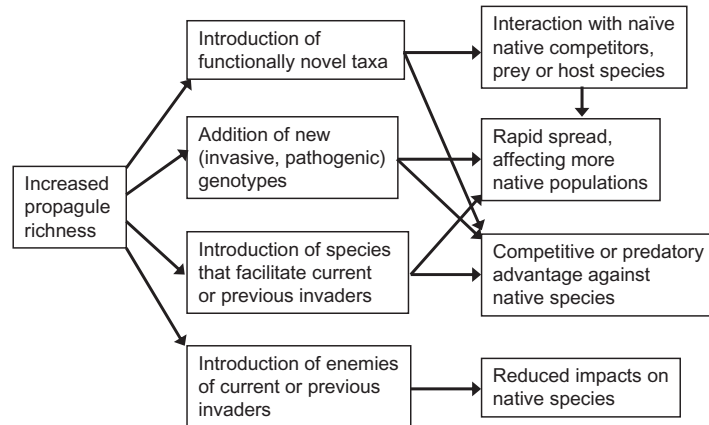
**The invader’s functional ecology relative to the recipient community**

A single transport vector, such as transoceanic shipping (Carlton & Geller 1993), can deliver hundreds of taxa simultaneously, and vectors from different source regions can carry multiple genotypes of a given species (Roman & Darling 2007). Variation in the supply of different taxa or genotypes of the same taxon has several consequences for recipient communities (Fig. 17.2), including the possibility of introducing an aggressive genotype (Fry & Smart 1999) or producing invasive hybrids (Ellstrand & Schierenbeck 2000; Facon et al. 2005). Such events may account for some of the observed long-term changes in the impacts of invaders (Strayer et al. 2006). Given that rapid evolutionary change in invaders is a common phenomenon (Whitney & Gabler 2008), the introduction of additional genotypes could increase functional diversity in populations of an invader (e.g. behaviour, morphology, physiological tolerances) so as to broaden its interactions with, and impacts on, native species by allowing it to invade new habitats (Sexton et al. 2002).

On the other hand, founder populations with low genetic diversity can also evolve rapidly (Dlugosch & Parker 2008) and produce major impacts. A notable example is the Argentine ant *Linepithema humile* introduced to California, where diminished genetic diversity in the invading population has reduced intraspecific aggression, allowing the formation of dense colonies that have expanded rapidly and replaced native species (Tsutsui et al. 2000). These examples underscore the important but poorly understood role of propagule pressure in the post-establishment evolution and impact of invaders.

Theoretical modelling reveals a potentially strong influence of propagule abundance and introduction rate on the impacts of invasive organisms that create or modify habitat (ecosystem engineers). Non-indigenous engineers affect the broadest range of species within the recipient community and can enhance both their own invasion success and impact on resident species by modifying selection pressures in their new environment (Byers 2002; Gonzalez et al. 2008). Their impact on native species will increase with the number of individuals initially released, if their rate of habitat transformation is density dependent. Furthermore, multiple introductions of engineers that fail to establish sustainable populations but persist for a short period of time may nonetheless exert impacts on the native community through cumulative transformations of habitat (Gonzalez et al. 2008).

Finally, an increase in propagule richness raises the probability of introducing a novel predator, competitor or pathogen. Functionally novel organisms are more



**Fig. 17.2** Potential pathways by which an increase in propagule richness (e.g. through an increase in vector or source region diversity) can alter the impact of an invader on native species.

likely to disrupt recipient communities (Ricciardi & Atkinson 2004; Cox & Lima 2006). Owing to ballast water transport from Europe, North American inland waters have been invaded in recent decades by several marine-like animals originating from the freshwater margins of the Black, Azov and Caspian Seas, including several species (e.g. the zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena bugensis* and round goby *Neogobius melanostomus*) whose unique functional ecology has contributed to strong impacts on native communities in the Great Lakes that lack evolutionary experience with such organisms (Ricciardi & MacIsaac 2000). Before reaching North America, each of these Ponto-Caspian species became abundant at European ports from whence originates the bulk of shipping traffic to the Great Lakes. This example is one of many that show how propagule richness is strongly influenced by the transportation vector activities and pathways between the donor and recipient regions (Wilson et al. 2009).

#### The invader's range size

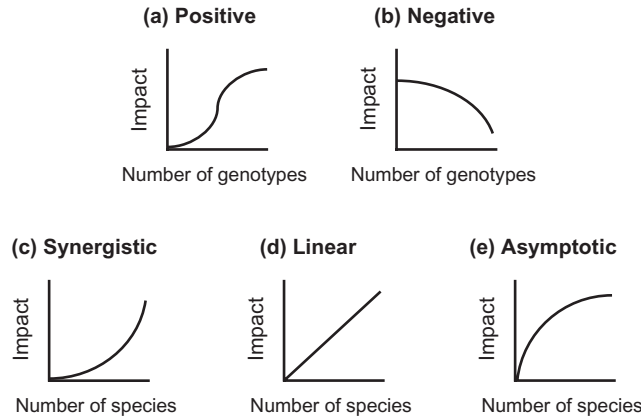
Both propagule abundance and frequency of introduction can have positive effects on an invader's range size (see, for example, Duncan et al. 1999). Through the delivery of multiple genotypes, propagule pressure can increase the potential for a non-indigenous species to adapt to local selective pressures (Sexton et al. 2002; Novak & Mack 2005; but see Dlugosch & Parker 2008), and thus governs the range of habitats in which native populations and communities are affected by the invader. Furthermore, a delay in the arrival of these genotypes can cause an invader's impact to change over time (Strayer et al. 2006). Secondary introductions from various sites in Europe raised the adaptive potential of canary grass *Phalaris arundinacea*, allowing it to invade a broader area of North American wetlands (Lavergne & Molofsky 2007). Even a long-established species can suddenly expand its range in the event of an infusion of genetic variation; multiple ballast-water introductions added genetic diversity to European green crab populations on the Atlantic coast of North America, apparently causing them to suddenly spread northwards into colder waters to which they were thought to be intolerant (Roman 2006). Variation in the source of propagules released in a given region may also lead to the creation of competitive hybrids that can rapidly expand their range

(Ellstrand & Schierenbeck 2000; Facon et al. 2005). On the other hand, continuous propagule pressure (gene flow) could also reduce local fitness and impede adaptation (Holt et al. 2005); the recipient habitat could become flooded with an inferior genotype, resulting in inferior hybrids or detrimental genetic swamping. These examples illustrate how frequent introductions of a species from different source populations can alter its invasion potential and the area over which its impacts occur.

#### 17.4 SYNERGISTIC OR ANTAGONISTIC EFFECTS OF PROPAGULE RICHNESS?

Propagule richness, as numbers of introduced genotypes or species, can have varied effects on the recipient community (Fig. 17.3). For a given species, the number of genotypes introduced may have a positive or negative effect on the probability and magnitude of its impact. As noted previously, propagule richness can elevate impact by (i) producing invasive hybrids, (ii) increasing an invader's functional diversity (e.g. physiological tolerances, morphology or behaviour) so as to give it a competitive advantage, or (iii) enabling or accelerating range expansion. However, high genetic diversity might also increase intraspecific aggression or competition, or cause detrimental genetic swamping or the production of inferior hybrids when incoming genotypes are maladaptive (e.g. after rapid adaptation of the invader).

Given that impacts are expected to accumulate with the number of invaders in an area, there should be a positive relationship between propagule richness (as species) and impact, but different situations may arise. An increase in propagule richness provides more opportunities for the introduction of natural enemies of a previously established or future invader, which can constrain the invader's spread and population growth (and hence its impact); but they might instead facilitate the invader if they harm resident species in the invaded range (Colautti et al. 2004). Multiple invaders can interfere with each other in such a way as to attenuate their impacts (Vance-Chalcraft & Soluk 2005; Griffen et al. 2008). Conversely, through a variety of positive interactions, multiple invaders can produce synergistic effects (Simberloff & Von Holle 1999; Richardson et al. 2000; Ricciardi 2005). For example, the establishment of functionally diverse



**Fig. 17.3** Hypothesized relationships between propagule richness (numbers of introduced genotypes and species) and the probability or magnitude of impact. For a given species, increased numbers of genotypes can elevate impact by enabling or accelerating range expansion (a). However, they may reduce impact when high genetic diversity increases intraspecific competition or genetic swamping with maladaptive genotypes (b). An increase in the number of species can produce a synergistic relationship (c), if the impacts of one or more invaders are amplified in the presence of other invaders. A linear relationship (d) is expected when impacts are additive and could describe a proportional sampling effect. An asymptotic relationship (e) is expected under at least two situations: mutually negative interactions (e.g. competition, interference) between introduced species may diminish their respective impacts; impacts may also attenuate through source pool depletion, if high-impact invaders colonize more rapidly than other species.

predators may increase the extinction risk of resident species through a nonlinear accumulation of deleterious effects (Blackburn et al. 2005). However, in aquatic systems, the number of invaders causing severe declines in native species populations is a linear function of the total number of introduced species in an area, after controlling for species–area effects (Ricciardi & Kipp 2008). This correlation likely reflects proportional sampling and suggests that the probability of receiving a high-impact species increases predictably with propagule richness.

Furthermore, an increase in propagule richness provides opportunities for reassembling co-evolved mutualistic, predator–prey or parasite–host combinations that produce synergistic impacts. In Western Europe, multiple vectors drove sequential invasions that completed the parasitic life cycle of a Ponto-Caspian trematode, *Bucephalus polymorphus*. The introduction of the trematode’s first intermediate host (the zebra mussel) and its definitive host (pike-perch *Sander lucioperca*) allowed it to establish and cause high mortality in local populations of cyprinid fishes, which serve as secondary intermediate hosts (Combes & Le Brun 1990).

Finally, an influx of non-indigenous species can alter the potential impacts of a previously established invader, even after a long time period during which it was relatively innocuous. An example is the European weed *Pastinaca sativa* that rapidly evolved an increase in toxicity in response to the introduction of one of its natural herbivores, two centuries after the weed became established in North America (Zangerl & Berenbaum 2005). The consequences of multiple invaders may also depend on the order of their introduction (Robinson & Dickerson 1987). Clearly, the effect of the delivery of multiple invaders to an area is one of the least understood elements of the relationship between propagule pressure and impact.

### 17.5 IMPLICATIONS FOR THE MANAGEMENT OF INVASIONS

The linkages we have highlighted here demonstrate how vector activity can affect the magnitude and scope of impact. A few predictions follow from these case studies. First, a change in the vector or pathway delivering propagules of a given species to a region can alter

the impact potential of the species long after it is established. The delivery of new genetic strains can impede the efficacy of management strategies by supplying potentially adaptive variation to a non-indigenous population that previously may have been benign for many years. Enhanced genetic variation promotes adaptive evolution that reduces vulnerability to enemies (such as biocontrol agents (Burdon & Marshall 1981)) and can trigger rapid growth and spread that make control unfeasible (Roman 2006). Therefore, even after the establishment of a non-indigenous species, efforts should be made to prevent repeated introductions, particularly from new source regions. Second, an increase in the diversity and intensity of vector activity over time will lead to a rise in the number of high-impact invaders (primarily through sampling effects (Ricciardi & Kipp 2008)), which will render ecosystems increasingly difficult to manage. Third, vector activities that transfer species across different biogeographical regions will generate greater impacts than those that transfer species within the same biogeographical region, because the former is more likely to introduce organisms that are functionally novel within the recipient community (Ricciardi & Simberloff 2009). However, this may not apply to freshwater species, because the naïveté of freshwater communities is manifested on a much smaller spatial scale (Cox & Lima 2006). Finally, the risk of receiving highly disruptive invaders will not be proportionally diminished by a simple reduction in propagule abundance, if the number of source regions or vectors is not reduced simultaneously.

The few cases for which long-term data are available do not reveal any straightforward empirical relationship between impact and propagule pressure for a given system. In the Great Lakes, most invasions over the past half century are attributable to shipping (Ricciardi 2006). However, the number of ship-borne invaders that have been implicated in population declines of native species is not correlated with intensity of shipping activity (A. Ricciardi, unpublished data). Most of these invaders are Ponto-Caspian species, which were discovered in the Great Lakes from the mid-1980s to the late-1990s (Ricciardi & MacIsaac 2000), as much as two decades after the peak in shipping activity; it seems unlikely that there was a 10- to 20-year lag between the introduction and detection of these species, given their high reproductive capacity and conspicuous populations. This case suggests that propagule source is at least as important as both prop-

agule abundance and the number of introduction events in influencing the impact of invasion (see also Colautti et al. 2006; Wilson et al. 2009).

## 17.6 EXPANDING THE CONCEPT OF PROPAGULE PRESSURE: NEW AND EMERGING RESEARCH DIRECTIONS

To advance invasion ecology as a predictive science, we advocate the extension of the propagule pressure concept to unite disparate research foci on the establishment, population dynamics, adaptation, range expansion and impact of invaders. By explicitly including impact, the revised concept would provide the context for addressing questions that have both theoretical and applied value, such as the following.

**1** How do different forms of propagule pressure (Table 17.1) vary in importance with respect to the establishment and impact of introduced species? This might be explored through the manipulation of the number, frequency and richness of propagules introduced to experimental mesocosms (see, for example, Drake et al. 2005) and relating these variables to subsequent changes in the structure of replicated recipient communities.

**2** Under what conditions does sustained propagule pressure result in a reduction of invasions and their associated impacts versus a rapid accumulation of invaders and their synergistic effects? Frequent introductions of a given species have been observed to overwhelm biotic resistance from the native community to invasion (Von Holle & Simberloff 2005; Hollebone & Hay 2007), but introductions of multiple species could generate resistance (Case 1990). Several hypotheses predict cumulative negative interactions, suggesting an attenuation of impacts among elevated numbers of invaders (Catford et al. 2009). An alternative hypothesis ('invasional meltdown'; Simberloff & Von Holle 1999) predicts an increased frequency of synergistic impacts with additional invaders (Ricciardi 2005).

**3** Is the introduction of propagules of co-evolved species more likely to generate synergistic impacts than propagules that do not share an evolutionary history? If co-evolution reduces the intensity of negative interactions (Case & Bolger 1991; Levin et al. 1982) and promotes positive interactions, then invaders with a common evolutionary history may be more facilitative and thus more likely to generate an invasional meltdown.



**4** How does propagule pressure interact with other abiotic variables (e.g. disturbance, resource availability, habitat fragmentation) to mediate impact? Anthropogenic disturbance can alter or exacerbate the impacts of introduced species (Byers 2002); habitat fragmentation, for example, can magnify the effects of propagule pressure on hybridization (Simberloff 1996). Complex interactions among the various forms of propagule pressure (Drake et al. 2005; Drury et al. 2007) or between propagule pressure and disturbance (Britton-Simmons & Abbott 2008) pose a challenge to experimental and statistical analysis.

**5** How does variation in different forms of propagule pressure affect time lags and long-term changes in the impacts of an invader? What are the mechanisms by which a change in propagule pressure can cause a previously benign invader to become ecologically disruptive? These questions stem from an increasing recognition of temporal variation in the effects of invaders (Strayer et al. 2006).

Such questions offer fertile ground for research that can inform management, even if general predictive models of impact remain elusive. Given its potential to enable a more comprehensive conceptual framework for understanding and managing invasions, the influence of propagule pressure on the short- and long-term effects of established non-indigenous species merits far more attention than it has received.

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