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Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework

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ABSTRACT

Aim Invasion ecology includes many hypotheses. Empirical evidence suggests that most of these can explain the success of some invaders to some degree in some circumstances. If they all are correct, what does this tell us about invasion? We illustrate the major themes in invasion ecology, and provide an overarching framework that helps organize research and foster links among subfields of invasion ecology and ecology more generally.

Location Global.

Methods We review and synthesize 29 leading hypotheses in plant invasion ecology. Structured around propagule pressure (P), abiotic characteristics (A) and biotic characteristics (B), with the additional influence of humans (H) on P, A and B (hereon PAB), we show how these hypotheses fit into one paradigm. P is based on the size and frequency of introductions, A incorporates ecosystem invasibility based on physical conditions, and B includes the characteristics of invading species (invasiveness), the recipient community and their interactions. Having justified the PAB framework, we propose a way in which invasion research could progress.

Results By highlighting the common ground among hypotheses, we show that invasion ecology is encumbered by theoretical redundancy that can be removed through integration. Using both holistic and incremental approaches, we show how the PAB framework can guide research and quantify the relative importance of different invasion mechanisms.

Main conclusions If the prime aim is to identify the main cause of invasion success, we contend that a top-down approach that focuses on PAB maximizes research efficiency. This approach identifies the most influential factors first, and subsequently narrows the number of potential causal mechanisms. By viewing invasion as a multifaceted process that can be partitioned into major drivers and broken down into a series of sequential steps, invasion theory can be rigorously tested, understanding improved and effective weed management techniques identified.

Keywords

Biological invasions, community ecology, Darwin, Elton, invaders, synthesis.

INTRODUCTION

Increases in international travel and trade have escalated the extent and frequency of species transfer around the world, and this shows no sign of abating (Mack, 2003; Lockwood *et al.*, 2005; Alpert, 2006). Species that expand beyond their natural range and population density are defined as invasive and may cause ecological or economic harm (Richardson *et al.*, 2000). Invasive species impact indigenous species, community dynamics and the overall structure and function of ecosystems. The impact of invasion is determined by the geographical range, abundance and the per-capita or per-biomass effect of the invader (Parker *et al.*, 1999). Numerous hypotheses address the reasons for successful biological invasion (Richardson & Pyšek, 2006), and most attribute it to characteristics of the invader or characteristics of the invaded ecosystems, with comparatively few integrating the two (but see Davis *et al.*, 2000; Colautti *et al.*, 2004; Blumenthal, 2006).

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Despite an increasing number of hypotheses that unite various arms of invasion ecology (Richardson & Pyšek, 2006), a holistic framework has largely been absent (Barney & Whitlow, 2008). Research studies have mainly focused on individual mechanisms (White *et al.*, 2006) and there has been no formal way to integrate findings. Rather than independent research projects trying to find the 'holy grail' of invasion (Sher & Hyatt, 1999; Davis *et al.*, 2000), greatest advances in invasion ecology would stem from a synthetic approach. Invasion success is likely to be context-dependent and due to a combination of factors and mechanisms (Williamson & Fitter, 1996; Daehler, 2003), so all of the possible reasons for successful invasion should be considered. A broader approach, where reductionist studies are placed within a robust, general theoretical framework, may advance understanding, and help to strengthen links within invasion ecology and with other subdisciplines of ecology.

The aim of this paper is to illustrate the major themes in invasion ecology and how they are dealt with by different hypotheses. By highlighting common ground among hypotheses, we demonstrate considerable overlap and redundancy in the theory of invasion ecology, where 'new' models and terms have been reinvented (albeit in different ways or with different foci). Rather than approaching a particular theme from many angles, we postulate that it is more useful to discuss causes of invasion in relation to a larger framework. We provide a simplified structure and contend that it will improve the understanding of invasion by placing hypotheses and mechanisms in context, and it will help to ensure that all mechanisms for invasion are considered. Our framework highlights the synergy between invasion and community ecology, and provides grounds for applying invasion theory to indigenous weeds as well as non-indigenous invaders, despite evolutionary differences. We conclude by showing how this approach can be used to organize and guide future research and weed management.

Definitions

Invasion is conceptualized as a staged process (Richardson *et al.*, 2000; Colautti & MacIsaac, 2004), although not necessarily a linear one (Colautti & MacIsaac, 2004). Invasion stages are perceived as being divided by barriers, or ecological filters, and species must pass these filters before progressing to the next stage (Richardson *et al.*, 2000; Mitchell *et al.*, 2006). As a result of this process, the number of species reaching each stage diminishes (Elton, 1958; Williamson, 1993; Williamson & Fitter, 1996; Levine *et al.*, 2004), although this has been attributed to a temporal artefact rather than filtering (Richardson & Pyšek, 2006). Viewing invasion as a staged process encourages ecologists to conceptualize factors that might enable a species to pass from one stage to another and can guide research and management (Table 1).

Based on a literature review, we have identified six distinct phases that lead to successful invasion (Table 1). The number of stages and their definitions vary among authors (Richardson *et al.*, 2000; Colautti & MacIsaac, 2004) and this has impeded generalizations and interstudy comparisons (Colautti & MacIsaac, 2004). Notwithstanding the differences, all of the definitions reviewed start with transport and introduction of plants, or plant propagules, into a new range and finish with spread and potentially negative impacts on other species. The notion of impact is based on human perception and can be subjective (Williamson, 1993), and economic and ecological impacts are not always synonymous (Pyšek & Richardson, 2006). We therefore understand 'successful invasion' to be the phase of invasion where a non-indigenous (alien, exotic, non-native) species undergoes spread outside the area of first introduction (Table 1, stage 5). Invasive species that harm other species or human interests (Table 1, stage 6) are termed pests. While the terms invasion, invaders and invasive only apply to non-indigenous species in this paper, indigenous (native) species can also reach stages 5 and 6 (Table 1, see Discussion; Richardson *et al.* 2000). We refer to non-indigenous species in stages 5 and 6 as invasive, indigenous species in stages 5 and 6 as indigenous weeds, and collectively refer to them as weeds.

Invasion ecology: themes in the theory

The literature on invasion ecology comprises many hypotheses designed to explain invasion success at a variety of temporal and spatial scales (reviews by Davis *et al.*, 2000; Alpert, 2006; Mitchell *et al.*, 2006; Richardson & Pyšek, 2006). Many hypotheses overlap, mirror, unite or share similarity with pre-existing hypotheses, a phenomenon not uncommon in ecology (Belyea & Lancaster, 1999; McGill *et al.*, 2007). The selection of hypotheses in Table 2, which is intended to illustrate patterns rather than to provide an exhaustive review of the literature, highlights commonalities among hypotheses.

For example, the empty niche hypothesis, which contends that non-indigenous invaders are successful because they use resources that indigenous species do not (Hierro *et al.*, 2005), is similar to the notion of invasion windows (Johnstone, 1986) and opportunity windows (Shea & Chesson, 2002). These hypotheses reflect the limiting similarity hypothesis, which supposes that successful invaders should be functionally different from species already present in the community (especially indigenous dominants; MacArthur & Levins, 1967; Emery, 2007). While Darwin (1859) initially expected the opposite (Procheş *et al.*, 2008), limiting similarity is embodied in what is now known as Darwin's naturalization hypothesis (Daehler, 2001; Ludsin & Wolfe, 2001; Procheş *et al.*, 2008).

In turn, limiting similarity is mirrored by biotic resistance where a recipient community is resistant to invasion, typically as a result of competition that stems from high local diversity and low niche vacancy (MacArthur, 1970; Hierro *et al.*, 2005). All of these hypotheses relate to resource availability and, as such, they also veer into the territory of hypotheses based on habitat heterogeneity (Melbourne *et al.*, 2007), fluctuating resource availability (Davis *et al.*, 2000) and disturbance (Sher & Hyatt, 1999). Using the same selection of hypotheses as Table 2, Table 3 lists the factors attributed to successful invasion. As well as illustrating considerable overlap and fragmentation, it is evident that there are four major factors (including human interference) that underpin invasion hypotheses (Table 3).

Table 1 Stages involved in invasion as related to various classification schemes and definitions.

<table>
<tr><th>Stage/Process</th><th>1/Transport</th><th>2/Introduction</th><th>3/Colonization</th><th>4/Naturalization</th><th>5/Spread</th><th>6/Impact*</th></tr>
<tr><td>Definition</td><td>Movement of plants or plant propagules to new location</td><td>Arrival of plant or plant propagules into new location</td><td>Survival of introduced plants</td><td>Survival and reproduction enabling pioneer population to be self-sustaining</td><td>Dispersal of propagules and spread of populations outside of area where first introduced</td><td>Harmful impact of species to ecology and economy</td></tr>
<tr><td>Driving factor†</td><td>P</td><td>P</td><td>PAB</td><td>pAB</td><td>PAB</td><td>paB</td></tr>
<tr><td>Spatial scale‡</td><td>Regional and continental</td><td>Local</td><td>Local</td><td>Local</td><td>Regional</td><td>Local and regional</td></tr>
<tr><td>Human-assisted</td><td>Yes, generally</td><td>Yes, generally</td><td>Yes, but not essential</td><td>No</td><td>No, but can exacerbate</td><td>No</td></tr>
<tr><td>Potential management actions</td><td>Quarantine and screening</td><td>Monitoring, detection and early eradication</td><td>Monitoring, detection and early eradication</td><td>Eradication and control of founding population; control of potential dispersal vectors</td><td>Dispersal and spread minimization; detection and eradication of satellite populations</td><td>Population control; dispersal and spread minimization; impact alleviation</td></tr>
<tr><td rowspan="5">Common terms used for non-indigenous invaders and the stages where they apply</td><td></td><td></td><td></td><td></td><td></td><td>Noxious/Pest</td></tr>
<tr><td></td><td></td><td></td><td></td><td colspan="2">Invasive</td></tr>
<tr><td></td><td></td><td></td><td colspan="3">Naturalized</td></tr>
<tr><td></td><td></td><td colspan="4">Weed</td></tr>
<tr><td></td><td colspan="5">Introduced</td></tr>
<tr><td rowspan="2">Requisite stages§</td><td></td><td></td><td></td><td></td><td colspan="2">Indigenous weeds</td></tr>
<tr><td colspan="6">Non-indigenous invaders</td></tr>
<tr><td colspan="7">Terms used for the six stages by various authors</td></tr>
<tr><td>Williamson (1993)</td><td>Imported</td><td colspan="2">Introduced</td><td>Established</td><td colspan="2">Pest</td></tr>
<tr><td>Richardson *et al.* (2000) – stages where barriers to invasion operate</td><td colspan="2">Geographic (A)</td><td>Environmental (local) (B)</td><td>Reproductive (C)</td><td>Dispersal (D)</td><td>Environmental [disturbed (E) and natural (F) habitats]</td></tr>
<tr><td>Levine *et al.* (2004)</td><td colspan="2">Introduction</td><td colspan="2">Establishment</td><td>Spread</td><td>Impact</td></tr>
<tr><td rowspan="2">Colautti & MacIsaac (2004) – Stages</td><td>Uptake and transport</td><td>Release and introduction</td><td colspan="2">Establishment and proliferation</td><td colspan="2">Spread</td></tr>
<tr><td>(0) I</td><td>II</td><td>III</td><td>III (IVb)</td><td>IVa</td><td>V</td></tr>
<tr><td>Lockwood *et al.* (2005)</td><td>Uptake and transfer</td><td>Release; arrival</td><td colspan="2">Establishment</td><td colspan="2">Population increase and range expansion</td></tr>
<tr><td>Mitchell *et al.* (2006)</td><td>Transport</td><td>Introduction</td><td>Colonization</td><td>Survival and reproduction</td><td colspan="2">Spread</td></tr>
</table>

*Stage 6, Impact, is based on human perceptions (a sociological notion, not a biogeographical one), so not all invasive species will necessarily reach stage 6. †Driving factor (discussed in text): P, propagule pressure; A, abiotic characteristics; B, biotic characteristics; capital letters indicate that the factor is primarily responsible for that invasion stage, small letters indicate that the factor usually has a secondary influence, although it can be a primary driver; more than one factor can drive invasion; H, human interference considered in separate row. ‡Spatial scale indicates the scale where factors important for that stage operate, which enable the associated process to occur. §Indigenous weeds do not have to negotiate stages 1–4 (and all of the associated terms, and processes) as they have effectively passed all of these hurdles already; only stages 5 and 6 apply to them (e.g. only Invasion terms 'Invasive' and 'Noxious/Pest'). Non-indigenous invading species must progress from stage 1 to reach stage 6, so all of the terms and processes relate to them. The stages that particular terms relate to are indicated by shading in the respective rows (e.g. Invasion term 'Invasive' refers to species in stages 5 and 6; Levine *et al.*'s (2004) 'Establishment' refers to stages 3 and 4).

Table 2 Summary of 29 leading hypotheses in invasion ecology with key references.

Hypothesis	Code*	E†	Explanation	Extent‡	Lag time§	Similar hypotheses	Notes	Key references
Propagule pressure	PP	+	High supply (size) and frequency (number) of plant propagule introductions increase chance of successful invasion due to high genetic diversity, seed swamping, continual supplementation, higher probability of introduction to favourable environment.	F/P	S/L	GC, IW	Propagules include adult plants, seeds or reproductive vegetative fragments. Reference to PP is generally species-specific, but not always. PP most effective in systems with available resources (e.g. primary succession).	Lonsdale, 1999; Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Pyšek & Richardson, 2006; Richardson & Pyšek, 2006
Global competition	GC	+	Based on PP, but noting that with an increasing number of species introduced, the higher the likelihood that a competitive species will be in the invading species pool.		S/L	PP, IW, PA, EN, BR, SP, DN	Rather than focusing on PP of individual species, GC focuses on the number of species that are introduced; the larger the species pool, the greater the chance that it will contain species that have traits that enable them to outcompete indigenous species.	Alpert, 2006; Colautti *et al.*, 2006
Sampling	SP	+	Like GC, but interspecific competition, rather than PP, drives invasion. Species identity is more important than species richness of the recipient community, and invasion occurs when invading species are able to exploit resources and avoid enemies more effectively than resident species.		S	IW, GC	With increased size of species pool, increased chance of containing a dominant species. Functional differences are irrelevant; it is a species' ability to dominate a community that enables it to be successful as an invader.	Crawley *et al.*, 1999
Ideal weed	IW	+	Life history, characteristics and traits of the invading species facilitate invasion by enabling them to outcompete indigenous species.	F	S	SP	Some traits that have been correlated with invasiveness include ruderal life history, small seed size, high genotypic and phenotypic plasticity, rapid growth, high and early fecundity and fertility.	Elton, 1958; Baker & Stebbins, 1965; Rejmánek & Richardson, 1996; Sutherland, 2004
Reckless invader	RI	–	Species characteristics that facilitate invasion under certain environmental conditions may be disadvantageous to invader when conditions change. Such tradeoffs may explain transient invasions.	P	L	BID, IW	Investment in ruderal characteristics, like rapid growth and high fecundity, help invader initially but they represent a trade off with stress tolerance. Even if invaders decline with environmental change, they may have already caused ecological harm.	Simberloff & Gibbons, 2004; Alpert, 2006

Table 2 *Continued*

Hypothesis	Code*	E†	Explanation	Extent‡	Lag time§	Similar hypotheses	Notes	Key references
Enemy release	ER	+	Upon entry into a new range, invader loses its natural enemies (herbivores, pathogens) that limit its population size in its home (native) range. Two types of ER: regulatory (ERr) and compensatory (ERc).		S/L	ERD, EICA, R-ER	ERr occurs when species are released from enemies that directly limit their home (native) populations, so they experience immediate benefits and population size increase when enemy constraints are absent. ERc occurs when species lose enemies that they have defended against. Resources previously used for defence are reallocated to growth and reproduction, thereby facilitating invasion albeit delayed and indirect.	Keane & Crawley, 2002; Colautti *et al.*, 2004; Joshi & Vrieling, 2005
Enemy reduction	ERD	+	Similar to ER in process and outcome, but rather than complete release, it is based on a reduction in the number of enemies (partial, not complete, release).	P	S/L	ER, DN		Colautti *et al.*, 2004
Enemy of my enemy	EE	+	Enemies have a stronger effect on indigenous species resulting in apparent competition. Invader accumulates generalist pathogens, which limit the invader's abundance, but limit indigenous competitors more.	P	L	IW, NAS	Also known as accumulation of local pathogens hypothesis. Enemies can be indigenous to recipient community or natural enemies of invader (i.e. also introduced). Can involve tri-trophic or tri-specific interactions, e.g. competition among plant species may be mediated by interactions between plants and soil biota.	Eppinga *et al.*, 2006; Colautti *et al.*, 2004
Enemy inversion	EI	+	Invader's natural enemies are also introduced into new range but are less effective, or may have an opposite effect, in the new biotic and abiotic conditions.	P	S	EICA	e.g. ineffective biocontrol agents.	Colautti *et al.*, 2004
Increased susceptibility	IS	–	Low genetic diversity and lack of specific defence of invaders increases their susceptibility to enemies in the invaded community.	P	S	NAS	Invaders unable to genotypically adapt to new enemies because of genetic bottleneck, and they are naive to their new enemies (overlap with NA).	Colautti *et al.*, 2004
Evolution of increased competitive ability	EICA	+	Similar to ERc, release or reduction of enemies that limit population in home range enables invader to allocate freed resources to adapting and enhancing its competitive ability in new ecosystem and community.		L	ER, ADP		Blossey & Notzgold, 1995; Callaway & Ridenour, 2004; Joshi & Vrieling, 2005

Table 2 *Continued*

Hypothesis	Code*	E†	Explanation	Extent‡	Lag time§	Similar hypotheses	Notes	Key references
Specialist–generalist	SG	+	Based on interactions between invader and recipient community, invasion success maximized when enemies in recipient community are specialists (unable to prey on introduced species) and indigenous mutualists are generalists (facilitate invasion).		S/L	NW, ER, NAS,	Specialist: absolute specialization at one extreme, e.g. preying upon or having symbiotic relationship with a single species; Generalist: absolute generalization in regard to community interactions e.g. relationships among any and all species. Mutualists can also be facilitative.	Callaway *et al.*, 2004; Sax *et al.*, 2007
New associations	NAS	+/–	Invading species form new relationships with species in the invaded community, which enhance or impede invasion success.	P	S/L	BID, IS	New commensalisms and mutualisms can facilitate invasion (e.g. introduced species benefit from relationships with generalist soil biota), whereas new enemies may impede it as invaders do not have specific or appropriate defence mechanisms.	Callaway *et al.*, 2004; Colautti *et al.*, 2004; Mitchell *et al.*, 2006
Missed mutualisms	MM	–	Upon entry into a new range invading species will lose the beneficial mutualistic relationships that they experience in home range, thereby impeding invasion.	P	S/L	ER, ERD	Same rationale as ER and ERD.	Mitchell *et al.*, 2006; Alpert, 2006
Biotic indirect effects	BID	+	Includes a range of mechanisms that can facilitate invasion as a result of indirect community interactions, i.e. how ‘a’ alters the effect that ‘b’ has on ‘c’.	P	L	ERD, EICA, ER, EI, EE, NAS, MM, IM	Four most commonly documented interactions are apparent competition, indirect mutualism/commensalism, exploitative competition and trophic cascades.	Callaway *et al.*, 2004; White *et al.*, 2006
Invasional meltdown	IM	+	Direct or indirect symbiotic or facilitative relationships among invaders cause an ‘invasion domino effect’. Often occurs over a range of trophic levels, where one species makes habitat or community more amenable for the other.	P	L	BID	Beneficial invader interactions may be pre-existing or not. Ecosystem engineers (transformers) can facilitate invasion of other non-indigenous species by altering ecosystem characteristics.	Simberloff & Holle, 1999; Mack, 2003
Biotic resistance	BR	–	Competitors, herbivores and pathogens in recipient community limit colonization, naturalization and persistence of invaders, impeding invasion.	P	S	EN, GC, LS, DN	Invading species are not adapted to indigenous competitors in new range, or defended against herbivores or pathogens. Community resistance mostly attributed to competition.	Levine *et al.*, 2004; Parker & Hay, 2005; Alpert, 2006
Novel weapons	NW	+	Invading species release allopatric chemicals that inhibit and repress potential competitors in new range. Indigenous species are not adapted to the novel chemical weapons, enhancing the invader’s competitive ability and success.	P	S	EN, OW, EVH, DN	Effect of allelopatry is usually relatively immediate unless invading species undergo genotypic or phenotypic adaptation.	Callaway & Ridenour, 2004; Hierro *et al.*, 2005

Table 2 *Continued*

Hypothesis	Code*	E†	Explanation	Extent‡	Lag time§	Similar hypotheses	Notes	Key references
Limiting similarity	LS	+	LS predicts that successful invaders are functionally distinct from species in the recipient community, so encounter minimal competition and can fill an empty niche. LS causes trait/phylogenetic overdispersion.	F/P	S/L	EN, OW, BR, EVH, DN	Inverse of BR essentially. Invaders may have different phylogeny, traits or belong to a different functional group compared to indigenous species. Ability to fix nitrogen (e.g. soil–biota mutualisms) is an example of a novel trait.	MacArthur & Levins, 1967; Emery, 2007; Darwin, 1859; Vitousek *et al.*, 1987; Mack, 2003; Callaway & Ridenour, 2004; Hierro *et al.*, 2005
Habitat filtering	HF	+	Invader successful as it is adapted to conditions of ecosystem and able to pass through the environmental filters. HF leads to trait underdispersion and phylogenetic clustering.	F	S	ADP	Habitat heterogeneity can promote invasion due to the vast range of conditions and niches. Probability of niche saturation is low.	Darwin, 1859; Weiher & Keddy, 1995; Melbourne *et al.*, 2007 Procheş *et al.*, 2008
Environmental heterogeneity	EVH	+	Habitats with high environmental variability contain a diverse array of niches that can host a variety of species. Invasion will be successful if there are an insufficient number of indigenous species to fill the available niches (i.e. indigenous species pool too small).	F	S/L	EN, HF	The spatial-scale-mediated pattern between diversity and invasion level has been attributed to higher habitat heterogeneity at large scales and the inability of the indigenous species pool to saturate the available niches, which leaves 'space' for invaders.	Melbourne *et al.*, 2007
Increased resource availability	IRA	+	Species require resources for colonization and establishment so an increase in resource levels provides opportunity for invasion.	F	S/L	DS, DE, ADP, OW	Also known as fluctuating resource hypothesis. Assumes that resources are fully utilized under 'normal' conditions. Resource levels increase by either an increase in supply (e.g. abiotic disturbance, eutrophication) or a decrease in resource use (e.g. die back of resident plants).	Sher & Hyatt, 1999; Davis *et al.*, 2000; Colautti *et al.*, 2006; Richardson & Pyšek, 2006
Disturbance	DS	+	Disturbance events increase resource availability and reset succession, giving invading species an equal chance of success at colonization and establishment.		S/L	OW, IW, IRA, DE	Disturbance events can be natural (e.g. floods, cyclones, fires) or anthropogenic (e.g. eutrophication, clearing). Invasion can be immediate unless species have to wait for disturbance. Disturbance-mediated invasion most effective when invaders are ruderals adept at primary succession (relates to IW).	Sher & Hyatt, 1999; Hood & Naiman, 2000; Colautti *et al.*, 2006

Table 2 *Continued*

Hypothesis	Code*	E†	Explanation	Extent‡	Lag time§	Similar hypotheses	Notes	Key references
Dynamic equilibrium model	DE	+/–	Disturbance and productivity interact to affect invasion, and each factor can reverse responses driven by the other. Invaders can readily establish in low disturbance–low productivity systems (but not very unproductive ones), but only become dominant in high productivity systems with high levels of disturbance (required to establish).		S/L	EVH, IRA, DS	Disturbance (biotic and abiotic) affects mortality; productivity (linked to resource availability and competitive displacement) affects plant growth rates. Likely that response to competition is only apparent at spatial scale where species interact. Modified from dynamic equilibrium model of species diversity; areas capable of high species diversity susceptible to invasion.	Huston, 1979, 2004
Empty niche	EN	+	Due to a limited indigenous species pool, the recipient, community and ecosystem are unsaturated so invaders can use the spare resources and occupy the unused niches (i.e. there is room for the invaders).	F	S	BR, EVH, DN	Inverse of some components of BR. Invaders able to use vacant niches, especially if they are novel (overlap with LS).	MacArthur, 1970; Hierro *et al.*, 2005
Opportunity windows	OW	+	Similar to EN, but niche availability is dynamic fluctuating through time and space. When opportunity arises, invading species colonizes and, once naturalized, invades.		S/L	EN, DS, IRA, EVH, NV, IRA	Also referred to as invasion windows. Invasion essentially occurs when there is a temporary increase in resource availability and community gap either in time or space. Invaders must be opportunistic.	Johnstone, 1986; Shea & Chesson, 2002
Adaptation	ADP	+	Invader pre-adapted to ecosystem conditions, or adapts post-introduction, enabling it to be successful in new range because of its specialization and associated competitive ability.		S	HF, DN		Duncan & Williams, 2002
Resource–enemy release	R-ER	+	Combines ER and IRA but notes that invasion can be accelerated and enhanced when both occur.	F	S/L	IRA, ER	Invasion can occur with just ER and IRA but will be enhanced if both occur together.	Blumenthal, 2006
Naturalization	DN	+	Invasion success attributed to human interference, high propagule pressure, suitable environmental conditions and favourable community interactions. HF is recognized but focuses on LS.	F	S/L	ER, IW, EN, ADP, LS, NV, HF, DS	Incorporates and integrates a number of different hypotheses. Ideas were articulated by Darwin so referred to as Darwin's Naturalization Hypothesis.	Darwin, 1859; Lonsdale, 1999; Pyšek & Richardson, 2006; Richardson & Pyšek, 2006

*Code, abbreviation for hypothesis name in column 1; †E, Effect indicates whether the hypothesis predicts a positive or negative effect on invasion success: +, facilitates invasion, –, inhibits invasion; +/– effect depends on conditions. ‡Extent: extent of the hypothesis; some hypotheses aim to provide a full explanation (F) of invasion, whereas others provide a partial explanation (P); blank indicates that the extent of the hypothesis has not been discussed. §Lag time indicates the relative length of time it takes for the invader to become invasive: S, short; L, long. 'Indigenous' refers to species in the recipient (invaded) community; 'natural enemies' refers to enemies of the invading species that come from its home range.

Table 3 Factors that influence invasion success according to 29 hypotheses of invasion ecology.

Hypothesis	Code	Human interference	Propagule pressure	Abiotic factors				Biotic factors							
				Conditions		Resources		Invader traits	Community interactions			Novel §			
				Present*	Modified†	Low uptake‡	High supply		Enemies	Mutualism	Competition	Evolution	Phylogeny	Functional group	Trait
Propagule pressure	PP	++	++					+							
Global competition	GC	+	++					++				++	++	++	++
Sampling	SP	+	+					++	+		+				
Ideal weed	IW	+	+					++							
Reckless invader	RI			–				–							
Enemy release	ER								++		+	++	+		
Enemy reduction	ERD								+		++	+			
Enemy of my enemy	EE								++		++	+			
Enemy inversion	EI								++	++		–			
Increased susceptibility	IS							–	–			–			
Evolution of increased competitive ability	EICA							++	++		++	++			
Specialist–generalist	SG								++	++		++			
New associations	NAS								–	++	–	+/–			
Missed mutualism	MM									–		–			
Biotic indirect effects	BID								++	++	++				
Invasional meltdown	IM			+	+			+		++	++	+			
Biotic resistance	BR								–	–	–	–			
Novel weapons	NW								+		+	++	++	++	++
Limiting similarity	LS								+		+	++	++	++	+
Habitat filtering	HF			++				+							
Environmental heterogeneity	EVH			++		++					+		++	++	
Increased resource availability	IRA	+				++	++	+			++				
Disturbance	DS	+				++	++	+							
Dynamic equilibrium	DE					++/–	++/–	+							
Empty niche	EN			+		+		+				+	++	++	++
Opportunity windows	OW	+		+	+	++	++	+	++	++	++	+	++	++	++
Adaptation	ADP			++	++			+	+		+	+	++	+	
Resource–enemy release	R-ER	+				++	++	+	++			+			
Naturalisation	DN	+				++	++	+	++			++	++		

Most of the hypotheses focus on factors that increase invasion success but a few focus on aspects that inhibit it. Example references for hypotheses in Table 2. Symbology: ++ major driver that facilitates invasion; + secondary influence that may facilitate invasion; – factor that impedes invasion; ++/– effect depends on ecosystem conditions. Abiotic factors: Conditions-Present* refers to environmental conditions at time of introduction/invasion; Conditions-Modified† refers to altered environmental conditions where 'natural' conditions no longer exist; Resources-Low uptake‡ refers to low or reduced use of abiotic resources by resident and indigenous plants. §Novel evolution relates to invaders that are non-indigenous; hypotheses that rely on novel evolution do not apply to indigenous weeds. Shading of the columns is for clarity of presentation only.

Unifying themes among hypotheses (PAB)

Invasion is essentially a function of propagule pressure (P), the abiotic characteristics of the invaded ecosystem (A) and the characteristics of the recipient community and invading species (biotic characteristics, B), and reflects positions in time and space (Pyšek & Richardson, 2006). Like the factors that affect community assembly (Belyea & Lancaster, 1999), P includes dispersal and geographical constraints, A incorporates environmental and habitat constraints and B includes internal dynamics and community interactions. For invasion to occur, all three factors must be accommodating, if not favourable (Fig. 1). The extent and intensity of invasion are determined by combination of the three factors, though their influence is unlikely to be equal, and is often mediated by humans (e.g. introduction and spread of propagules, alteration of environmental conditions and indigenous species abundance and diversity; Wilson *et al.*, 2007). The onset of invasion is controlled by temporal and spatial factors and, as PAB fluctuate and change in time and space, the timing, distribution and rate of invasion is dynamic (Hastings, 1996). Consequently, the phase, extent and severity of invasion are determined by the combined strength of PAB, and by the position in time and space (for spatial scale issues see Wiens, 1989; Pauchard & Shea, 2006; Richardson & Pyšek, 2006; for temporal scale issues see Kowarik, 1995; Rejmánek, 2000; Pyšek & Jarošík, 2005; Richardson & Pyšek, 2006).

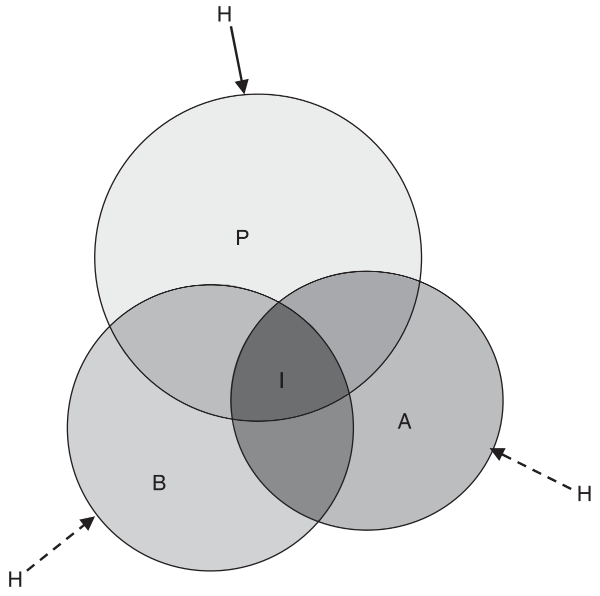

Figure 1 Schematic diagram illustrating how propagule pressure (P), abiotic characteristics (A) and biotic characteristics (B) interact to drive invasion (I), and how humans (H) may modify P, A and B. Invasion occurs where all three factors (i.e. circles) overlap. PAB must all be accommodating for invasion to be successful but the strength and extent of influence from each factor can vary. The circles also illustrate situations where one or two factors might limit invasion. The depth of shading represents the strength of factor influence and the size of the circles indicates the extent of their influence, both of which can change in space and time. In this example, the darker circle of A indicates that A drives invasion, followed by B, then P. P has the greatest extent (time and space) so limits invasion the least. The arrows indicate human interference, which may not necessarily occur but is highly likely with P (solid line; as opposed to dashed lines for A and B).

Propagule pressure (P)

Common to all theories of invasion ecology (Lonsdale, 1999; Davis *et al.*, 2000) is the understanding that successful invasion requires sufficient P (the number of individuals introduced in an event multiplied by the temporal frequency of these events; Eppstein & Molofsky, 2007). Though a single propagule could potentially lead to colonization (stage 3, Table 1), P is often important for the continued success of an invader, not just its introduction (Colautti & MacIsaac, 2004). Some authors suggest that it is the key driver of invasion (Crawley *et al.*, 1996; Lockwood *et al.*, 2005) and may explain the idiosyncratic nature of invasions (Lockwood *et al.*, 2005). This is corroborated by the significance of minimum residence time (time since earliest known introduction, Rejmánek, 2000, i.e. lag phase, Kowarik, 1995) as P generally increases with time (Pyšek & Jarošík, 2005; Richardson & Pyšek, 2006; however, the importance of MRT may also reflect temporal changes in A and B that advantage invaders, e.g. Crawley *et al.*, 1996; Keane & Crawley, 2002; Joshi & Vrieling, 2005).

High P may exacerbate invasion by enhancing genetic diversity of the non-indigenous population, thereby increasing the chance that the species will adapt to ecosystem conditions (Lockwood *et al.*, 2005). High P, especially the number of introduction events, also increases the chance that an invader will be introduced into a favourable environment. Continual introductions can act as a buffer if conditions are temporarily unfavourable (Lockwood *et al.*, 2005) or if populations suffer from a bottleneck (e.g. stage 4, Table 1). Regardless of A and B, high P may enable species to become established simply through seed saturation. Invaders are more successful with seedling–seedling competition than seedling–adult competition (Crawley *et al.*, 1999), so if invaders dominate the seed pool, they are more likely to dominate colonization and establishment. Such seed-swamping may at least partially explain why the majority of plant invasion occurs near human settlements in the UK (Crawley *et al.*, 1996).

Reflecting the importance of P for all stages of invasion (Tables 1 and 4), some researchers have advocated that P be considered as a null hypothesis of invasion (Colautti *et al.*, 2006; Wilson *et al.*, 2007). Most hypotheses, though, have considered P not so much as a driver but a prerequisite of invasion. One hypothesis primarily based on P is global competition; P is often correlated with the number of potential invaders and the larger their species pool, the greater the chance that some of the non-indigenous species will become invasive (Daehler, 2003; Mack, 2003). The ideas of global competition have been used to explain the high degree of invasion on oceanic islands by dominant species from the mainland (Pyšek & Richardson, 2006).

Table 4 Components of propagule pressure (P), abiotic characteristics (A) and biotic characteristics (B) that affect invasion success, matched with relevant hypotheses and weed management techniques.

Driver components*	Driver overlap†	Relevant hypotheses‡	Comments	Impact alleviation methods§
Propagule pressure				
Propagules per introduction	HB	PP, GC, DN	Species traits affect fecundity, phenology and propagule production.	Strict quarantine and screening measures.
Frequency of introductions	H	PP, GC, DN		Strict quarantine and screening measures.
Human use	HA	GC, SP, IW	Affects P, time and location of introduction and spread, e.g. horticulture, agriculture.	Increase awareness and education; strict quarantine and screening measures.
Propagule characteristics	B	PP, GC, IW	Species traits affect propagule characteristics.	Strict quarantine and screening measures.
Dispersal modes and avenues	HA	PP, GC, IW, LS, HF	Affected by location and A.	Strict quarantine and screening measures; concentrate weed control in dispersal corridors and at propagule source.
Abiotic characteristics				
Resource availability	HB	BR, IRA, EN, OW, DE, R-ER, DN	Recruitment success increases with IRA (primary succession).	Increase health and cover of indigenous species to increase resource uptake; time weed control efforts so it is concentrated post-disturbance; avoid/minimize anthropogenic resource increases.
Conditions and regimes	H	BID, IM, HF, EVH, IRA, DS, DE, EN, ADP, DN	Depends on invader traits.	Maintain/reintroduce 'natural' conditions of invaded ecosystem, or conditions that favour indigenous species; focus on the control/eradication of transformer species.
Episodic disturbance	HB	IRA, DS, DE, EN, OW, R-ER, DN	E.g. ruderals in disturbed environments.	Time weed control efforts so it is concentrated post-disturbance; minimize disturbance in uninvaded areas to reduce invader colonization and retain disturbance in invaded areas to destroy invaders.
Geographical location	HP	PP, GC, HF	Affects number of dispersal routes and avenues.	Concentrate control of weed species in dispersal corridors, at propagule source and in ecosystems deemed vulnerable.
Biotic characteristics				
Invader traits	PA	GC, SP, IW, RI, NW, LS, HF, ADP, DN	Affect propagule dispersal, longevity and viability; utility of invader traits depends on A.	Increase health of indigenous species to increase competition; strict screening measures to curb the introduction of potential invaders.
Enemies		ER, ERD, EE, EI, R-ER	Includes herbivores and pathogens.	Introduce/encourage indigenous and potentially natural enemies (natural enemies: from invader's home range)
Competition	A	GC, EICA, SG, BR, LS, DE, EN, ADP	Degree of competition depends on B and resource availability.	Increase health of indigenous species; concentrate weed control in the early stages of succession to minimize seedling–seedling competition.
Mutualism		SG, NAS, MM, BID, IM, BR, DN		Control/eradicate non-indigenous mutualists.
Commensalism		SG, NAS, MM, BID, IM		Control/eradicate non-indigenous facilitators.
Trophic cascades		NAS, BID, IM		Control/eradicate non-indigenous facilitators, especially transformer species (ecosystem engineers).

*Driver components are categorized into PAB based on the factor that is dominant. The driver components can either facilitate or inhibit invasion. †Driver overlap indicates that the component is affected by another PAB factor or by humans (H). ‡Hypothesis codes in Table 2. §Impact alleviation methods refer to management techniques that target the specific driver components.

Abiotic characteristics (A)

The environmental characteristics of a site must be hospitable for invasion to occur. If a species cannot survive the conditions of a site or pass through its environmental filters (Weiher & Keddy, 1995), invasion will fail. Many hypotheses attribute invasion to environmental characteristics (Table 3) and they are often based on a change in resource availability (Davis *et al.*, 2000; Hood & Naiman, 2000; Blumenthal, 2006). Increased resource availability enables population growth, provides invading species with an opportunity to colonize and can reset succession (Hood & Naiman, 2000). An increase in resource availability can occur at a variety of spatial and temporal scales and is usually associated with anthropogenic or 'natural' disturbance (e.g. eutrophication, regional cyclones, local tree-fall gaps; Sher & Hyatt, 1999).

Episodic disturbance can increase resource availability and it has long been associated with invasion (Elton, 1958; Rejmánek & Richardson, 1996; Davis & Pelsor, 2001; though not always, Sher & Hyatt, 1999; Huston, 2004; Buckley *et al.*, 2007). Plants, like other sessile organisms, need space to obtain resources, so any process that increases the availability of space may increase resource availability and invasion. Disturbance events reduce the cover of adult plants increasing space for colonization, and reducing competition, especially between indigenous adults and non-indigenous juveniles (Crawley *et al.*, 1999; Hood & Naiman, 2000). When high levels of disturbance are combined with high levels of ecosystem productivity (growth rates), an introduced species can become invasive (Huston, 2004). Even though indigenous and non-indigenous species undergo the same colonization process (Davis *et al.*, 2000; Meiners *et al.*, 2004), many invasive species are *r*-strategist ruderals (Rejmánek & Richardson, 1996). Consequently, invaders are particularly successful in the early stages of succession and can outperform indigenous species in high resource environments (Daehler, 2003).

Short-term increases in resource availability can drive invasion, but so can long-term changes to disturbance regimes (Tickner *et al.*, 2001) and environmental conditions in general (Williamson & Fitter, 1996). For example, changes to flow regimes have altered the structure of riparian communities (Planty-Tabacchi *et al.*, 1996) and have facilitated invasion (Tickner *et al.*, 2001).

Biotic characteristics (B)

Non-indigenous species may be novel and can both lose and gain biotic interactions on entry into a new range, so community and ecology–evolutionary interactions are important for invasion success and impact (Ricciardi & Atkinson, 2004; Joshi & Vrieling, 2005; Eppinga *et al.*, 2006; Mitchell *et al.*, 2006; Lau, 2008). Interactions like enemy release (Keane & Crawley, 2002), evolution of improved competitive ability (Blossey & Notzgold, 1995), allelopathy (Callaway & Ridenour, 2004), symbiosis (Richardson & Pyšek, 2006) and invasional meltdown (Simberloff & Holle, 1999) can facilitate invasion, whereas others like biotic resistance (Parker & Hay, 2005), biotic containment (Levine *et al.*, 2004) and interspecific competition (Burke & Grime, 1996), especially from dominant species (Emery & Gross, 2006), can constrain it (Table 2). These interactions can transcend trophic levels (e.g. trophic cascades, invasional meltdown; White *et al.*, 2006) and can be mediated by abiotic conditions (e.g. plant–soil biota interactions affecting plant competition; Callaway *et al.*, 2004; Eppinga *et al.*, 2006).

Interactions among PAB

Interactions among PAB affect invasion outcomes and should be central to the way invasion is viewed (Fig. 1). Competitive abilities that make an invader successful in one habitat do not necessarily make it successful in another (Sher & Hyatt, 1999), and without suitable characteristics, invading species will not be able to profit from favourable environmental conditions like increased resource availability (i.e. A*B interaction). Dispersal traits of invading species affect P (Crawley *et al.*, 1996; Rejmánek & Richardson, 1996), as do other traits that may cause some species or phenotypes to be introduced (intentionally or unintentionally) more than others (i.e. P*B interaction; propagule bias, Colautti *et al.*, 2006). Similarly, the physical characteristics of a site can increase P by concentrating propagules in certain areas or providing additional dispersal avenues (Lonsdale, 1999), as observed in riparian ecosystems (i.e. P*A interaction; Tickner *et al.*, 2001).

The interdependence and synergy of PAB are reflected in theory (Table 4). The global competition hypothesis is based on the P*B interaction (Alpert, 2006; Colautti *et al.*, 2006), and Burke & Grime (1996), Blumenthal (2006) and Davis *et al.* (2000) all attributed invasion to a combination of A and B, albeit in slightly different ways.

DISCUSSION

Benefits of a broader context

The roots of many key invasion hypotheses can be found in the texts of Darwin (1859) and Elton (1958) (Ludsin & Wolfe, 2001), but empirical research is yet to fully address the complexity of invasion they highlighted. By splitting biological invasion into study-sized fragments that likely coincide with researchers' fields of expertise, most work in invasion ecology has focused on identifying underlying individual mechanisms that explain invasion success. This detailed, albeit somewhat fragmented, approach has been fruitful in compiling a comprehensive list of likely explanations for invasion success. However, the high-resolution focus has also made it difficult to determine the relative influence of different mechanisms on invasion, and might have slowed down the rate of progress in invasion ecology (Davis *et al.*, 2001).

As well as greater connection among invasion studies, invasion ecology would benefit from more exchange and a stronger alliance with succession and community ecology (Chesson, 2000), landscape ecology (With, 2002) and conservation biology (Lockwood *et al.*, 2005). Despite theoretical synergy (Crawley *et al.*, 1999; Shea & Chesson, 2002), there has been little cross-citation between succession ecology and invasion ecology (Davis & Pelsor, 2001), to the detriment of both subdisciplines. The focus on mechanisms for colonization and establishment in studies of succession, as well as research on species additions in community assembly and food-web studies, is relevant for invasion ecology. A factor that has separated invasion ecology from succession and community ecology has been the distinction between indigenous and non-indigenous species.

Indigenous and non-indigenous weeds

Most evidence suggests that, overall, indigenous and non-indigenous colonization do not differ (Richardson & Bond, 1991; Meiners *et al.*, 2004; but see Colautti & MacIsaac, 2004) and both are affected by PAB (Belyea & Lancaster, 1999). Unlike non-indigenous invaders, indigenous weeds do not have to overcome long-distance dispersal barriers and establish self-sustaining populations in a foreign community and ecosystem (stages 1–4, Table 1). Indigenous species can become weeds by increasing their geographical range (Richardson *et al.*, 2000) and population density, which would result from changes in PAB (usually as a consequence of human activities).

Like the reasons for studying unsuccessful invasion (Duncan & Williams, 2002; Burns, 2008), we posit that research on indigenous weeds will be instructive for invasion ecology. First, comparative studies on indigenous and non-indigenous weeds can test hypotheses based on the separate evolutionary histories of non-indigenous invaders (e.g. specialist–generalist and novel weapons hypotheses, Table 3; Colautti & MacIsaac, 2004; Mitchell *et al.*, 2006), and may help to disentangle the effect of biotic interactions (B) from P and A. Second, acknowledging connections between indigenous and non-indigenous species will strengthen links between invasion ecology and subdisciplines of ecology that typically focus on indigenous species. While grounded in invasion ecology that is primarily concerned with non-indigenous species (Lodge & Shrader-Frechette, 2003), the PAB framework is also applicable to indigenous species that become weeds.

Mixed support for all hypotheses proposed

There is empirical support for most invasion hypotheses (examples in papers cited), but findings can differ among studies (Lockwood *et al.*, 2005; Emery, 2007), as the limiting similarity and enemy release hypotheses illustrate (Table 5). Inconsistent support for hypotheses can prompt doubts about hypothesis validity and, conversely, can lend weight to the notion that there are many reasons for successful invasion. Species can use several mechanisms of invasion that are driven by different factors (e.g. *Pinus* species in the southern hemisphere, Richardson *et al.*, 1994; *Tamarix* species in south-western USA, Stromberg *et al.*, 2007). If one

Table 5 Selection of theoretical and empirical observations illustrating that support for invasion hypotheses is often mixed. Hypotheses based around enemy reduction/release and limiting similarity are used as examples. Theoretical rationale and additional empirical evidence can be found in the references cited.

Support	Oppose
Enemy reduction	
Relevant hypotheses Enemy release hypothesis (ER) (Keane & Crawley, 2002); Resource-ER (Blumenthal, 2006); Evolution of Increased Competitive Ability/ERc (Blossey & Notzgold, 1995; Callaway & Ridenour, 2004; Joshi & Vrieling, 2005); Enemy reduction (Colautti *et al.*, 2004); Enemy inversion (Colautti *et al.*, 2004).	*Relevant hypotheses* Accumulation of local pathogens/enemy of my enemy (Eppinga *et al.*, 2006); Missed mutualisms (Alpert, 2006); Specialist–generalist (Callaway *et al.*, 2004; Sax *et al.*, 2007); New associations (Colautti *et al.*, 2004).
Empirical evidence Support from examples in the references listed above.	*Empirical evidence* Invaders lose and gain positive and negative relationships (Eppinga *et al.*, 2006); Altered interactions with enemies, mutualists and competitors all influence invader success (Mitchell *et al.*, 2006); ERH is too simplistic; other mechanisms at play e.g. plant and soil–biota interactions (Callaway *et al.*, 2004; Eppinga *et al.*, 2006).
Limiting similarity	
Relevant hypotheses Limiting similarity (MacArthur & Levins, 1967); Empty niche hypothesis (MacArthur, 1970; Hierro *et al.*, 2005); Darwin's naturalization hypothesis (Darwin, 1859); Hypotheses discussed by Vitousek *et al.*, 1987; Callaway & Ridenour, 2004; Hierro *et al.*, 2005; Mitchell *et al.*, 2006 among others.	*Relevant hypotheses* Habitat filtering (Mitchell *et al.*, 2006); Habitat heterogeneity (Melbourne *et al.*, 2007); Phylogenetic clustering (environmental filters) (Weiher & Keddy, 1995).
Empirical evidence Evidence from oceanic islands suggests that novel invaders are successful on islands because indigenous species are phylogenetically constrained (Mack, 2003); Dominant indigenous species have been found to limit establishment of phylogenetically similar species (Emery, 2007); Pine invasion in South Africa was greatest in vegetation communities (esp. grasslands) that lacked similar growth forms (Richardson & Bond, 1991).	*Empirical evidence* Inconsistent support for LS (Emery, 2007; Procheș *et al.*, 2008); Novel traits and absent life-forms are a partial explanation of invasion, not a complete one (Mack, 2003); Study in New Zealand found that invaders with indigenous congeners were more successful than phylogenetically 'novel' invaders (Duncan & Williams, 2002); Applicability of LS appears to be mediated by spatial scale (Mitchell *et al.*, 2006).

mechanism is tested in isolation, and if particular invasion cases are examined, it is likely that some support will be found (McGill *et al.*, 2007). Integrating hypotheses into an overarching theoretical framework will illustrate their context and how the suggested drivers and mechanisms relate to others.

Value of a simple, holistic framework

Barney & Whitlow (2008) recently proposed a holistic framework (the state factor model) that attributes invasion to the factorial relationship among propagule pressure (*p*), the invaded habitat (*h*), invader autecology (*a*), the invader's source environment (*s*) and time since introduction (*t*). While similar to our model in development and potential application, there are some key differences.

First, the inclusion of time as a driving factor in the state factor model seems misguided. The importance of invasion history (Rejmánek, 2000; Chase, 2003) and the time–invasion relationship are becoming increasingly evident (Castro *et al.*, 2005; Pyšek & Jarošík, 2005; Richardson & Pyšek, 2006; Wilson *et al.*, 2007) and should not be overlooked. However, time itself does not affect invasion outcomes – it affects the way outcomes are perceived. The factors that affect invasion vary across space and time. Therefore, if the scales of investigation change, the nature of an invasion observed will likely change, as will the factors found to be most influential (Wiens, 1989). While spatial and temporal scales must be factored into invasion ecology research and theory (Barney & Whitlow (2008) did not include space in their model, though they acknowledged its importance), it is important to distinguish the difference between scale-based issues and causal factors. Rather than being a weakness or oversight as Barney & Whitlow (2008) suggest, invasion hypotheses should not consider time as a driving mechanism, but as a scale that affects the way invasion is viewed.

Once time is excluded, the PAB framework differs from the state factor model in its segregation of living and non-living factors. Rather than including a separate factor to represent source habitat (*s*, the community and environment in which invaders evolved), we consider the invaders' evolutionary histories and genetic makeup as a component of invader characteristics and, hence, biotic characteristics (B). Barney & Whitlow (2008) combine community and abiotic characteristics in the habitat (*h*) state factor, whereas we separate them. Resident, indigenous communities influence invasion outcomes because of their interaction with invaders, making it essential to consider these biotic components independent of A. Separating A and B is more amenable to research and management, and it could reveal to what degree invasion is driven by invader–community dynamics or by physical characteristics of the invaded environment.

Given the complexity and multitude of interactions in invasion processes, there are many ways in which invasion theory could be organized. While the approach of Barney & Whitlow (2008) has merit, the hierarchical PAB scheme, using only three factors that complement theories of community assembly (Belyea & Lancaster, 1999), is simple and intuitive yet incorporates multiple layers of increasing complexity making it widely applicable.

Using PAB to guide empirical research

PAB are the primary factors that affect community assembly and species distribution, and they form the basis of invasion hypotheses (Table 3). Given that invasions are likely to result from multiple mechanisms, the challenge is to determine which mechanism is the chief driver. The sheer number of potential causal mechanisms is likely to preclude testing all of them relative to one another, but it should be feasible to determine the main factor (P, A or B) responsible for successful invasion. Once that is determined, the underlying mechanisms associated with that factor can be explored. For example, if A is found to drive invasion success, the relative importance of resource availability versus episodic disturbance could be gauged afterwards. A top-down approach, which starts with the three major drivers but increases in complexity as components of PAB are examined, is an efficient way to identify the chief mechanisms that drive invasion, making the PAB framework useful for guiding research. Depending on available resources, research aims, and the scale and breadth of investigation, this challenge can be approached in a stepwise fashion (incremental approach) or in its entirety (holistic approach). Although characteristics of invaders (B_I) and the recipient community (B_C) are interrelated, we suggest that it is easier, and more informative, to separate them for empirical research.

Incremental approach

Using the approach of frequentist statistics (Quinn & Keough, 2002), invasion can be examined as a series of increasingly complex hypotheses (legend of Fig. 2). Building up from the simplest hypothesis, factors and interactions can gradually be added until a complete model is produced. By determining the explanatory power (variance components; Quinn & Keough, 2002) of each of the factors and interactions, their relative importance can be estimated.

Figure 2 illustrates a set of increasingly more complex ideas for explaining how species become invasive. Some of these pathways may be invalid or of minor importance, in which case it is appropriate to move to the next pathway. The first box in the flow chart, human-mediated dispersal and propagule pressure, represents P of an invading species that does not relate to its biological characteristics, but rather to the quantity and distribution of its propagules that have been dispersed by human activities. This is the simplest hypothesis that attributes invasion success purely to P, coinciding with the null hypotheses advocated by Lockwood *et al.* (2005), Colautti *et al.* (2006) and Wilson *et al.* (2007). It is appropriate to examine P first, because invasion cannot occur without propagules, and P-related mechanisms, like seed swamping or global competition, may drive invasion. Examining P might help to tease apart P*A and P*B interactions where it is difficult to determine the direction of causality; does the high P of some species and in some ecosystems facilitate invasion, or do the characteristics of the species and ecosystems lend themselves to high P and high invasion (Lonsdale, 1999; Colautti *et al.*, 2006)?

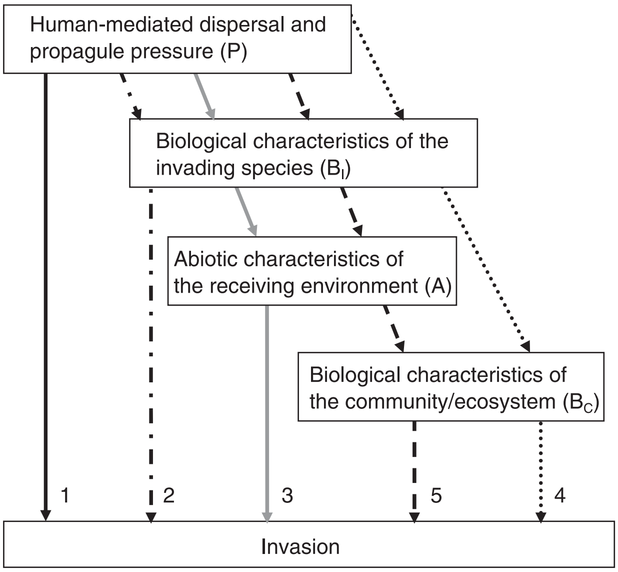

Figure 2 Potential invasion pathways increasing in complexity from 1 to 5. A suggested approach to studying invasion is to determine the validity of these individual pathways, ideally starting at 1, progressing to 5. Not every pathway is necessarily valid. Driving factors of each pathway are as follows: 1, $I = P$; 2, $I = P + B_I + P*B_I$; 3, $I = P + B_I + P*B_I + A + A*P + A*B_I + P*A*B_I$; 4, $I = P + B + P*B$; 5, $I = P + B + P*B + A + A*P + A*B + P*A*B$; notation follows Figure 1; * indicates interactions.

Pathway 2 is driven by biological characteristics of invading species (B_I), assisted by P, and attributes successful invasion to the innate characteristics of the invaders – these species can become invasive regardless of the nature of A or B_C. This hypothesis incorporates propagule bias, which occurs when species with a tendency to be invasive also have higher introduction rates (Colautti *et al.*, 2006). Hypotheses based on characteristics of an 'ideal weed' (Baker & Stebbins, 1965) coincide with this pathway. In practice (e.g. Sutherland, 2004; Richardson & Pyšek, 2006), it is unlikely that species can become invasive based on their characteristics alone, although there are some traits that are more common among invasive than non-invasive species (Rejmánek & Richardson, 1996).

Pathway 3 is driven by the physical characteristics of the receiving environment (A, Fig. 2). Relating to invasibility, it is also dependent on B_I and P, but does not include interactions between the invading and the resident species (B_C). As well as propagule bias, this pathway includes the interaction between A and P, where certain ecosystems tend to be exposed to higher P (Lonsdale, 1999). Invasion of highly disturbed, bare ground by ruderal invaders is an example of this pathway. Pathway 4 is driven by community interactions between the invading and the resident species (B_C), and is not affected by A. The enemy release, invasional meltdown and novel weapons hypotheses are based on this pathway (Fig. 2). The final pathway integrates all of the different factors that influence invasion (P, B_I, A, B_C; Fig. 2). Although it may be expected that this pathway will be the dominant one, relatively few modern hypotheses integrate all of these factors (Table 3), despite empirical findings that suggest that invasion follows pathway 5.

Following this scheme (Fig. 2), invader characteristics are included in all pathways except the first. Are there situations where invasions can be driven by P and A without any great input from B_I? A possible example may be disturbed environments, such as riparian zones where recurrent floods free resources and space for colonization. Perhaps as a consequence, riparian zones belong to the most invaded types of ecosystems (Crawley *et al.*, 1996; Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1998). However, not all invaders and invader populations will necessarily benefit from disturbance (Huston, 2004; Buckley *et al.*, 2007) and growing in riparian zones requires special adaptations, such as flood tolerance, pointing to the importance of B_I.

This incremental approach could be applied experimentally where factors are changed or added incrementally (e.g. using a setup similar to Fig. 3 but manipulating factors in accordance with Fig. 2), or for surveys where factors not being investigated can be controlled (e.g. Pathway 4: limit variation in A). Like all surveys, minimizing the influence of confounding factors and interactions will be challenging. To maximize the utility of the incremental approach, the effect size of interest must be defined *a priori*. It is likely that explanatory power of the model will keep increasing as additional factors are added, so the power of interest should be set in advance. For example, if the aim of research is to identify factors that account for 60% of variation in invasion extent, then testing (and progression from pathways 1–5) may cease once 60% of variance has been accounted for.

In reality, knowledge about invasion often grows through the collective work of independent research groups conducting a suite of surveys and experiments. A meta-analysis approach may be an effective way to utilize results and determine the dominant pathways that have been observed to date and may help to indicate the most influential factors. In this way, Fig. 2 could be followed in reverse, starting with the most complex pathways and gradually eliminating factors.

Holistic approach

The holistic approach examines the influence of PAB simultaneously and, in doing so, enables their relative influence to be ascertained from the outset. This approach is most easily achieved with experiments conducted over small spatial and temporal scales, where factors can be manipulated and the main effects and interactions examined. Propagule density (P) and the types of species introduced (B_I) can be altered in a controlled experiment, and A can be selected (Fig. 3). To examine the independent effects of B_C and A, which are normally confounded, replicate samples of B_C can be placed into different abiotic conditions. Figure 3 provides an example of how communities (B_C) normally nested with certain habitats can be extracted and moved to other habitat types (A). By calculating the proportion of total variance of invasion extent or intensity that can be attributed to each factor and interaction (Quinn & Keough, 2002), results from this experiment would enable the relative influence of the factors to be determined.

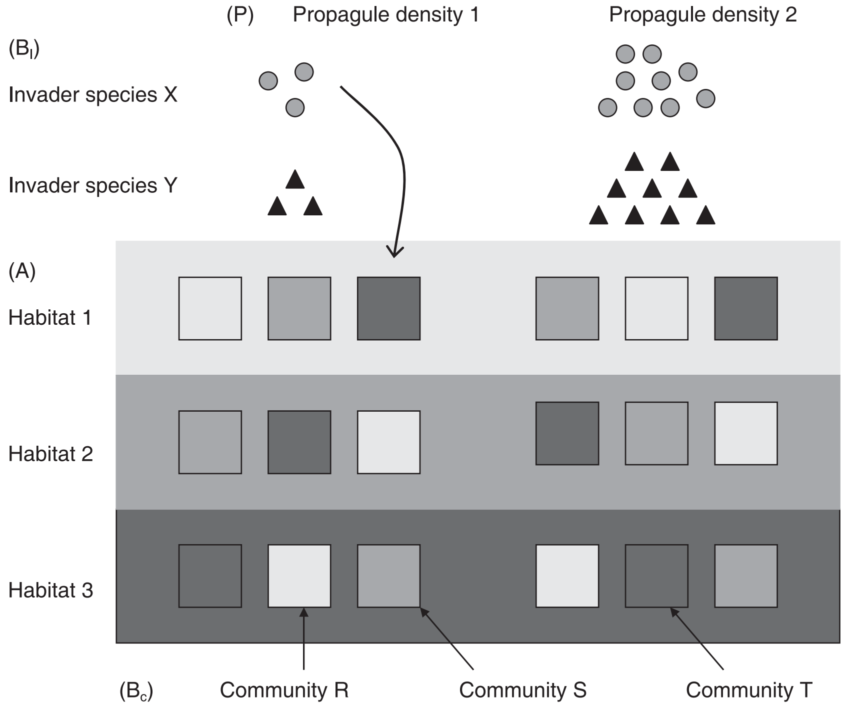

Figure 3 An example of an experimental setup that would enable assessment of the effects of propagule pressure (P), abiotic characteristics (A) and biotic characteristics [separated into invader traits (B_I) and invader–community interactions (B_C)] on invasion extent and severity. P is manipulated by changing the number of propagules that are added per introduction, or number of introduction events. B_I is manipulated by adding different invader species into the experimental quadrats. B_C and A are disentangled from each other by moving sections of each vegetation community into different habitats. P is represented by number of propagules; 3, Density 1; 9, Density 2. B_I is by different shapes; circle, Invader X; triangle, Invader Y. B_C is represented by shading; light grey, Community R; mid grey, Community S; dark grey, Community T. Habitat type is represented by location of strips; upper, Habitat 1; middle, Habitat 2; lower, Habitat 3.

The hypotheses reviewed in this paper (Tables 2 and 3) do not necessarily fit into the structure of the incremental or holistic approach, but that was not the intention. Figure 2 provides a way to graphically illustrate and conceptualize how the PAB framework might be tested in a systematic way, and Fig. 3 shows a holistic way. One major limitation in invasion ecology to date has been the somewhat haphazard way of ascertaining which factors affect invasion; by targeting single, or a few, hypotheses, empirical work has tested certain slices or sections of the PAB framework. The two approaches discussed are intended to illustrate a couple of ways in which empirical and theoretical invasion ecology can progress; by partitioning the various aspects of the PAB framework into testable questions (but also expressing the links among these questions) or by viewing them as whole, cumulatively we move closer to determining what drives successful invasion and under what circumstances.

If the prime aim of a study is to identify the main cause of invasion success, we argue that a top-down approach that focuses on PAB maximizes research efficiency by identifying the most influential factors first, which subsequently narrows down the number of potential causal mechanisms. If working from the bottom up by exploring the significance of components of PAB on invasion (Table 4), the PAB framework highlights that these components may be influential for a number of reasons (e.g. hypotheses and mechanisms that relate to each component in Table 4). Therefore, instead of solely attributing invasion that results from high resource availability to disturbance, for instance, the PAB framework indicates that at least six other hypotheses may be applicable (Table 3). To complicate matters, the estimated 10% of invaders that are transformers (invader that alters the conditions of an ecosystem in its favour due to its growth form, ecology or life-history characteristics; also known as ecosystem engineers; Richardson *et al.*, 2000), may act as a form of disturbance (Lockwood *et al.*, 2005) modifying the invasion process and response (Vitousek *et al.*, 1987; Tickner *et al.*, 2001). By modifying an ecosystem, transformers can obscure the pathways used for invasion (Richardson *et al.*, 2000).

The PAB framework suggests that there is a high probability that invasion stems from interactions among factors. Although inconvenient for research studies that use the top-down approach, the components that underlie interactions can still be identified, and they can be addressed in management (Table 4). Recognizing the complexity of invasion highlights the importance of integrated weed management. Successful weed management in situations with multiple interacting drivers (i.e. pathways 4 and 5 in Fig. 2) may require quarantine and screening, restoration of natural habitats, and eradication and control (Holmes *et al.*, 2005). Knowing the relative influence of factors and components on invasion outcomes will aid decision-making and management resource allocation, and will indicate the limitations of certain management techniques. For example, if enemy release (component of B) accounts for 60% of an invader's success, enhancing predation or herbivory would not eradicate the invader or stop its spread. However, it may be a moderately effective management strategy, especially when combined with other techniques (Table 4). Identifying the end-points that control measures are likely to achieve will increase stakeholder confidence in management and will also ensure that expectations are realistic.

CONCLUSION

Despite a considerable research effort by empirical and theoretical ecologists (Shea & Chesson, 2002), the relative contribution of different mechanisms to invasion success is unknown. Integrating hypotheses into an overarching framework, rather than testing them in isolation, will illustrate their context and assist quantification of their importance compared with other hypotheses. A unified framework will help advance invasion ecology by fostering links with other aspects of ecology, consolidating ideas and removing theoretical redundancy. By viewing invasion as a multifaceted and complicated process that is composed of a series of sequential steps and major drivers, invasion and community assembly hypotheses can be rigorously tested. Identifying the chief causes of invasion will enhance understanding of factors that shape community assembly and affect species coexistence, and will indicate factors that should be targeted in weed management.

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