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REVIEW AND SYNTHESIS

Emergent insights from the synthesis of conceptual frameworks for biological invasions

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Abstract

A general understanding of biological invasions will provide insights into fundamental ecological and evolutionary problems and contribute to more efficient and effective prediction, prevention and control of invasions. We review recent papers that have proposed conceptual frameworks for invasion biology. These papers offer important advances and signal a maturation of the field, but a broad synthesis is still lacking. Conceptual frameworks for invasion do not require invocation of unique concepts, but rather should reflect the unifying principles of ecology and evolutionary biology. A conceptual framework should incorporate multicausality, include interactions between causal factors and account for lags between various stages. We emphasize the centrality of demography in invasions, and distinguish between explaining three of the most important characteristics by which we recognize invasions: rapid local population increase, monocultures or community dominance, and range expansion. As a contribution towards developing a conceptual synthesis of invasions based on these criteria, we outline a framework that explicitly incorporates consideration of the fundamental ecological and evolutionary processes involved. The development of a more inclusive and mechanistic conceptual framework for invasion should facilitate quantitative and testable evaluation of causal factors, and can potentially lead to a better understanding of the biology of invasions.

Keywords

Biological invasions, demography, lags, monocultures, propagule pressure, rapid population increase.

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INTRODUCTION

Biological invasions have dramatically altered the natural world, threatening native species and communities, affecting human health and costing enormous amounts of money to control. Confronting these important applied problems has made this a compelling area for ecological research. Invasions also offer unique opportunities to probe fundamental ecological and evolutionary questions on an unprecedented spatial and temporal scale.

The literature on invasions has grown exponentially over the past half century, with over 10 000 papers published over the last 30 years (Fig. 1; exact numbers depend on definitions of what constitutes a study in invasion ecology). This work on biological invasions encompasses empirical studies particular to specific systems and organisms as well as theoretical and conceptual work. More than two dozen hypotheses for biological invasions have been proposed, based on specific individual drivers of invasions [e.g. resource fluctuation, enemy release hypothesis, evolution of increased competitive ability (EICA); reviewed by Inderjit *et al.* 2005; Catford *et al.* 2009]. It has become increasingly clear that no one individual explanation is sufficient to account for all biological invasions, however compelling the argument for and evidence consistent with that explanation might be. The individual hypotheses partially overlap in mechanism and prediction, and may contribute additively or interactively to invasions. Different mechanisms may contribute to the invasion of different species, or to the same species in different places or at different times; they may also act simultaneously. Milbau *et al.* (2009) point out that researchers may be 'studying different pieces of the same invasibility puzzle' and that progress would be more rapid if results were integrated. Invasion biology is clearly ripe for conceptual synthesis and integration, by subsuming these individual hypotheses in a broadly applicable conceptual framework grounded in basic principles of ecology and evolutionary biology.

Real progress has been made towards developing a general, synthetic conceptual framework for invasions within the last few years. We review this effort, focusing on 19 papers with a diversity of approaches but the shared goal of finding general explanations for invasions that unify and provide a more overarching context for single-factor hypotheses. In addition, we propose a novel conceptual framework that incorporates many of the important elements of previously proposed frameworks, explicitly based on the fundamental ecological and evolutionary processes involved in invasions. We use the term 'fundamental' in its common English meaning: that is, 'relating to a basic phenomenon, foundation or basis; underlying principles'. We mean that biological invasions can be explained in terms of (ordinary, basic) ecological and evolutionary processes such

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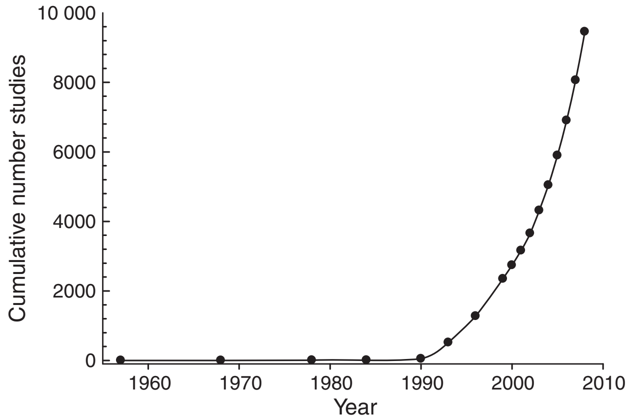

Figure 1 Cumulative number of studies in invasion ecology from 1958 to 2008 from a Web of Science search on key terms 'inva*' and '(ecol* or plant or invert*)' after eliminating all non-ecological subject categories (engineering, oncology, etc.), for 10-year intervals through 1978, 5-year intervals from 1987 to 1990, 3-year intervals to 1999 and 1-year intervals from 2000 to 2008.

as rates of population increase, competition and natural selection without invoking processes or phenomena unique to invasion biology. Ideally, but not necessarily, these are single irreducible elements.

Conceptual frameworks are more common in business and the social sciences than currently in ecology, but recognition of their utility in ecology has been increasing (e.g. see papers in Table 1). A conceptual framework is a theoretical entity closely tied with empirical applications. It is not a formal model *per se*, but can lead to the development of formal models, to empirical or experimental studies, to the generation of new hypotheses or to the comparison and evaluation of existing hypotheses (see, e.g. Dewey 1938; Kaplan 1964; Merrill *et al.* 1981; Botha 1989). Conceptual frameworks encompass the assumptions, laws and ideas that underlie the construction of a broad concept. In practice, they define connections and elements of knowledge in a general area of inquiry, giving coherence and direction to the study of empirical problems. Particular conceptual frameworks are typically described as works in progress, propelling the advancement of thinking on complex topics and providing guidelines for future research and action. The invasion syntheses that we review here are not all full conceptual frameworks, but all contain elements of what conceptual frameworks can achieve.

It is not our goal to compare or explain the many single-factor hypotheses for invasion. Rather, we focus on reviewing and expanding the conceptual frameworks that seek to integrate these hypotheses. We focus on syntheses of explanations for invasion and only touch on other important issues in invasion biology, including invasion impacts and large scale patterns (e.g. Stohlgren *et al.* 1999; Sax & Gaines 2003; Fridley *et al.* 2007).

Each of the invasion syntheses or conceptual frameworks that have been proposed offers important advances. There are overlaps among them, points upon which they disagree, and gaps and limitations in what they encompass, as is true for the single-factor hypotheses they seek to unify. These papers offer insights into how to begin to frame a general understanding of invasions. One of the challenges to creating useful frameworks for invasion is the tension between generality and specificity: overly general efforts risk explaining nothing very well, while overly specific contributions risk explaining only a limited range of cases. The papers discussed here fall at various points along the continuum between specificity and generality. For instance, papers by Hobbs & Humphries (1995) and Doren *et al.* (2009) are cast in an explicitly applied context, and focus on plants, although both include many important elements; others focus on a single over-arching cause for invasions. Some papers are more general and are intended to apply broadly (e.g. Catford *et al.* 2009).

ESSENTIAL FEATURES OF A GENERAL FRAMEWORK FOR INVASIONS

What is essential for a general conceptual framework for biological invasions? We believe that a general framework should put the mechanisms and processes contributing to invasion into the context of basic ecology and evolutionary biology. Population interactions such as competition and predation, ecosystem processes and community and landscape ecology are important basic factors in invasions. Demography of the invading populations is central. The functional ecology, ecosystem, community and landscape processes associated with an invasion must have demographic consequences – increasing the population growth and dispersal of the invader – if they are to contribute to an invasion. Evolutionary processes are integral to a general understanding of invasions, and both the invasive species and the natives in the communities they invade are subject to them.

A general framework should account for the fact that multiple factors often contribute to invasions, and that there can be interactions and feedbacks among these factors. Scale is an important element as well, because the processes governing different aspects of invasion (e.g. establishment vs. geographic spread) occur on different spatial and temporal scales, and their consequences (some direct, some emergent) also occur on distinct scales. A unified approach must in some way accommodate a consideration of how spatial and temporal heterogeneity facilitate invasion, and the role of stochastic variation in space and time. A conceptual synthesis can integrate the study of stages of invasion with other aspects of invasion biology (e.g. Inderjit *et al.* 2005), and explicate the causes of lags at all invasion stages, not only initially. A general conceptual framework of invasions should facilitate explaining the success of invasives relative to natives in the novel environment, the success of invasives in the novel environment contrasted with their home environment and the success of invasive species or populations relative to non-invasive aliens in the novel environment (e.g. Van Kleunen *et al.* 2010).

One barrier to reaching a broad understanding of invasions is that different researchers may be explaining different phenomena when identifying invasions or proposing explanations for them. Invasions are identified – indeed, defined by – three distinct major characteristics: rapid local population increase, the establishment of local dominance or monocultures and/or rapid range expansion. These three characteristics of invasions differ in both causes and impacts. (Major ecosystem alteration also characterizes some biological invasions, and this might be considered a fourth characteristic, depending on whether it is considered to be an outcome of invasion or a causal factor.) We are not referring here to invasion stages – temporal sequences in invasions – but rather, to the major phenomena that define invasions. When populations of a non-native species are observed to demonstrate one or more of these defining characteristics – rapid local population increase, establishment of monocultures, or range expansion – scientists, managers and the general public recognize that an invasion has occurred or is ongoing. These three phenomena that define invasions do not inevitably occur together or lead to one another; any one may occur alone or in

Table 1 Conceptual frameworks of invasion differ in focus, emphasis, generality and in the elements considered. Listed in order of date of publication

Citation	Main elements and focus	Ecological level(s) emphasized	Taxonomic focus	Framework or model type	Aspect(s) of invasion success implied or emphasized	Evolution integral to model or framework?	Emphasizes multicausality?/ interactions between causal factors included?	Explicitly addresses geographic scale at multiple levels?
Hobbs & Humphries (1995)	Management and human role	Population, ecosystem, community	Plants	Verbal, graphical	Range expansion	No	Yes/yes	No
Davis *et al.* (2000)	Disturbance, resources, temporal variation	Ecosystem, community (competition)	Plants	Verbal, graphical	Population increase	No	Two: resource variation and competition	No
Shea & Chesson (2002)	Links to basic community ecology; 'niche opportunity'	Community	Broad	Verbal, mathematical	Population increase	No	Yes/yes	Yes
Marvier *et al.* (2004)	Fragmentation, habitat loss and management	Meta-population	Broad	Mathematical	Population increase	No	No/no	No
Davis *et al.* (2005)	Invasibility as a fundamental property of communities, determined by abiotic conditions, resources, population interactions	Population interactions, community, meta-community, regional, biogeographic patterns	Plants	Systems model, mathematical	Population increase	No	Yes/yes	No
Inderjit *et al.* (2005)	Overview of prior proposed hypotheses for invasion, put into framework of stages of invasion	Life histories, population interactions, community	Plants	Verbal	Population increase, dominance, range expansion	Yes	Yes/implied only	No
Blumenthal (2006)	Interaction of two hypothesized causes of invasion	Ecosystem (response to resources); population interactions (with enemies)	Plants	Graphical	Population increase	Yes	Two: resources and enemy release	No
Facon *et al.* (2006)	Match of invader with habitat due to pre-adaptation or evolutionary change; removal of dispersal barriers	Organism traits, population community, life histories	Broad	Graphical	Population increase	Yes	Yes/interactions between pairs of factors	No
Mitchell *et al.* (2006)	Population interactions, abiotic conditions	Population interactions, community, ecosystem	Plants	Verbal, mathematical, graphical	Population increase	Yes	Yes/yes	No
Richardson & Pyšek (2006)	Naturalization-invasion as points on a continuum, temporal scale and invasion, invasiveness, invasibility and propagule pressure	Organism traits, population community	Plants	Verbal	Population increase, range expansion	Yes	Yes/yes	Yes
Dietz & Edwards (2006)	Differences in causality between distinct stages of invasion	Population, community	Plants	Verbal, graphical	Population increase, range expansion	Yes	Yes/yes	Yes

Table 1 (*Continued*)

Citation	Main elements and focus	Ecological level(s) emphasized	Taxonomic focus	Framework or model type	Aspect(s) of invasion success implied or emphasized	Evolution integral to model or framework?	Emphasizes multicausality?/ interactions between causal factors included?	Explicitly addresses geographic scale at multiple levels?
Eppstein & Molofsky (2007)	Frequency-independent, Frequency-dependent and competitive effects on population growth rates, propagule pressure	Population, community	Plants	Mathematical	Population increase, dominance	No	Yes/yes	Yes
Melbourne *et al.* (2007)	Heterogeneity (in space and time), spatial and temporal scale	Meta-community, population interactions, community, landscape	Broad	Mathematical	Population increase, range expansion	No	Yes/no	Yes
Theoharides & Dukes (2007)	'Filters' at different invasion stages (propagule pressure, abiotic, biotic resistance, human)	Population interactions, community, ecosystem, landscape	Plants	Verbal, graphical	Population increase, range expansion	No	Yes/no	Yes
Barney & Whitlow (2008)	'State factors': propagule pressure, novel habitat, organism traits, source habitat, time since introduction	Population, ecosystem, community	Broad	Mathematical	Population increase	Yes	Yes/implied only	No
Moles *et al.* (2008)	Suites of species' traits, match with environmental conditions, vacant niches	Organism traits, abiotic conditions, community	Plants	Mathematical, graphical	Population increase	No	No/no	No
Catford *et al.* (2009)	Propagule pressure, abiotic, biotic and human factors; hierarchical, synthesizes 29 major hypotheses	Population interactions, community, abiotic conditions, ecosystem	Broad	Verbal	Population increase, range expansion	Yes	Yes/yes	Yes
Doren *et al.* (2009)	Abiotic and human drivers of invasion, invasives as ecosystem engineers, restoration	Abiotic conditions, ecosystems	Plants	Systems model	Population increase	No	Yes/ cross-scale	Yes
Milbau *et al.* (2009)	Invasibility, hierarchy of levels of spatial scale acting as filters	Abiotic conditions, population interactions, community	Plants	Verbal	Population increase	No	Implied only/yes	Yes

combination with either of the others. Management as well as basic science will benefit if we are explicit about which of these distinct aspects of invasion we are attempting to model, explain, understand or control.

APPROACHES AND SCOPE OF PROPOSED SYNTHETIC FRAMEWORKS

We carried out a search for synthetic frameworks for biological invasion by first compiling a list of papers with which we were familiar, then searching the *Web of Science*, using combinations of the search terms 'invasion', 'synthesis', 'conceptual' and 'framework' as well as shortened parts of those terms (e.g. invas*). We examined citations from the papers we selected for additional references. Readers of earlier drafts of this paper suggested references as well. Papers were selected based on whether: (1) their stated aim was to provide or suggest a conceptual framework or comprehensive synthesis of hypotheses explaining biological invasions, (2) other papers cited them as providing conceptual syntheses or (3) we felt that they had done so, regardless of the stated goals of the authors. We excluded papers that proposed or tested single-factor hypotheses for invasions. We attempted to identify papers providing syntheses that introduced novel ideas or added to our general understanding of invasions.

We found 19 papers that included synthetic frameworks for biological invasions that sought to place invasion hypotheses on a common conceptual basis (Table 1), summarizing and categorizing them based on our own interpretations. None of the proposed frameworks include all of the components discussed in the previous section. Most of the papers conceive of biological invasions in terms specific to this subject rather than in a more general ecological context. Elements common to many of the papers include propagule pressure, general abiotic effects, and either biotic effects in general or particular species interactions. Several papers conceive of invasions in terms of successive 'filters' or barriers to invasion in the novel habitat. Invader dispersal ability and habitat connectivity are recognized as important elements in invasion in a number of the frameworks.

The majority of these conceptual frameworks address phenomena at the level of population interactions; many include abiotic effects, and some incorporate functional ecology and species traits (Table 1). Almost half include ecosystem effects, and several consider meta-populations and landscape ecology. Although there is a substantial literature on demographic analyses of invasive populations that helps to shed light on factors contributing to invasions (e.g. Parker 2000; Sakai *et al.* 2001; Buckley *et al.* 2003, 2005, 2006; Neubert & Parker 2004; Rose *et al.* 2005; Shea *et al.* 2005; Jongejans *et al.* 2008; Ramula *et al.* 2008; Shea & Kelly 2008), only a minority of the frameworks explicitly pose demographic processes as essential to a general understanding of invasions (Shea & Chesson 2002; Marvier *et al.* 2004; Mitchell *et al.* 2006; Eppstein & Molofsky 2007; Melbourne *et al.* 2007).

Evolution plays a central role in about a third of the frameworks. One key notion is the importance of evolutionary processes in explaining stages of invasion or lags (e.g. Facon *et al.* 2006). The converse is not true: of the ten frameworks considering stages or lags, evolution is integral to only half of them. Frameworks in which evolution is central may consider it as operating on a different timescale than ecological processes, although there is mounting evidence (Pelletier *et al.* 2009) that evolutionary and ecological processes at least sometimes occur on the same timescale, with interacting dynamics. Lambrinos (2004) called attention to the potential for interaction between evolutionary and ecological mechanisms, even on short time scales. None of the frameworks consider evolutionary responses of native species to invasions.

It is becoming more widely recognized that multiple factors may contribute to invasions, and that different causal factors may interact. About half of the frameworks address this directly. Dietz & Edwards (2006) emphasize that causal factors can be very different depending on the stage of invasion: initial introduction, naturalization or rapid spread.

Fewer than half of the papers (and none published before 2006) explicitly address questions of spatial scale. This seems surprising, given the emphasis on the importance of spatial and temporal scale in the ecological literature over at least the past decade. The role of temporal and spatial environmental heterogeneity in invasions is central to some influential theoretical and empirical work on invasibility, and is included in or the focus of several of these papers. Davis *et al.* (2000) proposed that fluctuations in resource availability can provide a general theory of invasibility. Chesson (2000) proposed a body of theoretical work that offers insight into how such variation can facilitate invasions (and see also Melbourne *et al.* 2007). Blumenthal (2006) casts invasions in terms of the interaction between fluctuating resources and enemy escape.

Melbourne *et al.* (2007) outline a comprehensive view, in which both temporal and spatial stochasticity (unpredictability in the environment from one location to another) may determine not only the degree to which a community is invasible (cf. Davies *et al.* 2005, 2007), but also the impact of invaders on the community. They also discuss cases in which invasions may not depend on stochasticity. Marvier *et al.* (2004) incorporate spatial environmental heterogeneity in another way, considering the interaction between species with relatively specialized habitat requirements and an invasive habitat generalist. The key result of this explicitly mathematical approach is that limitations to habitat fragmentation and habitat destruction can effectively limit the spread of habitat generalist invaders.

The papers reviewed here all offer valuable conceptual advances, but are subject to a variety of limitations. A large majority deal specifically only with plant invasions. Most of the papers implicitly discuss invasions as a single phenomenon, while few explicitly define or identify which of the three main elements that define biological invasions (rapid local population increase, monocultures and range expansion) they are seeking to explain. Strikingly, all but one of the frameworks focus largely on population growth. Range expansion is addressed in a few of the frameworks, often relating it to (although not always distinguishing it from) rapid population growth. Only two frameworks focus on the development and establishment of monocultures or local dominance by the invader population.

PROGRESS TOWARDS MORE SYNTHETIC FRAMEWORKS

More general frameworks have been proposed by several authors that include many of the important components discussed above and highlighted in Table 1. Questions of scale are explicit in several of these, underscoring the growth of interest in this new and active area of ecological research. Scale is an intrinsically important component of the analysis by Melbourne *et al.* (2007), as is spatial and temporal heterogeneity, and their 'hierarchical meta-community concept' considers dominance, rapid increase and range expansion at different hierarchical and spatial scales. Theoharides & Dukes (2007) emphasize that the processes controlling different stages of plant invasions operate over a range of spatial and temporal scales. Milbau *et al.* (2009) present a hierarchical framework based on spatial scale, with the goal of integrating the results of experimental studies on plant invasions and identifying research gaps. Eppstein & Molofsky (2007) also explicitly address issues of spatial scale.

Proposed frameworks by Facon *et al.* (2006) and Barney & Whitlow (2008) emphasize that invasions depend on a match between invasive organisms and their environment. This match can either be present at initial contact between a species in a novel environment, or may develop subsequently through changes to the invasive species, the environment or both (Facon *et al.* 2006). The concept of the centrality of a match between the invader and the invaded environment provides a context that applies broadly, is not limited to specific organisms or systems, and incorporates evolution explicitly. It offers an explanation for time lags, but does not explicitly include scale or interactions between factors, and is unspecific about mechanisms. It is related to the idea of the importance of the niche of an invader matching the opportunities in the novel environment (e.g. Shea & Chesson 2002). While it may seem hard to argue against the idea that invading organisms must match their environment [also an assumption of species distribution (niche) modelling], it may be difficult to predict such matches or their dynamic consequences. For example, in considering invasions by 'ecosystem engineers', Cuddington & Hastings (2004) found that invasions may be especially fast when organisms can invade suboptimal environments but modify them to become more favourable, a special case of changes in the novel environment as proposed by Facon *et al.* (2006). Melbourne *et al.* (2007) and Eppstein & Molofsky (2007) also discuss the impacts of alteration of the environment by invasive 'ecosystem engineers'.

Any truly general framework for understanding invasions must grapple with the large number of hypotheses that have proposed single-factor explanations for the process of invasion. Inderjit *et al.* (2005) were among the first to emphasize that the various hypotheses are not mutually exclusive. They identify whether the mechanisms posited for invasion are ecological, evolutionary or both, whether the explanation is at a species, population or community level, and the invasion stages at which the hypotheses could function. They set the stage for, but do not propose, a framework that encompasses the various hypotheses. Mitchell *et al.* (2006) construct a unified framework based on enemies, mutualists, competitors and abiotic factors that aims to integrate 20 single-factor hypotheses for plant invasions.

Catford *et al.* (2009) propose a comprehensive framework for categorizing 29 individual hypotheses for invasion. They cast invasions in terms of three causal factors: propagule pressure, abiotic and biotic factors (PAB), each of which is affected by a fourth factor, human actions. This framework is conceptualized at the community level, as are many of the other syntheses. Catford *et al.* (2009) pull together many disparate ideas in invasion ecology, explicitly incorporate scale and invasion stages and point out that invasions are generally likely to be due to multiple causal factors and to interactions between factors. Catford *et al.*'s PAB framework is organized around stages of invasion rather than fundamental ecological and evolutionary processes, and although the authors discuss the latter, they are not integral to the framework.

This framework offers an effective way to summarize the large variety of single-factor invasion hypotheses, but we believe that the key terms of the PAB categorization are too divorced from specific mechanisms for it to constitute a fully comprehensive conceptual framework. Two of these terms, biotic factors and propagule pressure, are not really distinct from one another, because biotic factors play a major role in propagule pressure (as discussed below). While clearly 'biotic factors' play a role in invasions (e.g. Levine *et al.* 2004), we believe that this term is of limited utility as an organizing principle for invasion, because it includes so many different kinds of conditions, interactions and processes with so many different kinds of consequences for invasions. It becomes much more useful when analysed and recast into specific fundamental ecological and evolutionary elements. Nevertheless, this paper represents an important advance in our thinking about how to go about unifying the wide diversity of ideas and approaches in invasion biology into a coherent framework.

While these more synthetic frameworks contain important components that are essential to developing more general and more synthetic frameworks, none includes all of the components of a truly general framework. Various important elements may be missing; most focus on population interactions and community ecology and none include a wide range of ecological hierarchical levels. Few incorporate interactions between causal mechanisms (particularly multiple interacting causal mechanisms, including feedbacks). Most are unspecific about mechanisms; e.g. 'propagule pressure', 'biotic factors' and unspecified 'state factors' tell us little about the specific mechanisms by which invasions proceed. The gap between the existing literature and the development of a fully satisfactory conceptual framework for biological invasions is at least in part due to the challenges inherent in the tension between specificity and generality in framing such a conceptual synthesis.

TOWARDS A UNIFIED VIEW – A SYNTHESIS OF CONCEPTUAL FRAMEWORKS FOR INVASION

Shea & Chesson (2002) pointed out that invasion ecology is not distinct from community ecology, but rather is conceptually situated within it (see also Huston 1994; Davis *et al.* 2001; MacDougall *et al.* 2009). Consistent with and extending this insight, we believe that the study of invasions should be situated broadly within a framework that includes not only community ecology, but population and ecosystem ecology and evolutionary biology. There are many papers on invasion that touch on this idea, but no previous efforts have squarely placed a conceptual framework for invasion in these terms. The basic structural elements of several of the frameworks discussed above are: biotic factors, abiotic factors and propagule pressure (e.g. Theoharides & Dukes 2007; Barney & Whitlow 2008; Catford *et al.* 2009). In synthesizing these ideas and moving forward, we can show how these elements (and others) fit together in a single synthetic, integrated ecological and evolutionary framework.

Invasion biology developed, to some extent, independently of the rest of ecology (as pointed out, e.g. by Davis *et al.* 2001; Shea & Chesson 2002). While fundamental ecological concepts have been part of invasion biology since the field began (e.g. competition, the niche), invasion biology also developed a strong reliance on terms and concepts unique to this field: e.g. invasion filters, propagule pressure, biotic resistance and even disturbance. We believe that all of these terms can be made more useful by expressing and analysing them in terms of more general ecological and evolutionary concepts. 'Invasion filters' (Theoharides & Dukes 2007) provides an interesting metaphor, but is not a fundamental ecological process or principle. Disturbance, a familiar explanation for invasions, is also arguably not a truly fundamental ecological concept, and more importantly, it is not one specific thing. The consequences for terrestrial organisms and ecosystems and the mechanisms of action for a disturbance due to canopy removal are very different from those of a disturbance to the soil caused by the removal of rooted plants, from the effects of wave action on a rocky shore or from those of a major oil spill on benthic marine organisms. It is inexact and ineffective to use one word for all of these cases. Carnap (1950) defines the term *explicating* as transforming an inexact, prescientific concept with a more specific and exact concept. By explicating the concept of disturbance we will progress in our understanding of the roles of these different factors in invasion. It might be more accurate and productive to evaluate the effects of 'increased light and reduced competition resulting from canopy removal', or 'reduction in predation on an invading invertebrate due to higher mortality in seabirds resulting from an oil spill' than to attribute such disparate examples to 'disturbance'. We will make more rapid progress by reframing invasion biology in terms of basic ecology and evolution, rather than in terms of special processes and factors unique to invasion biology.

We can illustrate how fundamental ecological and evolutionary processes create the foundation for a conceptual framework for invasions by outlining how they contribute to invasions (Fig. 2). The boxes indicate basic ecological and evolutionary conditions or processes that are major contributors to invasions. The arrows in the illustration outline causal or contributory connections, rather than temporal sequences.

Figure 2 illustrates a general conceptual framework for biological invasions. Here, a synthetic invasion meta-framework (SIM) – synthesizing previously proposed conceptual frameworks and incorporating their insights in a meta-framework – is constructed from fundamental ecological and evolutionary processes and states, and the causal transitions between them. This SIM is not a formal model, but rather a conceptual framework that proposes a general way to think about invasions. We view this as a fluid work in progress and not a final end product.

Ecological factors at individual, population, population interaction, community and ecosystems levels are incorporated in the proposed SIM, as are major evolutionary factors. These fundamental elements

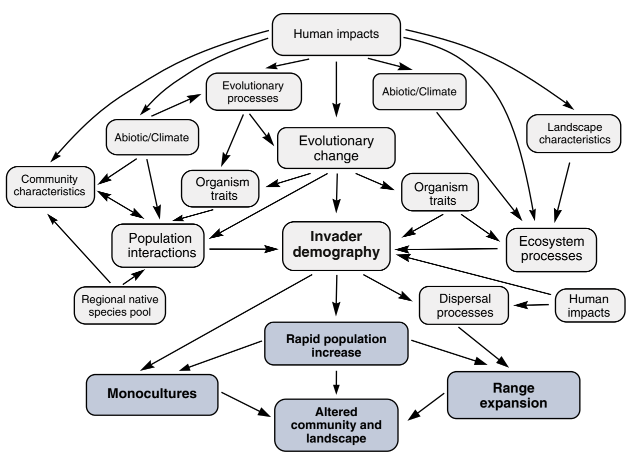

Figure 2 A conceptual synthetic invasion meta-framework (SIM) based on fundamental ecological and evolutionary processes and states. The three different characteristics of invasions and their effect on altering communities and landscapes are in bold capital letters. Transitions between the processes and states are indicated by arrows. Components found in more than one position affect or are affected by more than one set of other processes.

underlie all of the frameworks in Table 1, as well as the many different single-explanation invasion hypotheses. Human influences affect many of the ecological and evolutionary conditions and processes involved in invasions, both directly and indirectly, altering physical, abiotic factors such as climate and soils, community characteristics such as vegetation cover and native species diversity, fragmentation and other landscape characteristics, and evolutionary processes such as selection. Human impacts also include transporting the invaders to the novel environment originally, whether intentionally or unintentionally, and often, dispersing them in the new environment as well.

Demography is central in this SIM, because demographic processes determine whether an invasion proceeds or fails. Demographic parameters such as survival and reproductive rates determine population growth, and life history traits such as growth, survival, dormancy and clonality help define demographic parameters. Population interactions including altered herbivory or predation affect invasions by altering vital rates such as survival and reproduction; vital rates are also affected by evolutionary (e.g. selection) and ecosystem (e.g. nutrient cycling rates) processes. Initial colonization and establishment of the invading organisms, clearly a key step in any invasion, fit well into this framework as they depend on the same sorts of basic processes as other aspects of invasion. Evolutionary processes, population interactions and suitability of the abiotic environment, tempered by human actions, create the conditions that lead to demographic changes resulting in establishment and initial population growth.

The demographic processes of successful invading organisms, coupled with dispersal to new regions of the novel environment, result in one or more outcomes: rapid local population increase, the establishment of monocultures or local dominance and/or range expansions. Ultimately, these three aspects of invasion may alter the character of the community or landscape (Fig. 2).

Evolutionary processes may include bottlenecks, genetic architecture, hybridization and selection in the novel environment. The degree of plasticity of the introduced organisms may be a pre-adaptation or evolve in the novel environment. These evolutionary factors may lead to evolutionary change in the novel environment, distinguishing the introduced organisms from populations of those species in their home environments. Selection resulting from the effects of the invaders in the novel environment may result in evolutionary changes in the native species as well. Evolutionary change may directly affect the demography of the invading population (e.g. juvenile survival, clutch size), or alter organisms' physiological and morphological traits, leading indirectly to demographic change.

Ecosystem processes may affect and be affected by a number of other components in the figure, including organisms' physiological and morphological traits, as well as larger scale landscape characteristics. Natural and anthropogenic alteration of 'disturbance' regimes (e.g. fire return intervals, nutrient flushes, flooding) at the ecosystem level may cause or be caused by biological invasions. These processes relate directly and indirectly to other ecological processes. For example, alterations in disturbance regime (canopy removal, increases in dissolved oxygen) can affect ecosystem processes and thus change physiological processes (increased photosynthetic and respiration rates); these changes alter demographic processes (changes in reproductive output) and lead to rapidly increasing local population sizes of the invader.

It is widely recognized that lags occur during initial establishment, but they may also occur between other stages. Although the processes in Fig. 2 do not represent stages, lags might be inherent both within the components (boxes) or at the linkages between components (shown by arrows) of this SIM. For example, as a population increases, there are likely to be lags before the population is dominant enough to cause ecosystem changes, long after the initial stages of invasion and even after the population is large and widespread. The box for invader demography may incorporate lags due to various factors, such as stochastic events during early establishment, or the time needed to reach stable age distribution, while the link between dispersal and its consequences for range expansion may likewise involve long time periods.

No one specific example of an invasion, no single invasion hypothesis and no predictions about invasions will call upon all or even most of the components outlined in Fig. 2. This flexible framework, or SIM, can be used in a number of different ways to better understand biological invasions. One can map different hypotheses onto this framework to see where they overlap or are distinct. One could use a SIM to compare different specific invasions in a particular system, or general cases of invasion processes in different systems (e.g. terrestrial plant communities and invasions by freshwater invertebrates) to highlight their essential similarities and differences. In contrast, it would be difficult to map such comparisons where the central components of the framework are limited to PAB, or enemies, mutualists, etc. because these categories are not truly fundamental or are too general to be sufficiently explanatory.

A SIM facilitates consideration of the many ways in which stochasticity can affect both the conditions and process that contribute to invasions. The conditions that set the stage for invasions – from abiotic factors like climate change or N deposition, to the genetic composition of populations and the species composition of a local community – vary in both time and space. Some of this spatial and temporal variation is predictable, and some is stochastic. This spatial and temporal variation affects not only the rates at which populations grow and spread, but can also affect the opportunities for invasion (e.g. Chesson 2000; Davis *et al.* 2000; Shea & Chesson 2002). Our framework facilitiates the formulation of new hypotheses, including those that consider how stochastic variation may affect invasions. As an example, the illustration of the SIM in Fig. 2 might prompt a consideration of how stochastic spatial variation in landscape conditions or ecosystem processes could facilitate or inhibit invasions, depending on its relationship to the scale of within-population heterogeneity in individual functional traits.

Multiple causal factors, interactions between factors, direct and indirect effects and feedbacks are integral to this SIM. For example, an invading population may already possess (pre-adaptation) or evolve (after invasion) traits that are advantageous in the novel environment; such traits would contribute to invasiveness by affecting the demography of the invader, contributing ultimately to increasing the rate of population increase of the invading population. These traits could be morphological, physiological, in allocation and defense, or in life history characteristics (e.g. age of first reproduction, clutch size). Organisms' traits can also, of course, affect population interactions such as competition and predation, or alter the ecosystem in ways that favour the population of the invader (e.g. Ashton *et al.* 2005).

As is generally true for a conceptual framework, this SIM is meant to be easily modified to include additional feedbacks, sub-components, etc. in specific applications. It can be used to elucidate invasion hypotheses or empirical examples in terms of fundamental processes. An important advantage of this framework is it allows the comparison of different contributing factors in an invasion (or to invasions in general). One could, for example, use methods such as structural equation modelling (e.g. Shipley 2002; Grace 2006) to quantitatively evaluate the relative contributions of different factors in an invasion, or to compare competing hypotheses. The SIM we propose, as illustrated in Fig. 2, is deceptively familiar, but in fact recasts our understanding of biological invasions in a way that has not been done before, in terms of familiar things we knew all along. This could be called the 'Wizard of Oz phenomenon' for the classic 1939 film in which the protagonists are finally made to realize that the things they were seeking were familiar ones they already possessed.

We envision that any specific application of this SIM will involve ignoring some of its components, focusing on some of them and possibly expanding on certain other components. For instance, if population interactions are the focus of a particular invasion hypothesis, field study or literature review, those components in the figure could be expanded into sub-components; the decision to include or ignore each component must be explicit. Most importantly, a SIM facilitates comparisons by identifying what aspects, factors, conditions and processes are similar, and which are different, for a wide variety of applications. The overlaps and discrepancies among invasion hypotheses can be identified; different specific or general cases of invasion can be compared (e.g. the means by which two species of invasive crabs succeed, or the causal factors and mechanisms of marine invertebrate invasions contrasted with those of terrestrial plants); and the important components operating at different scales can be identified.

ENEMY ESCAPE, SCALE, PROPAGULE PRESSURE AND THE EVOLUTION OF INCREASED COMPETITIVE ABILITY IN THE CONTEXT OF A GENERAL FRAMEWORK

We illustrate how this framework can be applied using three hypothetical examples. These examples illustrate how different components in the framework may be relevant in different situations, or function to address different questions in a common context, and show how applying the framework can change the way we understand a given problem.

Consider a case in which enemy escape leads to reduced seed and seedling predation (Fig. 3a). We would want to focus in this event on several key components of Fig. 2, while most other processes and conditions would not be relevant in this application of the SIM. In this hypothetical example, reduced seed and seedling predation (a population interaction) result in increased survival at these life history stages (demographic processes). The population of the invader will grow if the rate of population increase is sensitive to these demographic transitions, if so, this can result in high local population growth rates and rapid population increase; larger population sizes may alter community properties (Fig. 3a). If conditions are favourable for establishment beyond the extent of the local population, and means exist for dispersal, this may ultimately lead to range expansion and in turn alter landscape characteristics. Thus, the black box of 'enemy escape' can be understood more transparently and mechanistically. This perspective can lead not only a clearer understanding of what may be involved in a given case of invasion resulting from 'enemy escape' (e.g. Rose *et al.* 2005; Shea *et al.* 2005; Buckley *et al.* 2006), but also to guiding empirical studies to ask whether, for example, reduced seed predation actually leads to changes in population growth parameters,

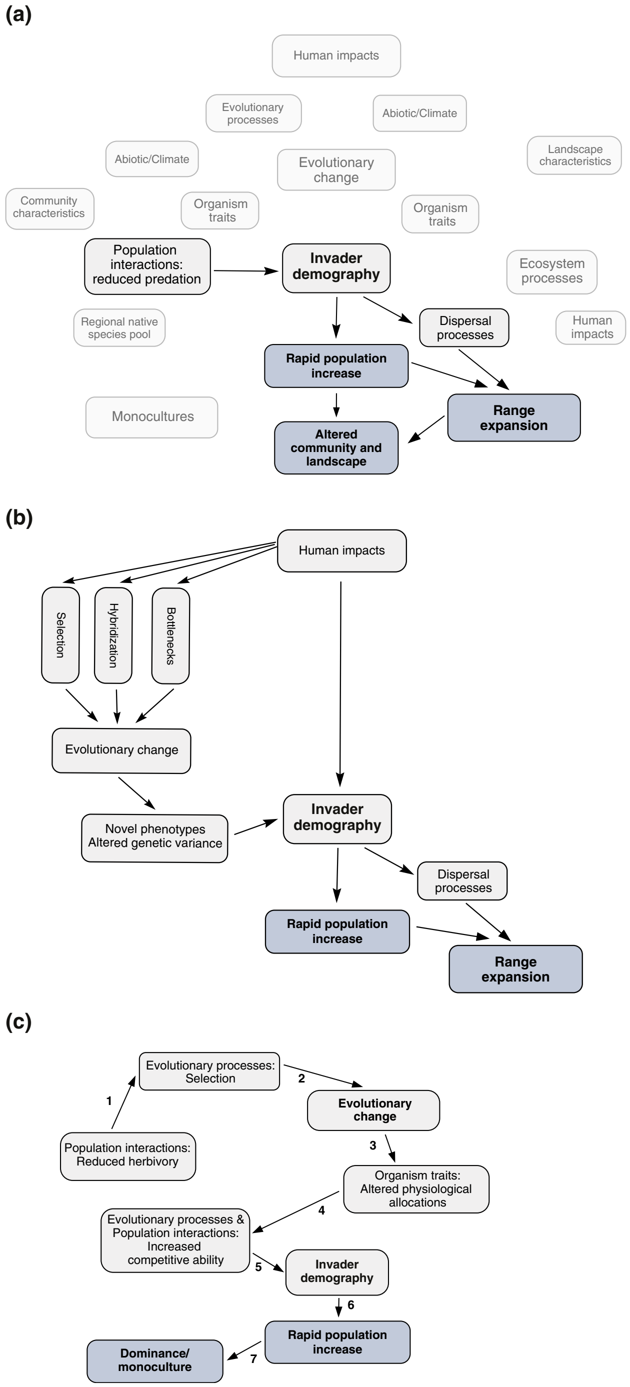

Figure 3 Examples of how the synthetic invasion meta-framework (SIM) might be applied in three hypothetical invasion scenarios. (a) A simple case of enemy escape resulting in an invasion. (b) An example of the ecological and evolutionary components that may be involved in 'propagule pressure' (see text). (c) The hypothesis of the evolution of increased competitive ability (EICA) invokes many different components; the application of the SIM reveals the underlying complexity of the EICA. See text for explanation of the steps required for the EICA to be fully supported.

rather than just observing lower rates of seed predation in an introduced population.

A second example is thinking more mechanistically about the role of propagule pressure in promoting invasions. A number of authors consider 'propagule pressure' (Lockwood *et al.* 2005; Colautti *et al.* 2006) to be a simple null hypothesis for the success of invasives, and it is incorporated as such in a number of the syntheses in Table 1 (Richardson & Pyšek 2006; Eppstein & Molofsky 2007; Theoharides & Dukes 2007; Barney & Whitlow 2008; Catford *et al.* 2009). The idea is essentially that the introduction of propagules is a simple explanation for successful invasion. But propagule pressure is not a single irreducible phenomenon, and as a concept or explanation for invasion it does not elucidate or clarify any specific mechanisms. We believe that it is most useful to directly address actual causal factors rather than to invoke what is really a conglomeration of multiple ecological and evolutionary factors acting in different ways.

We illustrate the variety of ways in which propagule pressure can affect the course of an invasion in a hypothetical case (Fig. 3b). In adapting Fig. 2 to consider propagule pressure, we focus on the essential components involved in the process, while various other components of Fig. 2 are omitted. Here, an invasion is initiated when humans introduce propagules of the invader to a novel environment. How many propagules are introduced, and the number of introduction episodes, are both important in determining the chance of establishment (Catford *et al.* 2009), and stochasticity from various sources will affect the fate of the population founded by the propagules. The box for evolutionary processes has been expanded into several specific processes: bottlenecks, selection and hybridization between organisms brought together in the novel range from different parts of the native range. The response to these processes results in evolutionary change, and may create new phenotypes or alter population genetic variance. The demography of the invader changes in response to these evolutionary and ecological factors, determining the chances for successful local establishment, rapid local population increase and dispersal to new regions. These components and the connections between them are aspects of how propagule pressure influences the progress, and ultimately success or failure, of an invasion.

Examining the mechanisms by which propagule introductions affect invasion reveals some important insights. Counter-intuitively, sustained propagule introductions from a non-adapted source may swamp out locally adapted alleles, thus slowing or even stopping the growth and spread of a population (e.g. Travis *et al.* 2005; Hammershøj *et al.* 2006). Thus, propagule pressure may promote invasions, result in invasions only after considerable lags (caused by both evolutionary change and demographic processes), or may actually act to slow invasions. The introduction of propagules will lead to self-sustaining population increase only if the population is capable of growing, regardless of how often or how many are introduced. The fate of the population will depend on whether λ is > 1; if not, the population will simply act as a sink for the propagules. Depending on Allee effects, the population may grow, or it may decline to extinction. Whether populations produce sufficient numbers of offspring – new propagules – capable of dispersing to new areas will determine the potential for range expansion. Evaluating these various components of propagule pressure and their contributions in an actual empirical case of an invasion would not be simple, but it would be very valuable. Examined this way, propagule pressure is not a simple null hypothesis: propagule pressure is a complex phenomenon composed of many ecological and evolutionary factors.

By examining the different specific components contributing to the role of propagule pressure, we open the black box. In addition, by framing propagule pressure in the context of fundamental ecological and evolutionary processes and conditions, we can facilitate direct comparison with the components involved in other causal factors contributing to invasions (such as enemy escape), rather than viewing propagule pressure as a null hypothesis or single factor responsible for invasions.

Other explanations for invasion may also appear to be deceptively simple, but upon examination in this framework their complexity is made more explicit. The well-known hypothesis of the EICA (Blossey & Nötzold 1995) makes intuitive sense, but demonstrating it requires evidence for at least six causal links between seven and eight conditions or processes (Fig. 3c); these must all be demonstrated for the EICA to be fully validated. In the hypothetical case illustrated in Fig. 3c, reduction in herbivory or predation (a population interaction) leads to (1) changes in the selective regime (an evolutionary process), resulting in (2) evolutionary change and thus to (3) altered physiological allocations (organism traits). These altered physiological allocations result in (4) enhanced competitive ability (evolutionary process plus population interactions), leading to (5) demographic changes which (6) result in an increase in population growth rates. The establishment of dominance or monocultures may follow (7). Demographic processes are again essential to the transition to invasiveness.

Demonstrating greater herbivory in the native range, for instance, even if correlated with increased size in the invaded range, might be suggestive, but is insufficient evidence to conclude that this hypothesis was supported. This version of the SIM emphasizes the connections and the order in which they follow conceptually. The relevant evolutionary process is selection; the relevant population interactions are both reduced herbivory and increased competitive ability. The organism traits most affected in this scenario are altered physiological allocations. The boxes (conditions and processes) of the SIM shown in Fig. 2 have been expanded or more narrowly defined in Fig. 3c, as called for in the analysis of this particular example.

Consideration of Fig. 3c makes it clear why scientific evaluation of the EICA conclusively is difficult. The elegant body of work on the invasive plant *Hypericum perforatum* by Vilá, Maron, and their colleagues tested many of these aspects of the EICA and found that while some components of this complex hypothesis were validated, others were not (e.g. Vilá *et al.* 2003; Maron *et al.* 2004a,b). Papers which cite support for this hypothesis sometimes test only one or two of the components in Fig. 3c (as discussed by Inderjit *et al.* 2005), which is insufficient evidence to rule out other causes of invasion.

The spatial and temporal scale at which invasions are examined may influence both the nature of the questions and the answers sought. The conceptual framework proposed here can be used to address issues relevant at much larger as well as at smaller scales. In some instances, the outcomes of invasion at larger scales may simply be addressed within the conceptual framework from the platform of demographic processes and dispersal at local scales, as when local demographic and dispersal processes result in range expansions of invaders at landscape and regional scales. Demographic processes can also directly influence larger scale phenomena such as alpha and beta diversity at landscape and regional scales, or native species declines and extinctions. In other instances, while the demography of invaders still underlies the process of invasion, this may be more of a background consideration, with the focus instead on larger scale factors. For instance, one might ask whether regional species richness is decreased by the presence of invasive alien plants or predators in the context of regional native species richness (e.g. Sax & Gaines 2003), or whether invasive species richness is affected by heterogeneity at a landscape scale (e.g. Davies *et al.* 2005). Interest might centre on the how the interaction between climate change and invasive species alters ecosystem properties such as decomposition rates and CO_2 efflux from soils, or changes landscape properties by increasing fire frequency. In studies like these, the focus is on larger scale phenomena, even though these phenomena ultimately rest on demographic and other processes at smaller scales.

SUMMARY, PRESCRIPTIONS AND PROGNOSIS

Research on invasion biology has produced an enormous literature, and clearly a single explanatory factor for invasions is not expected to emerge. Invasions open a window on fundamental ecological and evolutionary questions, and present enormous applied problems. The literature on biological invasions is large, diverse and can be very confusing. Better conceptual tools may help to better understand the biology of invasions, and more effectively control and manage an increasing number of invasive species, given finite resources.

Conceptual frameworks are useful theoretical tools for distilling current understanding, guiding future research efforts, developing control strategies and in prioritizing management schemes. Recent efforts to develop such frameworks highlight both the growing recognition of the need to identify essential underlying principles, and the difficulty of achieving that distillation. A number of common themes emerge in the way invasions are currently conceived: invasions proceed in stages, most frequently recognized when time lags slow the transition to subsequent stages. There is no single cause of invasion; the invasiveness of species and invasibility of communities both vary with context and across temporal and spatial scales. Propagule pressure, abiotic factors and biotic interactions, with both ecological and evolutionary components, can act as filters that control the match of a particular individual or population of a colonizing species to the novel habitat. We have tried to show here that we can incorporate this current understanding of biological invasions and move beyond it by framing these insights in terms of the basic ecological and evolutionary elements on which they rest.

Demographic processes are central to invasion and play into all of its aspects (population increase, local dominance and range expansion), suggesting that mechanistic explanations of invasion success can benefit from careful demographic analyses. Population level factors can be linked to community ecology by measuring differential success (e.g. Ramula *et al.* 2008) of invasives relative to natives in the novel environment, invasives in the novel vs. home environment and invasives vs. non-invasives that have been transported to the novel environment. Extending such studies to meta-populations, especially those embedded in a spatial framework, can advance our understanding of the particular features that speed up or limit the spatial spread of species across heterogeneous landscapes.

Our contribution towards the development of a more inclusive and mechanistic conceptual framework for invasion should facilitate quantitative and testable study of causal factors. This will be particularly valuable if the goal is to determine the relative contributions of multiple causal factors to invasion under different circumstances, as opposed to merely evaluating whether data are consistent with particular single hypotheses. Such conceptual unification, situated within the larger fields of ecology and evolution, is essential, and can lead to improved explanatory power and precision in the study of invasions. Lacking an adequate conceptual framework, important aspects of invasion biology can be overlooked and predictions can be incomplete, ambiguous, inaccurate or misleading. The development of general conceptual frameworks will also facilitate protocols for pressing applied research on topics such as restoration (Doren *et al.* 2009) and the influence of climate change on biological invasions. The SIM presented here also offers an enhanced perspective for addressing basic questions, such as what determines the limits to community diversity and species' ranges (Shea & Chesson 2002). The benefits of conceptual unification in invasion theory are potentially very great.

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