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Propagule pressure: A null model for biological invasions.

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Propagule pressure:

a null model for biological invasions

By

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Abstract

Understanding the mechanisms by which a species invades, establishes in, spreads through, and dominates novel habitats has been a priority for invasion biology, but there are surprisingly few empirical generalizations. I begin with a review of recent attempts to identify characteristics of species 'invasiveness' (i.e., the ability to invade) and habitat 'invasibility' (i.e., the susceptibility to invasion), and find little support for an emerging consensus on species- or habitat-specific characteristics. Moreover, I find that few studies consider hypotheses based on the concept of 'propagule pressure' (i.e., introduction effort), despite its potential as a confounding factor. Another barrier to generalizations may be the divergent use of operationally important terms like 'invasive', 'naturalized', or 'nuisance'. I therefore introduce a framework that conceptualizes biological invasions as a series of obligatory stages. This stage-based framework can aid in identifying characteristics that are confounded by 'propagule biases' (i.e., non-random variation in introduction effort), and can serve as common ground for an operational lexicon. I use this framework to investigate the enemy release hypothesis (ERH), which relates invasion success of a host species with the number of co-occurring enemies. I show that patterns of enemy release may be confounded by propagule biases, leading to 'apparent' release from enemies with no fitness consequences for the host. A more detailed analysis shows that assumptions underlying the ERH often do not hold true. A short review suggests that recent studies that test for enemy release are divided; biogeographical studies tend to reveal patterns of enemy release that are largely unsupported by community-level studies. This suggests that alternative scenarios for the success or failure of nonindigenous species may be important. Finally, I apply genetic markers to assess the importance of 'propagule pressure' to the spread of the invasive

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crustacean *Bythotrephes* in Ontario's inland lakes. Introduced populations are found to have no genetic variability at microsatellite loci, suggesting either a bottleneck during invasion, or a species that is genetically depauperate at microsatellite loci. Thus, *Bythotrephes* represents a highly successful invader in spite of, or due to, low genetic diversity.

Pour Nathalie

Ma passion, ma force, mon amour

Acknowledgements

I am told by some that the only way to survive in science is to specialize, to focus on one particular area of a small sub-field, and thereby develop a research *niche*. The present thesis brings together data and ideas from plant ecology, animal ecology, aquatic ecology, molecular ecology, parasite ecology, and the philosophy of ecology, all to question some of the current paradigms in the study of biological invasions (I never liked niche theory). While I strongly believe that there is a need for a multidisciplinary approach to ecology, I have come to realize that the more I learn, the less I know -- mostly because questions quickly exceed answers. And this is where collaborators become invaluable. Hugh MacIsaac and Dan Heath have, of course, been instrumental in my professional development, through the erudition of new skills and techniques and the discussion and refinement of my flighty plans and ideas. On this note, I should also add Dr. Igor Grigorovich, lab colleagues, and faculty and graduate students in the department too numerous to mention, all of whom, in one way or another, are responsible for the scientist that I am becoming. Vicky Rixon and other undergraduate assistants provided the kind of laboratory and field aid that is often monotonous, but invaluable nonetheless. Dr. Grigorovich also helped me to develop the theory behind Chapter 2. Dr. Ian Duggan and Denis Roy helped edit early manuscripts of Chapter 3. Dr. Anthony Ricciardi and Dr. Grigorovich provided invaluable insight into the development of assumptions and alternative hypotheses to the ERH presented in Chapter 4, while Dr. Charles Mitchell provided stimulating conversation on the ERH. Mike Rawson and George Cimbura provided resources beyond my requests and expectations to aid in my collection of *Bythotephes* from the Kawartha Lakes area, as did Cam Willox. And, of course, what self-respecting student wouldn't thank his family and friends!

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Chapter 1

Introduction

Virtually all the world's natural habitats - from tropical islands in the south Pacific to freshwater lakes in northern Europe - are threatened by the invasion of nonindigenous species (NIS). Biological invasions are now seen as a potent threat to global biodiversity, second only to habitat destruction (Sala et al. 2000, Rahel 2002, Stachowicz et al. 2002). Extending beyond ethical arguments for preserving the integrity of natural ecosystems, profound changes to natural ecosystems have followed the establishment of particular invaders. Countless examples exist of potent invaders that have transformed ecological communities. Examples include Nile perch (*Lates niloticus*), zebra mussels (*Dreissena polymorpha*), water hyacinth (*Eichhornia crassipes*), leafy spurge (*Euphorbia esula*), purple loosestrife (*Lythrum salicaria*), Argentine ant (*Linepithema humile*), and European starling (*Sturnus vulgaris*).

The level of disruption caused by NIS can be dramatic, with important implications for human health and welfare. Perhaps the most obvious and direct effects come from the invasion by nonindigenous diseases. In Canada, recent nonindigenous diseases of special concern include the potato wart, SARS, and the west Nile virus. In many cases these effects can be far-reaching: the discovery of potato wart in a single field in Prince Edward Island in 1999 shut down U.S. potato exports from the province for over a year. But perhaps the most significant and underappreciated effect of NIS are the numerous indirect impacts. Disruptions to the biotic composition of natural ecosystems has strong implications for the production of aquaculture, agriculture and forestry products in Canada (MacIsaac et al. 2002) and the rest of the world (Pimentel et al. 2002). Including both direct and indirect effects, the cost of NIS to the global economy conservatively exceeds $1.4 trillion worldwide (Pimentel et al. 2002).

Biological invasions also serve as natural experiments, presenting unique opportunities to study ecological and evolutionary processes. Indeed the fact that biological invasions are so common represents somewhat of a paradox in ecology and evolution (Sax and Brown 2000). How is it that so many native species, which should be well adapted to their environment, come to be displaced by NIS with completely different evolutionary histories? Furthermore, how do so many NIS become abundant in completely alien territories? Some common explanations for this apparent paradox include the pre-adaptation of NIS for human-altered environments, a reduction in co-occurring enemies, the invasion of empty 'niche' space, or the superior competitive ability of widely successful invaders. Despite the attractiveness of these ideas, many of which were promoted long ago by Elton (1958), there remains a serious dearth of strong empirical evidence to support them (see Lodge 1993, Levine and D'Antonio 1999, Williamson 1999).

Although it is perhaps underappreciated, resolving this paradox of invasion could prove to be an important step in refining the discipline of invasion biology. Such attempts however, have proven difficult given the enigmatic and sometimes contradictory patterns of invasions. Even Darwin (1859) appreciated these seemingly unpredictable patterns, writing:

> "From the extraordinary manner in which European productions have recently spread over New Zealand, and have seized on places which must have been previously occupied by the indigenes, we must believe, that if all the animals and plants of Great Britain were set free in New Zealand, a multitude of British forms would in the course of time become thoroughly naturalised there, and would exterminate many of the natives. On the other hand, from the fact that hardly a single inhabitant of the southern

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hemisphere has become wild in any part of Europe, we may well doubt whether, if all the productions of New Zealand were set free in Great Britain, any considerable number would be enabled to seize on places now occupied by our native plants and animals. Under this point of view, the productions of Great Britain stand much higher in the scale than those of New Zealand. Yet the most skilful naturalist, from an examination of the species of the two countries, could not have foreseen this result" Despite his brilliant insight on all matters of evolutionary biology, it is ironic that Darwin hadn't seriously considered the most basic explanation for his conundrum: that species may have been asymmetrically introduced to New Zealand from Britain than in the reverse direction.

Surprisingly, the significance of propagule pressure (i.e., introduction effort) to the establishment of NIS has only begun to be addressed, but there are already some striking examples of high predictability in patterns of the establishment and spread of NIS, using propagule pressure and habitat suitability (Veltman et al. 1996, Lonsdale 1999, Forsyth and Duncan 2001, Rouget and Richardson 2003).

This thesis is firmly rooted in the concept of 'propagule pressure'. The concept is admittedly simple, yet frustratingly absent from many current syntheses on invasion concepts (e.g., Sax and Brown 2000, Keane and Crawley 2001, Shea and Chesson 2002, Bruno et al. 2003). In the chapters that follow, I reassess some current procedures and paradigms in the literature on biological invasions and argue for the importance of 'propagule pressure' as a key to understanding patterns of invasion success.

Below I briefly outline each chapter of this thesis; I do not include references here because they are merely summaries of the chapters, which are of course fully referenced. Chapters are written as stand-alone articles, complete with separate abstracts and

introductions. References sections have been combined at the end of the thesis to reduce redundancy.

Chapter 2

A common criticism of invasion biology is its lack of strong empirical models and useful generalizations. Much recent work has focused on identifying factors that enable a) introduced species to become established; b) established species to become widespread; or c) established or widespread NIS to become dominant. Similar efforts have been directed toward particular communities or habitats, to identify mechanisms that render them susceptible to invasion. In chapter 2, I try to address this problem by reviewing characteristics of invasive species or susceptible habitats in studies published since 1991. This analysis reveals only equivocal support for species- or habitat-specific characteristics. It also reveals that 'propagule pressure' is an important factor that may have often been underestimated or overlooked in these published studies. Based on these results, I argue that 'propagule pressure' hypotheses may help us better understand current patterns of invasions, and should be universally incorporated into future studies. I find that although 'propagule pressure' hypotheses have rarely been examined empirically, there exists a strong possibility that variation in 'propagule pressure' confounds patterns of establishment or spread of NIS. I conclude the chapter with a framework to better conceptualize this problem.

Chapter 3

Another important problem in invasion biology is the use of poorly defined terminology, a problem that has plagued much of the science of ecology. In chapter 3, I

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address some of the problems posed by a lack of operational terminology in the English lexicon on biological invasions. I suggest that this failure stems primarily from a lack of consensus on terms with *a priori* definitions. Consensual definitions are unlikely, given on-going debates on operationally important terms like 'invasive'. Based on the framework developed in chapter 2, I suggest that a 'propagule pressure'-based approach could be used to form an operational terminology that views biological invasions as a sequential series of stages. A focus on the stage of interest will help to develop a common understanding of the determinants of invasion success (stages 0 to V). Furthermore, while I believe it is generally undesirable to the English lexicon on invasion biology, I hold that the introduction of terms with no *a priori* meaning can greatly aid in a unified conceptualization of biological invasions.

Chapter 4

Chapter 4 applies the criticisms developed in chapters 2 and 3 to the enemy release hypothesis (ERH) – an idea that has recently gained much attention. The ERH seeks to relate the abundance and dominance (i.e., invasiveness) of NIS in their invaded range to a reduction in the number of co-occurring enemies (pathogens, parasites, predators, etc.). Presumably, enemies are lost owing to bottlenecks during the invasion process, with a resultant increase in vigour or survival for the target species (i.e., 'host'). However, these patterns may also be a result of the 'propagule biases' that I define in chapter two, leading me to question the evidence for the ERH as a predictor of invasiveness. Patterns of enemy release may be a sampling artefact that is essentially a series of propagule biases (defined in chapter 2) acting on the potential introduction of enemies. I also suggest

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alternative scenarios for bottlenecks during the invasion process to predict the success of particular invasion events.

Chapter 5

I shift gears somewhat in chapter 5, and apply the concept of 'propagule pressure' to the spread of a particular species, *Bythotrephes longimanus*. *Bythotrephes* is a large-bodied, nonindigenous zooplankter that is strongly affecting plankton communities in the Great Lakes region through predation on other species. Since its initial discovery in Lake Huron in 1984 (later found in Lake Ontario samples from 1982), it has since spread to over 50 inland lakes in Ontario, and several more in the United States. My original focus was to develop microsatellite DNA markers to resolve the population genetic structure of Ontario populations of *Bythotrephes*. With the level of resolution afforded by microsatellite DNA, I could more closely examine the role of 'propagule pressure' in shaping both the geographic and genetic patterns of *Bythotrephes* establishment. My failure to find polymorphisms in 24 microsatellite loci tested on 9 populations from across Ontario precluded a test of the 'propagule pressure' model. However, these findings, combined with previous genetic work on *Bythotrephes*, suggest a severe bottleneck during its introduction to North America. Thus, *Bythotrephes* represents a highly successful invader despite, or perhaps due to, its low genetic diversity.

Chapter 2

Propagule pressure: A null model for biological invasions

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Abstract

To explore factors determining invasion patterns, I conducted a review of recent invasion literature that examined characteristics of invasiveness (i.e., the ability of species to establish, spread or dominate novel communities) and 'invasibility' (i.e., the susceptibility of habitats to invasion). Only one of twelve species characteristics - invasion history - was always positively associated with invasiveness across a variety of taxa. Two characteristics - generation time and asexual reproduction - were concordant over a few studies within taxa or when results were divided into establishment and post-establishment stages. All other characteristics examined, namely taxonomic over-representation, physiological tolerance, body size, length of growing/breeding season, growth rate, the rate or success of germination or hatching, seed or egg size, reproductive output, and consumption efficiency, contained results with contrasting patterns within taxa, or contained too few studies to draw conclusions. None of four characteristics of invasibility - disturbance, nutrient levels, species diversity or species abundance - were concordant among all studies. Though examined in only ~17% of studies, 'propagule pressure' (i.e., introduction effort) was a consistent predictor of establishment success for NIS. This factor was correlated with characteristics of invasiveness and invasibility in numerous studies, raising the possibility that reported determinants of establishment success are confounded by propagule biases. I contend that 'propagule pressure' should serve as a null model for invasion patterns and that studies should consider propagule biases before examining invasiveness or invasibility. I conclude with a conceptual framework to better identify potential confounding factors among species- and habitat-specific characteristics, and to more explicitly define the invasion process as a logical sequence of events.

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Introduction

Human-mediated biological invasions are occurring at an historically unprecedented pace,

with some estimates up to 50,000 times higher than background levels of natural

colonization (Hebert and Cristescu 2002). As such, invasions represent a significant

threat to global biodiversity, and a potent agent of biotic homogenization (e.g., Carlton

and Geller 1993, Rahel 2002, Stachowicz et al. 2002). Invasions also impose an

'invisible tax' on national economies (Perrins et al. 2000) that may exceed $1.4 trillion

per year worldwide (Pimentel et al. 2002). Given the extent of these problems, any

ability to make general, *a priori* predictions about potential invaders or susceptible

habitats would be of tremendous value to policy makers and resource managers, and

could provide novel insights into processes important to ecology and evolution.

Charles Darwin (1859) was among the first to identify invasion patterns, noting

that habitats containing 'naturalized' nonindigenous species (NIS) seemed to have few

native congeners, and that habitats varied in their number of established NIS. Elton

(1958) later emphasized biotic resistance and niche theory as processes underlying these

patterns. Theoretical arguments have been invoked to characterize 'weedy' species

(Baker 1965, 1974), and to discriminate potential NIS from unlikely invaders (e.g., Gray

1986, Ehrlich 1989, Lodge 1993, Mack 1996, Williamson and Fitter 1996, Rejmának

2000). Similar attempts have been made to predict the susceptibility to invasion of

particular habitats (e.g., Grover 1994, Moyle and Light 1996, Richardson et al. 2000*a*,

Shea and Chesson 2002). Many of these models are rooted in the biotic resistance

paradigm and emphasize competition for limited resources among native and

nonindigenous species. But these models have recently been challenged by studies of

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facilitative interactions (Simberloff and von Holle 1999, Ricciardi 2001, Bruno et al. 2003). Perhaps ironically, few predictive efforts have examined empirical relationships between 'propagule pressure' (i.e., introduction effort) and invasion success (e.g., Lonsdale and Lane 1994, Veltman et al. 1996, Wonham et al. 2000, Forsyth and Duncan 2001, Rouget and Richardson 2003).

I present a brief review of recent literature reporting characteristics correlated with the ability of species to invade (i.e., invasiveness) and the susceptibility of habitats to be invaded (i.e., invasibility). These analyses are combined with studies of 'propagule pressure' to better examine factors affecting invasion success, including the establishment of species and the degree to which they spread to and become dominant in new habitats. These studies are addressed in a systematic fashion that is broad in taxonomic scope. My intention is not to present a comprehensive summary of the current invasion literature, but to draw general conclusions regarding the interplay between human influences and natural factors affecting species invasions. I conclude with a critique of the current state of predictive invasion biology, and propose a framework to aid in future efforts.

Methods

I reviewed the modern invasion literature by searching the titles, abstracts, and keywords of articles characterizing invasive species or invaded habitats. I searched articles published since 1991 from a list of 56 ecological journals (see Appendix 1 for a complete list of titles), using the Institute for Scientific Information (ISI) Web of Knowledge (v1.2) search of the 'Science Citation Index Expanded' database. These searches resulted in over 700 studies from which I chose only papers that included an objective contrast of

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two or more species (e.g., nonindigenous and native species, invasive and non-invasive species, etc.). Thus, I excluded theoretical papers, studies of natural colonisations by native species, *post hoc* analyses of specific invaders, impact assessments, and reviews or syntheses lacking empirical data. I included only studies that explicitly examined characteristics of successful invaders or susceptible habitats and those that explored the role of propagule pressure. For the purposes of this paper, 'propagule pressure' is defined by the number of discrete introductions, and the total number of individuals introduced. In total, I reviewed 140 studies of which 54 dealt primarily with invasiveness, 82 with invasibility, and 2 with results relevant to both. Of these, 11 invasiveness and 13 invasibility studies examined the role of propagule pressure (Appendix 2).

All papers examined in Appendix 2 were categorized in terms of theme (i.e., invasiveness, invasibility or propagule pressure) and taxon studied, as well as by the contrast groups used (i.e., established NIS vs. resident native species, established NIS vs. native species from the same source region, established NIS vs. failed introductions, or invasive vs. non-invasive species). I also examined abstracts to identify characteristics associated with successful invaders or susceptible habitats (e.g., seed size, species diversity) and measurements of propagule pressure. For each of these measurements, I recorded whether associations with invasiveness or invasibility were reported as positive, negative, or not significantly different.

I organized NIS characteristics into five groups: plants, invertebrates, fishes, birds, and mammals. Similarly, studies of invasibility were grouped based on the type of invaders examined: plants, birds, fishes, invertebrates and micro-organisms, mammals, or multiple taxa. Results for invasiveness characteristics were categorized into one of two

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stages of the invasion process (i.e., established or post-establishment), following Kolar and Lodge (2001, 2002).

Invasiveness Traits

Analyses of invasiveness characteristics used either replicated experiments (11 cases) or *post hoc* (i.e., observational) comparisons (43 cases). Studies were considered to be tests of the establishment success if they involved contrasts between established NIS and one of the following: 1) species found in the same source region(s) as the NIS; 2) native species in the invaded region; or 3) from a list of global congeners; or 4) other introduced species that failed to establish self-reproducing populations (Appendix 2A). Additionally, some studies examined characteristics of established NIS that varied in their rates of spread or their ability to dominate natural habitats. I considered these as tests of the post-establishment stage (Table 1).

Only one invasiveness characteristic (i.e., invasion history; Table 1) was concordant across a broad range of taxa. Growth rate and hermaphroditic (or asexual) reproduction varied between, but were concordant within, invasion stages (i.e., establishment vs. post-establishment). For the most part, however, contradictory patterns remained even after separating characteristics based on invasion stage and taxon (Table 1). For example, physiological tolerance was positively correlated with establishment or post-establishment success in four plant studies and three fish studies, but was negatively correlated in three plant studies and one study of invertebrates.

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Invasibility Traits

To identify differences in habitat invasibility, 14 experimental and 68 *post hoc* analyses characterized susceptible habitats based on one or more of the following measurements: 1) abundance of NIS, including area of cover, biomass, or number of individuals; 2) diversity of NIS, including diversity indices or other measures of the number of NIS; 3) survivorship and/or reproduction of particular NIS in different habitats; and 4) presence/absence of particular species among habitats (Appendix 2B).

Characteristics of invasibility fell primarily into one of the following categories: disturbance, nutrient levels, resident species diversity, or resident species abundance (Table 2). One additional class, which I termed 'anthropogenic exposure', compared measurements of human activity (e.g., proximity to roads or urban areas) with invasibility. In these cases, the mechanism underlying invasion patterns may be 'propagule pressure', disturbance or some interaction between them. No characteristics were consistent among all studies of invasibility, and results were heavily biased toward the plant literature (Table 2). Of characteristics represented by more than one taxon or more than three studies, only anthropogenic exposure did not contain studies reporting both positive and negative relationships with invasibility. Interestingly, the effects of species diversity and species abundance were almost evenly divided among positive and negative relationships with invasibility (Table 2).

The role of propagule pressure

I identified 24 studies that specifically examined the effects of 'propagule pressure' on establishment success (Table 1 and 2). Several other studies considered 'propagule

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pressure' as a confounding variable, but did not test it explicitly. In all cases, 'propagule pressure' was addressed in one of four ways: 1) deliberate introduction of a known number of propagules into replicated plots (e.g., Mesleard et al. 1993, Miller et al. 2002); 2) replicated plots were colonized by both native and nonindigenous species, but the number of propagules was not controlled *per se* (Shurin 2000); 3) historical records of the number of individuals introduced, or some proxy of it. These included records of introduction by regional governments or 'acclimatization societies' (e.g., Veltman et al. 1997, Duncan et al. 2001), propagules identified in a transport vector (e.g., Wonham et al. 2000) or historical data on intensity of use (e.g., Richardson 1998, Prinzing et al. 2002); and 4) analysis of anthropogenic activity or correlates thereof, including economic data and areas of human use (e.g., urban areas, proximity to roads). In the latter case, effects of disturbance versus introduction effort were often impossible to distinguish (Table 2). For example, Vilà and Pujadas (2001) successfully accounted for over 60% of European and North African plant invasions using a general 'Human Development Index'.

Where 'propagule pressure' was explicitly examined, 22 of 24 studies found positive associations with establishment or post-establishment success (Tables 1 and 2), and one study found no relationship. Additionally, 29 of 30 studies that examined human activity (i.e., representing disturbance and/or propagule pressure) found positive associations, while one study found no relationship (Table 2). Thus, 'propagule pressure' was positively associated with the establishment of NIS, the post-establishment success of NIS, and the susceptibility of habitats to invasion. Furthermore, studies that identified invasiveness and invasibility characteristics rarely considered 'propagule pressure' hypotheses (Fig. 1). It is important to note, however, that many studies were from the same region (e.g. bird introductions to New Zealand) and therefore do not represent

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independent samples. Additionally, studies finding no difference between invasiveness and invasibility characteristics are likely under-reported in the literature.

Critique of methodologies

The overall lack of consistent relationships between characteristics of invasiveness and invasibility in this review mirrors a general lack of predictability in invasion biology -- a problem highlighted by others (e.g., Enserink 1999, Williamson 1999). To address this problem, Kolar and Lodge (2001, 2002) advocated that NIS characteristics be assessed at each stage of the invasion process. Results from this review show support for this method, but contradictory patterns for similar taxa at similar stages suggest that characteristics of invaders may still be confounded (e.g., physiological tolerance and body size in Table 1). Additionally, contradictions of factors affecting invasibility cannot be addressed under this methodology. For example, disturbance is not always positively associated with invasibility, and may be system-specific (e.g., Table 2; see also Lozon and MacIsaac 1997).

This lack of consensus among invasion patterns at a topical level may also reflect a difference in analysis procedures. For example, Cassey (2001) noted that smaller birds tended to be more successful at establishing than larger ones, but after controlling for taxonomic similarity the pattern was reversed. Another possible explanation for this lack of consensus is the inherent complexity of biological invasions. Predicting invasions might necessarily be confined to particular species-by-habitat interactions (Tucker and Richardson 1995, Kolar and Lodge 2002). A lack of clear, operational definitions in invasion biology may also be a source of confounding of invasion paradigms because

poor definitions have likely led to the splitting of common phenomena and the lumping of unique ones. Finally, an inability to find generalities may stem from a failure of the assumptions underlying the ways in which characteristics of invasiveness and invasibility are addressed. Below I explore this possibility in more detail.

Habitat invasibility is typically inferred from the number or abundance of established NIS (e.g., Lonsdale 1999, Symstad 2000, Davis and Pelsor 2001). But habitat invasibility is characterized by an inherent susceptibility to invasions rather than the number or abundance of established species *per se*, independent of whether invaders are native or nonindigenous. In a similar manner, species invasiveness reflects an inherent ability of species to establish and proliferate in novel habitats. Establishment success is thus an inherent prediction of both the invasiveness of species and the invasibility of habitats, but other mechanisms can produce a similar pattern. Studies that infer a causal relationship from these patterns alone suffer from the non-sequitur, logical fallacy 'affirming the consequent' (Copi and Cohen 1990). In other words, affirming a predicted pattern (e.g., finding a correlation between a habitat characteristic and the number of NIS) is not sufficient to infer causation (e.g., inferring biotic resistance or competition) when other explanations are possible. Propagule pressure is a consistent predictor of establishment (e.g., Veltman et al. 1996, Duncan et al. 2001, Forsyth and Duncan 2001); therefore it is likely correlated with many characteristics of successful invaders or susceptible habitats. In addition to statistical correlations with establishment (e.g., Blackburn and Duncan 2001), propagule pressure has been shown to strongly influence the probability of establishment in a number of experimental studies (e.g., Hopper and

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Roush 1993, Memmot et al. 1998, Grevstad 1999). Patterns of invasion may therefore be confounded if propagules are chosen non-randomly.

Species that are deliberately introduced represent non-random samples of all possible invaders because they are chosen according to human preference. When processes underlying invasion success are inferred from *post hoc* analyses, there is a high risk for spurious correlations between habitat- or species-specific characteristics and invasion success. Studies that examine characteristics of deliberately introduced NIS are therefore prone to 'propagule biases', which I define as non-random variation in the delivery of propagules, resulting in spurious correlations between invasion success and some characteristic or pattern of interest (e.g., habitat diversity, flower size, introduced range).

Due to the likelihood of non-random variation in the propagule pressure of deliberately introduced organisms, propagule biases may confound studies of numerous taxa. For example, globally invasive birds tend to belong to just seven families (of ~204 worldwide; Clements 2000), including Anatidae (ducks and geese), Phasianidae (pheasants) and other taxa commensal with human activity (Lockwood 1999). Similarly, Mack and Erneberg (2002) estimated that between 57 and 67% of nonindigenous flora were intentionally introduced to the United States. In Argentina, NIS tend to be those utilized by humans (Prinzing et al. 2002), and the most problematical globally invasive *Pinus* species tend to be those planted the most widely and for the longest times (Richardson 1998). Perhaps the best example is the study of globally introduced birds from Blackburn and Duncan (2001), who suggest that patterns of taxonomic over-representation, disproportionate invasions to temperate and island locations, and

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geographical range are highly constrained by non-random variation in introduction effort. In other words, species with large ranges and from a restricted number of families are disproportionately introduced to temperate and island locations.

Accidental introductions also may be prone to propagule biases. In the Great Lakes, for example, approximately 85% of established NIS are the result of unintentional introductions, primarily through discharge of contaminated ballast water (Mills et al. 1993, Ricciardi 2001, Grigorovich et al. 2003). However, the majority of these introductions originate from relatively few regions of the world (MacIsaac et al. 2001, Colautti et al. 2003), and are thus non-random samples of the species pool. An additional propagule bias arises because species characteristics likely reflect their propensity for uptake and survival in the (ballast) transport vector, rather than inherent ecological or evolutionary advantages (Carlton 1985, Ricciardi and MacIsaac 2000). Thus, the majority of deliberately and accidentally introduced NIS likely represent non-random samples before they even reach the establishment stage where community and environmental variables may become important.

Habitat and species characteristics important to the outcome of invasion may vary with invasion stage (Kolar and Lodge 2001, 2002). I take this one step further, and argue that patterns apparent at any stage of the invasion process may be confounded by propagule biases at any of its preceding stages. To help conceptualize this, Fig. 2 combines Carlton's (1985) ballast water transport model, Williamson and Fitter's (1996) 'tens rule', barriers to invasion in Richardson et al. (2000b), and Kolar and Lodge's (2001) 'transitions' model. The invasion process is thus broken into stages where filters may preclude species from reaching each subsequent stage. Factors affecting transition

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between each stage can be categorized as propagule pressure (A; Fig. 2), physico-chemical conditions (B), or community composition (C). Particular invasion determinants act to promote or impede the transition of species to each stage (Fig. 2).

To demonstrate how determinants drive invasion patterns, Fig. 3a shows a propagule bias arising from four determinants influencing which species establish (commercial value and popularity in the case of deliberate introduction, pelagic life stage and survival of transport in the case of accidental introduction). Even ignoring any species-ecosystem interactions, by assuming a 15% flat rate of establishment success, confounding effects might emerge if two contrast groups are not exposed to the same filters and are, therefore, not subject to the same determinants at similar intensities. Fig. 3b demonstrates how the choice of contrast groups can lead to spurious patterns of NIS characteristics, independent of any ecological interactions (e.g., competition, facilitation).

Logically, determinants may only confound patterns at the same or subsequent stages of the invasion process. Thus, identifying the important determinants based on *post hoc* analyses (i.e., observational studies) could be difficult. For example, several determinants can result in significant differences in flowering period between Stage III (established) plants and resident native species. One possible explanation is that a long flowering period confers a competitive advantage by allowing more time for pollination. However, a trend toward longer flower duration could also emerge if there was a strong commercial market for plants with extended flowering. Thus, the same pattern could result from an ecologically significant interaction or from a simple propagule bias, or both. Table 3 lists a number of oft-cited characteristics that may be directly confounded by propagule biases.

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In addition to these *direct* biases, some characteristics correlated with invasion success may be *indirectly* confounded by propagule biases. Such a case might exist, for example, if smaller seed size was correlated with long flowering time. Disproportionate importation of long-lived flowers could thus result in an *indirect* propagule bias toward smaller seed size. Characteristics that are prone to a *direct* propagule bias are likely to reflect human influence or transport survival (Table 3), whereas virtually any characteristic may be confounded by an *indirect* propagule bias.

Studies of invasiveness and invasibility may suffer from the causal fallacy of 'joint effect' (Copi and Cohen 1990), where one parameter such as body size is held to cause another (e.g., invasion success) when in fact they are both resultant from an underlying cause (e.g., propagule bias). In complex systems like ecological communities, several factors often work in concert, rendering difficult, or impossible, attempts to infer causation from observed patterns. Even where observations are not compatible with predicted patterns, *ad hoc* arguments are often invoked to explain discordant results. Such a practice can lead to erroneous predictions and extraneous complexity, a pervasive problem in ecology that has been criticized elsewhere (Peters 1991).

Given an historic lack of predictability among invasion studies, recent attempts have been made to predict high-risk species using characteristics of successful and unsuccessful invaders (Tucker and Richardson 1995, Reichard and Hamilton 1997, Kolar and Lodge 2002). Such studies are likely system-specific, but represent significant advances in invasion biology as they offer testable, *a priori* predictions. However, I feel the need to stress the inherent danger in developing management strategies when causation cannot be proven. This is particularly poignant in the case of invasions, where

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patterns of invasion success may be confounded by propagule biases. In such cases, innocuous species may be blacklisted simply because they share traits with species that are commensal with human activity (i.e., type I error). Alternatively, species that are not commensal with human activity, including those with a potential to become invasive or even a nuisance, may be allowed entry because they do not share traits common among historically introduced species (i.e., type II error). This might occur if models were inadvertently built on characteristics reflecting the common geographic origins of NIS found in a particular region (e.g., Ponto-Caspian species in the Great Lakes). If import origins then changed, as might be the case with an emerging third world economy, then predictive models could fail. More importantly, the ability of imported species to establish and spread may be at least partially dependent upon propagule pressure. As such, classifying a species as harmless could actually serve to increase its rate of importation, thereby facilitating its invasion!

Propagule biases may also confound theoretical expectations. For example, some ecosystems have experienced a series of successful invasions by species native to one particular geographic area, as has happened in the Great Lakes (Ricciardi and MacIsaac 2000). While this pattern is consistent with an 'invasional meltdown' scenario in which early invaders facilitate later ones (Ricciardi 2001), it also could result from a propagule bias in which species from a particular donor area are differentially transported to the recipient ecosystem. However, these processes needn't be mutually exclusive; propagule pressure might be more important in determining which species invade and become widespread (i.e., stages 0-IVa) while facilitative interactions determine which species become dominant or prevalent (stage IVb or V).

Framework for future studies

From this review, it is clear that 'propagule pressure' is a significant predictor (in 23 of 24 studies) of establishment success. Furthermore, non-random variation in 'propagule pressure' may result in propagule biases capable of confounding patterns of invasion success. Given this potential for confounded patterns at every stage of the invasion process, I suggest a propagule pressure-based approach to act as a starting point for the study and management of invasions. This suggestion in no way pre-supposes that physiological attributes of NIS or interspecific interactions among NIS and recipient communities are unimportant. Rather, questions of invasion success (i.e., successful transition of each stage of the invasion process) ought to be explored in a logical manner beginning with 'propagule pressure'. At a minimum, propagule pressure ought to be considered as a covariate in studies exploring other mechanisms.

The likelihood of covariance among 'propagule pressure' and patterns of invasiveness and invasibility suggested by this review also raises an analytical dilemma in that there is a reciprocal possibility for cause-and-effect. In other words, introduced species may be more successful because more propagules are introduced, or invaders may be introduced more because they are better at establishing. However, two factors suggest to me that this latter scenario cannot adequately explain correlations between 'propagule pressure' and establishment. First, propagule biases that affect unintentionally introduced NIS are not part of this dilemma, yet unintentional introductions are often strongly correlated with measurements of 'propagule pressure'. For example, Lonsdale (1999) found that invasibility of nature reserves was strongly correlated with the number of visitors, and Vilà and Pujadas (2001) and Levine and D'Antonio (2003) found a strong

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correlation between the intensity of commodity import and the number of established NIS. Invasions in the Laurentian Great Lakes and many navigable waterways are likewise biased toward invasion from biota linked by dominant shipping vectors (e.g., MacIsaac et al. 2001, Grigorovich et al. 2003*b*, see also Carlton 1996 and Ruiz et al. 2000). Second, experimental studies that have explicitly tested 'propagule pressure' for individual species (e.g. biological control experiments) have consistently found a positive effect on establishment success (e.g., Hopper and Roush 1993, Memmot et al. 1998, Grevstad 1999).

Until sufficient data exist to suggest otherwise, I maintain that 'propagule pressure' should form the basis of a null model for invasion studies because it holds such potential to confound invasion patterns and because it models invasions simply as a probabilistic process. Thus, future attempts to distinguish characteristics of invaders should first attempt to dismiss confounding propagule biases before other processes are implicated. The 'propagule pressure' model presented here is not mutually exclusive of other biological and environmental processes; rather it forms a basis on which such processes can better be explored in supplement. Such a protocol may seem daunting, but compared to the myriad possibilities underlying biological interactions it may prove useful in harmonizing discordant characteristics of successful invaders or susceptible habitats.

For example, this review reveals that invasibility is equally associated with species-rich and species-poor communities; this pattern is analogous to the highly controversial diversity-stability debate (e.g., McGrady-Steed et al. 1997, Hector et al. 1999, Stachowicz et al. 1999, Huston et al. 2000). Levine and D'Antonio (1999)

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reviewed studies relating species diversity to invasibility and noted that experimental studies tended to find diverse communities more resistant to invasion, while observational studies often found the opposite - a positive correlation between species diversity and the number of NIS established. Levine (2000, 2001) later demonstrated that more diverse communities were less resistant to, but not exempt from, invasions at a local scale, but that this pattern could be confounded by variation in propagule pressure at a regional scale.

Progress is already being made toward eliminating propagule biases. Several experimental studies have correlated species characteristics to invasion success even after considering 'propagule pressure'. This has been accomplished either by controlling the number of propagules (e.g., Grotkopp et al. 2002), or through a multi-step regression analysis when introduction effort was known (e.g., Sol and Lefebvre 2000, Duncan et al. 2001). Similarly, experimental studies of invasibility have found significant relationships between habitat characteristics and invasion success, even when plots received equal numbers of propagules. Using experimental plots with equal numbers of seeds propagules, for example, Burke and Grime (1996) and Davis and Pelsor (2000) found strong support for the importance of resource availability to invasibility. These types of studies should form the basis for future exploration of factors affecting invasiveness and invasibility. However, it is important to question the biological significance of these findings in natural ecosystems, how they may be confounded by 'propagule pressure', and at which stages (from Fig. 2) they are most important. Thus, there remains a large intellectual gap in experimental tests of the relative importance of propagule pressure and

other biotic and environmental factors to the success of NIS at each of the invasion stages.

Conclusion

My intention is not to repudiate the importance of biological processes as determinants of invasion success; rather I propose that propagule pressure-based hypotheses represent the appropriate starting point to predict successful transition of the invasion stages. Instead of focusing on complex, system-specific biotic interactions, management efforts may be better spent reducing opportunities for unintentional introductions and escapes, while activities that deliberately introduce NIS should be re-examined. Given the implications of 'propagule pressure' for invasions, eradication programs should weight heavily the importance of propagule pressure on the spread of established NIS. For example, prescribed burnings designed to open space for native species may prove futile if propagules from nearby populations of NIS are not precluded (e.g., Simberloff et al. 2003).

A comprehensive, scientific understanding of ecosystem dynamics can only benefit from the inclusion in future analyses of quantified 'propagule pressure' and acknowledgement of its potentially confounding effects. I anticipate that this suggestion will not be universally accepted, but it should provide a framework to guide invasion biologists to a better understanding of patterns and processes underlying the ecology of invasions.

TABLE 1. Reported characteristics of 'invasiveness'. Summary of observations (usually separate studies) implicating positive (+), negative (-), or no (n.d.) relationship between characteristics of successful invaders during establishment or subsequent stages (post-establishment). Results are identified by taxon as follows: plants (p), birds (b), fishes (f), invertebrates (i), and mammals (m).

Characteristic examined	Relationship with invasiveness					
	Establishment			Post-establishment		
	+	-	n.d.	+	-	n.d.
Propagule pressure	1p,1i,1f,6b,1m			1p		
Taxonomic over-representation	3p,2b		1p			
Physiological tolerance	3p,1f	3p,1i	1p	1p,2f		
Body size	1p,3b	1i,1b	1p		1b	1f
Length of growing/breeding season	2p		1p	1p		1f
Growth rate	1p,1f				1f	
Generation time	1b	4p,1i,1m			1p,1b	1f
Invasion history or widespread	4p,1i,1g,2b			1b		
Germination/hatch success or rate	7p		1p			

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TABLE 1 (continued)

Seed/egg size		2p		1p	1f
Reproductive output	2p,1i		1p		
Consumption efficiency	6p,1i	1p	1p		
Hermaphroditic/asexual reproduction	3p			1p	

TABLE 2. Reported characteristics of 'invasibility'. Summary of observations (usually separate studies) implicating positive (+), negative (-), or no (n.d.) relationship between characteristics of habitats susceptible to invasion. Results are identified by taxon as follows: plants (p), birds (b), fishes (f), invertebrates/micro-organisms (i), mammals (m), and multiple taxa (s).

Characteristic examined	Relationship with 'invasibility'		
	+	-	n.d.
Propagule pressure	9p,2b,1s		1p
Anthropogenic exposure	24p,2b,1f,1m,1s		1p
Disturbance	24p	3p,1f	1p
Nutrient levels	10p,1b,2i	1p	2p
Species diversity	10p,1b	9p,1b,1f,3i,1m,1s	4p,1f,1i
Species abundance	4p,1s	6p,1f	1p,1i

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TABLE 3. Some commonly cited characteristics that may be confounded by a *direct* 'propagule bias' (i.e., non-random variation in propagule pressure; see text for further explanation). Characteristics are separated by stages of the invasion process from Fig. 2 (bold), and some possible propagule biases (italics) driving non-random variation in propagule pressure at each stage. Note that virtually any characteristic may be a result of an *indirect* propagule bias because characteristics may be indirectly correlated with propagule pressure (see text).

Stage I (transport) biases

Ease of cultivation, desirability, or covariates thereof

    competitive ability

    growth rate

    reproductive rate

    time to maturity

Stage II (introduction) bias

Survival of transport

    competitive ability ('hardiness')

    reproductive rate

    vegetative/asexual reproduction

    presence of a dormant stage

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TABLE 3 (continued)

vegetative/asexual reproduction

size of propagules

presence of dormant stage

number of propagules

size of propagules

dispersal mode/efficiency

number of propagules

physiological tolerances

presence of predators/parasites

pre-germination treatment

phenology compared to native species.

taxonomic over/under-representation

Stage (spread) IVa bias

physiological tolerances

Human-mediated dispersal

body size

growth rate

ability to utilize local pollinators

reproductive rate

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TABLE 3 (continued)

root density

time to maturity

vegetative/asexual reproduction

Attainability and factors affecting accidental transport

presence of dormant stage

reproductive rate

size of propagules

vegetative/asexual reproduction

number of propagules

presence of dormant stage

dispersal mode/efficiency

size of propagules

invasive elsewhere

number of propagules

dispersal mode/efficiency

invasive elsewhere

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FIGURE 1. Studies describing characteristics of successful invaders or habitats susceptible to invasion. Studies in which propagule pressure was explicitly considered (white bars) make up only a small proportion of most types of studies. A) Characteristics of successful invaders: 1 – taxonomic over-representation, 2 – physiological tolerance, 3 – body size, 4 – length of growing/breeding season, 5 – growth rate, 6 – generation time, 7 – invasion history or widespread, 8 – germination/hatch success or rate, 9 – seed/egg size, 10 – reproductive output, 11 – consumption efficiency, 12 – hermaphroditic/asexual reproduction. B) Characteristics of habitats susceptible to invasion: 1 – anthropogenic exposure, 2 – disturbance, 3 – nutrient levels, 4 – species diversity, 5 – species abundance.

FIGURE 1

A)
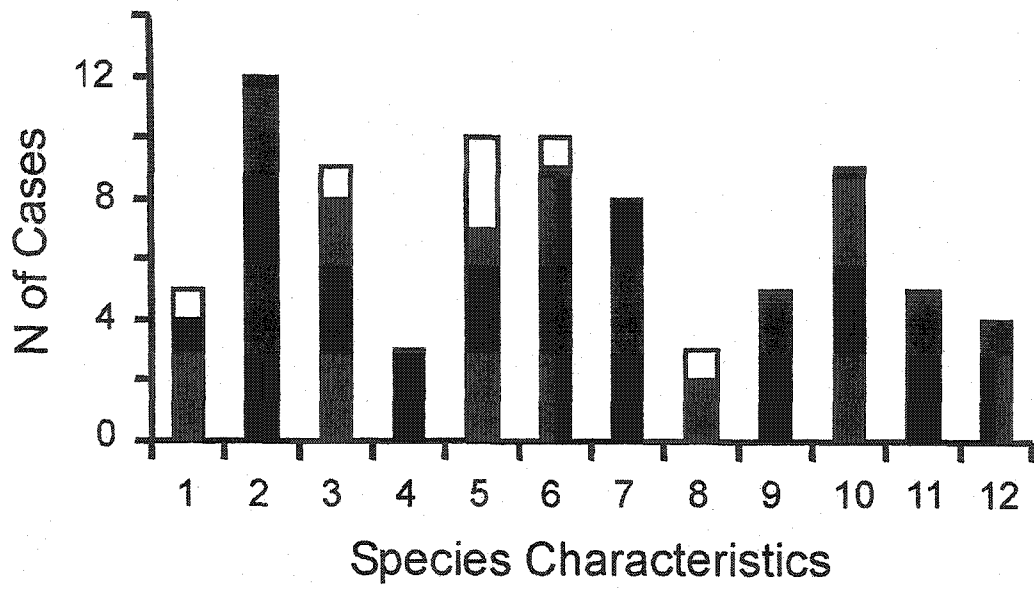
B)
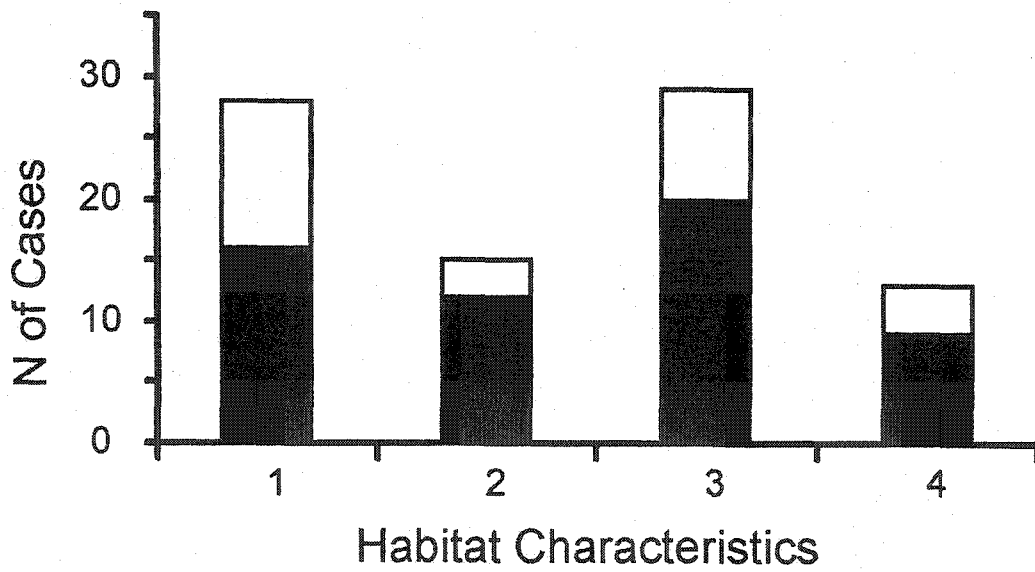
FIGURE 2. Stage-based model of the process of biological invasions. Invasions are

modelled as a series of successive stages (0-V). Beginning with a pool of species in a

source region, sub-sampling of species occur at early stages of the invasion process.

Three classes of determinants may act to aid (+) or impede (-) the transition of

species to each subsequent stage: propagule pressure (A), physico-chemical factors

(B) and community interactions (C). Additionally, filters act at each stage to preclude

transition between stages. Note that species may be widespread but rare (stage IVa),

localized but dominant (stage IVb) or widespread and dominant (i.e., stage V).

FIGURE 2

STAGE 0
(source pool)

A+ | UPTAKE FILTER

STAGE I
(transported)

A+
B± | TRANSPORT VECTOR SURVIVAL
AND RELEASE FILTER

STAGE II
(introduced)

A+
B±
C± | ENVIRONMENT SURVIVAL AND
REPRODUCTION FILTER

STAGE III
(established)

DISPERSAL FILTER   A+

STAGE IVa
(widespread)

B±
C± | ENVIRONMENT AND COMMUNITY
SUITABILITY FILTER

STAGE IVb
(dominant)

ENVIRONMENT AND COMMUNITY   B±
SUITABILITY FILTER   C±

STAGE V
(prevalent)

A+   DISPERSAL FILTER

STAGE V
(prevalent)

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FIGURE 3. Graphical representation of the confounding effects of propagule pressure.

Each symbol represents a different species. A) Assuming a flat establishment rate

(i.e., not species-specific), propagule biases (i.e., non-random variation in introduction

effort) such as 'commercial value' or 'popularity', may result in the transport (stage I)

and introduction (stage II) of NIS with similar characteristics (e.g., flower size or

colour). B) Established NIS may therefore differ dramatically from their congeners,

owing to propagule biases. One of three groups of species are typically contrasted

with NIS to identify characteristics of established nonindigenous species: 'native' -

native to the invaded region, stage 0 – native to the source region, and stage II –

introduced but not established. Characteristics confounded by propagule pressure are

expected to increase with the number of propagule biases, thus there should be more

differences between NIS and native species in the recipient community than between

NIS and failed invaders (i.e., those that are introduced but fail to establish).

FIGURE 3
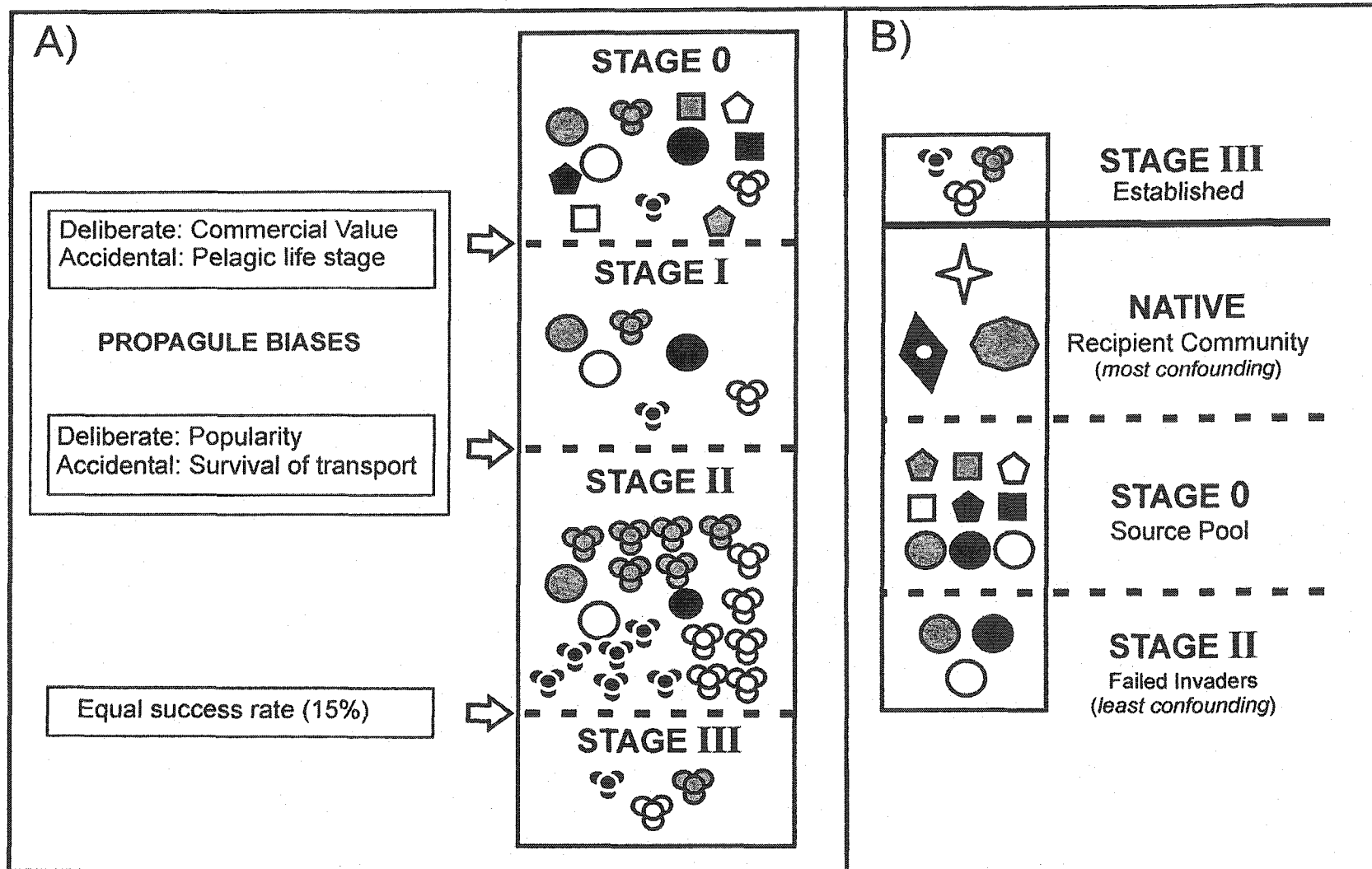
Chapter 3

A process-based approach to biological invasions

Abstract

The use of simple terms to articulate ecological concepts can result in liberal or divergent definitions that confound conceptual debates. This problem is particularly acute in studies of nonindigenous species, which alternatively have been called 'exotic', 'introduced', 'invasive' and 'naturalized', among others. Because attempts to redefine commonly used terminology have failed, I introduce a synthetic framework that instead focuses on the invasion process. Operationally important terms in this framework are based on a model that breaks the invasion process into a series of consecutive, obligatory stages and identifies factors affecting success of species at each stage. Under this framework, invasions can be more objectively defined as a biogeographical phenomenon, and different preferences in the use of existing terminology can be addressed.

Introduction

Terms and concepts crucial to understanding ecology have often been criticized for their tautological, ambiguous or non-operational nature. Classic examples of problematic ecological terminology include concepts like ecosystem, diversity-stability, and the ecological niche (see McIntosh 1985, Peters 1991, Grimm and Wissel 1997). While the widespread use of ordinary words in the English ecological literature has allowed rapid dissemination of novel ideas, it also has impeded progress of objective scientific theory (Peters 1991). Invasion ecology has enjoyed a rapid ascension in the public domain, owing in part to the extensive use of adjectives like 'invasive', 'alien', 'noxious' and 'exotic' (Chew and Laubichler 2003). However, subconscious associations with preconceived terms, particularly emotive ones, can also lead to divergent interpretations and a confusion of concepts and theory. These differences can become problematic if

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they cloud conceptualization of the processes they are meant to describe (see McIntosh 1985, Peters 1991, Pyšek 1995, Richardson et al. 2000a, Shrader-Frechette 2001). This problem is perhaps best highlighted by the recent publication of widely divergent perceptions of the criteria for 'invasive' species (Davis and Thompson 2001, Rejmánek et al. 2002, Chew and Laubichler 2003).

Lack of consensus

Many important terms relevant to invasion biology theory, like 'invasive', 'weed' or 'transient', include qualities that are open to subjective interpretation. For example, it is generally accepted that the adjectives 'noxious' and 'nuisance' are used to imply adverse effects on humans, either directly (e.g., species that produce toxins that are harmful to humans) or indirectly (e.g., species that infest nature reserves). However, this reliance on human interaction has three important analytical consequences. First, definitive criteria may vary dramatically, ranging from species with aesthetically displeasing effects (e.g., Civeyrel and Simberloff 1996), to those that are vectors for serious human diseases (e.g., Lounibos 2002). Second, species may be considered a nuisance (or weedy, invasive, etc.) in areas where they have little or no effect simply because they were identified as a nuisance elsewhere (e.g., Morton 1996). Indeed, the screening model developed to identify possible harmful plants imported to Australia depends heavily on previous invasion history (Pheloung et al. 1999). Finally, a particular species can have both beneficial and detrimental effects, depending on criteria employed. For example, the mosquitofish *Gambusia affinis* has been widely introduced because of its supposed suppression of larval mosquitoes (Fuller et al. 1999), yet it also has negative affects on native species of insects, fish and amphibians (e.g., Rupp 1996, Goodsell and Kats 1999).

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Given this wide range of subjective criteria, terms like 'nuisance' may have more to do with human perception than with any inherent ecological parameters. As such, these subjective terms may complicate or confound investigations of invasion patterns and processes.

In addition to a lack of empirically defined criteria, other terms also lack consensus on a more basic level. Ironically, the greatest confusion surrounds the common term 'invasive' and its various derivatives (Richardson et al. 2000a). Explicit or implicit definitions for 'invasive' include: 1) a synonym for 'nonindigenous' (e.g., Goodwin et al. 1999, Radford and Cousens 2000); 2) an adjective for native or nonindigenous species that have colonized natural areas (e.g., Burke and Grime 1996); 3) discrimination of NIS established in cultivated habitats (as 'non-invasive') from those established in natural habitats (e.g., Reichard and Hamilton 1997); 4) NIS that are widespread (e.g., van Clef and Stiles 2001); or 5) widespread NIS that have adverse effects on the invaded habitat (e.g., Davis and Thompson 2000, Mack et al. 2000). The latter definition has gained popularity with some international conservation organizations (e.g., IUCN 1999, McNeely et al. 2001), but has been criticized by others (Rejmánek et al. 2002). Richardson et al. (2000a) similarly noted that the term 'naturalized' is equally confused, including uses as a synonym for 'alien', a synonym for 'invasive', a synonym for 'established', or specifically for NIS able to establish in undisturbed habitats. Richardson et al. (2000a) advocated for a biogeographical approach to defining established, naturalized and invasive species, a concept with which I agree.

Table 1 identifies a non-exhaustive series of adjectives commonly used in the English literature on invasive species. Many of these terms have been used interchangeably to describe the same concept (e.g., nonindigenous, exotic, alien), while

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the same term has been used to describe different processes (e.g., invasive, naturalized, imported). Although this criticism may at first seem semantic, varied definitions can cloud theoretical issues. This leads to the lumping together of different concepts, and the splitting of similar ones, which in turn makes generalization difficult or impossible. For example, a particular species may have a widespread region of introduction in which it is only found at low abundance, or may be established in only one area where it is locally abundant. The term 'invasive' has been used in both cases, but the underlying processes accounting for these two patterns may be quite different; human-mediated transport is likely most important in the former case, whereas biological processes (e.g., competitive ability, lack of natural enemies) may be more important in the latter (see also Richardson et al. 2000a). Indeed the very terms used to describe NIS (e.g., exotic, non-native, introduced, etc.) are misnomers in that nonindigenous species are really nonindigenous populations of species. In other words, the same 'species' that are nonindigenous, naturalized, or invasive in one area are native somewhere else. A focus on invasions at a population level has important implications for both invasion biology and ecological theory.

Problems with invasion terminology reflect a more general dilemma in ecology: the 'non-operational' or casual use of important terms and concepts (McIntosh 1985, Peters 1991). Furthermore, recent attempts to redefine 'invasion' and its derivatives have only reinforced division among invasion biologists (Davis and Thompson 2000, Richardson et al. 2000a, Daehler 2001, Davis and Thompson 2001, 2002, Rejmánek et al. 2002). A complete restructuring of invasion terminology is beyond the scope of this essay. However, I maintain that failure to operationalise definitions is sufficiently harmful that a consensus on definitions must be achieved in order to reduce confusion and

allow for unambiguous generalizations and predictions. Such a consensus would greatly reduce confusion among researchers, and would facilitate a more directed approach to finding generalizations and better understanding of phenomena associated with biological invasions. Considering the conservation implications of biological invasions, it is imperative that workers in the field provide clear, objective definitions and models to managers and other officials charged with protection of native biodiversity.

Consensus for an operational lexicon

Davis and Thompson (2000) classified colonizing species into eight categories based upon dispersal distance, novelty, and impact. As such, their 'colonizer' model assumes that NIS are simply colonizing species, moved over long distances. This use of categories may be key to uniting invasion paradigms, as their explicit definitions help eliminate inferential 'baggage' associated with common words and the subtle, subconscious definitions that often vary between authors. However, I disagree with the assumptions of the 'colonizer' model, as have other workers (Daehler 2001, Rejmánek et al. 2002). Contrary to the Davis and Thompson (2000) colonizer model, I argue that NIS are inherently different from native colonizers, owing to separate evolutionary histories and different propensities for commensal interactions with humans. Furthermore, the process of becoming 'invasive' (i.e., both widespread and locally dominant), even if it includes negative effects, is always the climax of a process that includes establishment and local spread, followed by an increase in abundance (Fig 1; see also Richardson et al. 2000a, Kolar and Lodge 2001). Once established, however, processes that determine species distribution and abundance are conceptually similar for both native and nonindigenous species.

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In a seminal contribution, Richardson et al. (2000a) proposed a comprehensive model that described invasions as a sequential process in which NIS progress through a series of invasion stages. Their model was specific to plants, but is conceptually similar to other, more general models (i.e., Carlton 1985, Williamson and Fitter 1996; Kolar and Lodge 2001; reviewed in chapter 2). However, these studies attempted to clarify terms already common to the invasion literature. Previous efforts to redefine invasion terminology have been largely unsuccessful (e.g., Shafland and Lewis 1984, Binggeli 1994). Thus, I maintain that proposals for universal definitions are unlikely to succeed unless authors forego their individual preferences. Consequently, I suggest that a useful invasion framework should be process-based and include operational terms with no *a priori* meaning (i.e., as 'stages').

In chapter 2, I developed a conceptual framework synthesized from Carlton's (1985) ballast water transport model, Williamson and Fitter's (1996) 'tens rule', Richardson et al.'s (2000a) barriers to invasion, and Kolar and Lodge's (2001) 'transitions' model. I suggest that future studies explicitly refer to the invasion stages of interest (Fig. 1). Such an approach utilizes novel terms with no *a priori* definitions and builds upon existing invasion models (Carlton 1985, Williamson and Fitter 1996, Richardson et al. 2000a, Kolar and Lodge 2001). Such a protocol wouldn't replace current terminology, but could greatly ease confusion by supplementing terms with the invasion stage of interest. An example might be: "We examined distribution data to identify differences between invasive species (stages IVa, and V) and non-invasive species (stages III and IVb)". By explicitly stating the stage of interest, it would be clear that the 'invasive' species include those that are widespread, whereas 'non-invasive' species refer to localized populations, regardless of local abundance. This model of the

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invasion process is roughly analogous to the stages of tumour progression used in the cancer literature. The conceptual framework for cancer, which ranges from localized (stage I) to malignant and widespread (stage IV) tumour growth, is less explicit than the synthetic model presented here, but has undoubtedly aided in the understanding and treatment of cancer progression among specialists and the general public.

Besides introducing a framework for operationally important terminology, this invasion framework aids in conceptualizing factors that affect invasion success (i.e., determinants in Fig. 1). For example, the transition of propagules from introduction (stage II) to establishment (stage III) requires survival and reproduction in the recipient region. To predict success at this stage, invasion models have historically focused on biotic resistance of recipient communities (e.g., Elton 1958). Biotic resistance predicts that species interactions hinder the establishment of NIS due to the negative effects of predation, competition or parasitism. Thus, the C-class of determinants (Fig. 1) may have a negative value, indicating that biotic resistance can hinder the transition of propagules from introduction to establishment. Alternatively, facilitative interactions can increase the probability of invasion success by creating new niches (e.g., Simberloff and von Holle 1999, Richardson et al. 2000b, Bruno et al. 2003). Therefore, the same determinants (C-class) may have a positive value at the same stage. Physicochemical requirements (B-class determinants) of the potential NIS may similarly affect establishment success either positively or negatively, depending on the physicochemical properties of the recipient environment or of the transport vector. For example, lakes with low calcium concentration may be relatively invulnerable to invasion by zebra mussels (*Dreissena polymorpha*), while nutrient-rich grassland habitats may foster establishment of both native and NIS plants (Ramcharan et al. 1992; Stohlgren et al. 1999). Finally, the

probability of establishment success may increase with the introduction of more propagules (A-class), which reduces or eliminates the likelihood of Allee effects and stochastic extinctions (Mack 1995, Courchamp et al. 1999a, Keitt et al. 2001).

Under this framework, the designation of 'Stage 0' (Fig. 1) should be reserved for species found in the same source region as the NIS of interest (i.e., potential introductions from the same source pool), thus discriminating species in the source region from species native to the recipient region (i.e., resident species native to the invaded region). This distinction is important in better conceptualizing 'propagule biases' that may confound patterns of invasion (see chapter 2).

Invasive vs. native

A focus on invasion stage also has the added benefit of stressing the view that invasions represent biogeographical rather than taxonomic phenomena. As such, invasion stages should refer to individual populations, and not entire species. Such an approach is crucial if invasion biology is to move beyond the current, widespread practice of contrasting species to identify characteristics of good invaders. Species-level analyses have provided valuable insights because the same species are often invasive in different parts of the world (i.e., invasive populations are a non-random sample of the global species pool). Nevertheless, a biogeographical focus is imperative because populations of the same species can differ in their population dynamics (Crawley 1987, Thébaud and Simberloff 2001, Torchin et al. 2001, Leger and Rice 2003), and because determinants of invasion success (Fig. 1) act at the level of populations.

Processes that affect local spread and establishment in novel areas may be independent of species origin (i.e., native or nonindigenous). As such, stages III to V

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(Fig. 1) could be used to model three types of potential colonizers that might be available from a regional species pool: (i) NIS that have only recently established in the region of interest; (ii) NIS that have been resident for a long period of time; and (iii) native species. Ecologically important concepts like competition, facilitation, and disturbance may therefore prove useful in modelling the latter stages (III to V) of the invasion process where similar mechanisms operate on populations, independent of their origin or residence time. Alternatively, processes that are unique to the ecology of invasions by populations of nonindigenous species (e.g. human import preferences, survival of harsh transport vectors) would act at the early stages (0, I and II) of the invasion process (Fig. 1).

The approach to defining NIS that I describe here still requires explicit criteria for 'nonindigenous' status. Such criteria are crucial, but likely will be case-specific initially, and standardized criteria may prove to be a source of continued debate (e.g., Webb 1985, Shrader-Frechette 2001). However, this shift of focus to invasion stages renders moot the issue of whether the taxa involved are native regionally or originate from other biogeographic areas. Using this framework, even resident native species and established (Stage III) NIS might be modelled by the same or similar factors affecting later stages within a given system. Nevertheless, a consensus on operational terminology is required if invasion biology is to evolve into a more objective discipline.

TABLE 1. List of some common terms in the English literature on invasion biology, along with their suggested stage(s) from Fig. 1.

Term	Stage
Adventive	Stage I-V
Alien	Stage I-V
Casual	Stage II
Colonizing	Stage IVa
Cryptogenic	A species whose origin is uncertain; may be modeled as Stage III-V
Escaped	Stage II-V
Endemic	Not defined by the model
Established	Stage III-V
Exotic	Stage I to V
Foreign	Stage I to V
Immigrant	Stage I to V
Imported	Stage I to V
Introduced	Stage I to V
Invasive	Stage IVa, IVb or V
Native	Not defined by the model
Naturalized	Stage III-V
Nonindigenous	Stage I-V
Noxious	Not defined by the model
Nuisance	Not defined by the model
Pest	Not defined by the model

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TABLE 1 (continued)

Spreading	Stage IVa
Temporary	Stage II
Tramp	Used to describe a species that is widespread globally, not defined by the model
Transferred	Stage I-V
Transformer	Not defined by the model
Transient	Stage II
Translocated	Stage I-V
Transplanted	Stage I-V
Transported	Stage I-V
Waif	Stage II
Weedy	Not defined by the model

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FIGURE 1. Suggested framework for defining operationally important terms in invasion studies (based on chapter 2). This model is based on Fig. 2 in chapter 2, but focuses on invasion stages.

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FIGURE 1
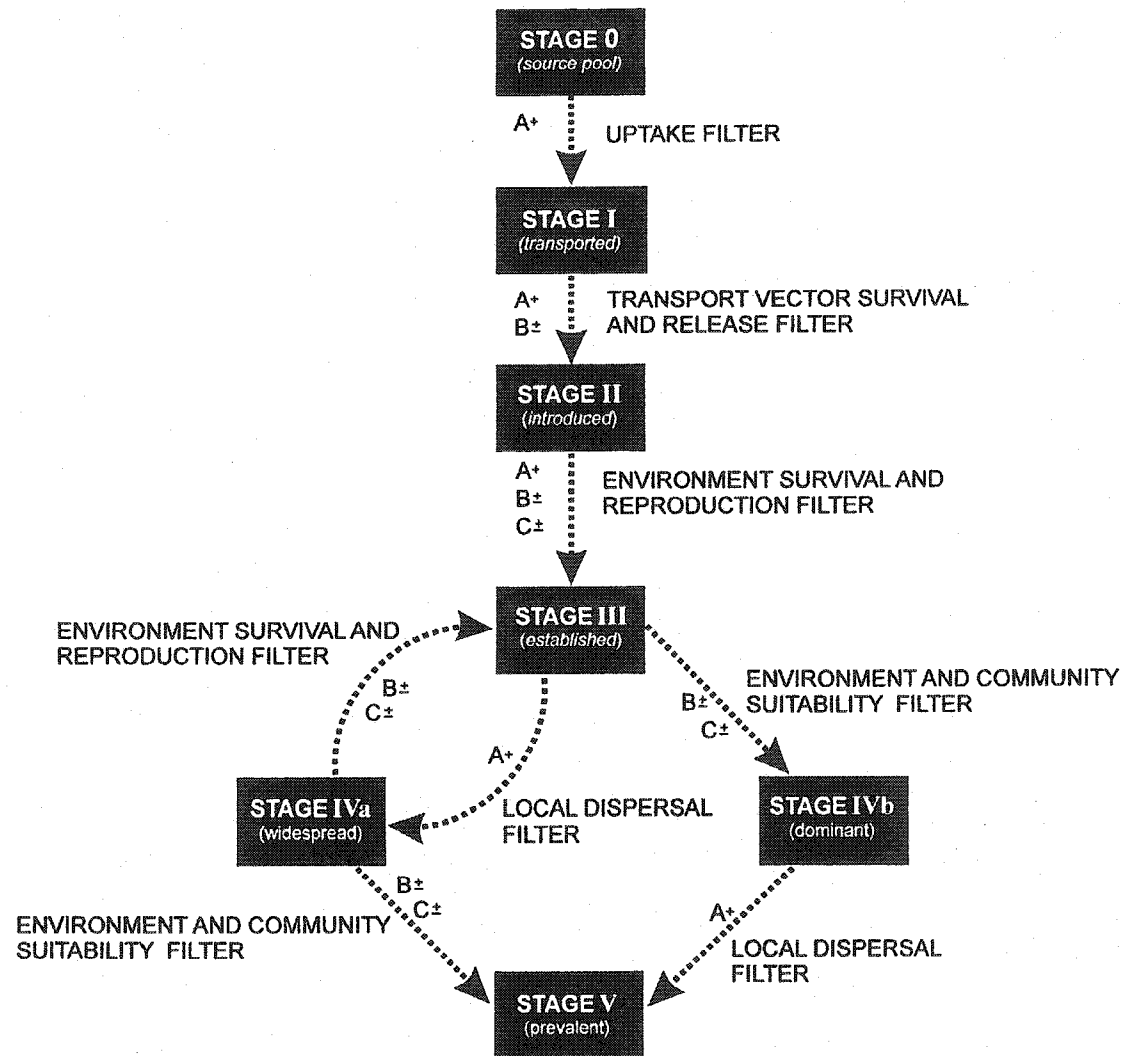
Chapter 4

Does the enemy release hypothesis predict invasion success?

Abstract

A recent trend in the invasion literature relates the success of nonindigenous species (NIS) to the number of co-occurring enemies (i.e., the enemy release hypothesis; ERH). Several case studies suggest that release from particular enemies can result in increased vigour or survival. However, the predictive ability of the ERH rests on four assumptions: (i) compared to native populations, nonindigenous populations harbour fewer co-introduced enemies; (ii) enemies already present in the invaded region will affect native species more than NIS; (iii) enemies co-introduced with their hosts will behave similarly in the invaded and source regions; and (iv) release from enemies results in increased fitness with a resultant advantage over native competitors. A literature review finds that these assumptions often do not hold true. Furthermore, the putative mechanism of enemy release – bottlenecks during invasion – implies a number of alternative scenarios that may have either positive or negative consequences for the host species. Taken together, these results suggest that loss of natural enemies attendant with biological invasion may not yield benefits to the host species.

Introduction

Understanding factors that affect the ability of nonindigenous species (NIS) to invade novel environments, where they may become widespread and abundant (i.e., invasive), holds important implications for both resource management and theoretical ecology. Perhaps the most straightforward and intuitively appealing explanation for the rapid establishment and proliferation of NIS is that they are introduced into environments with fewer natural enemies. The enemy release hypothesis (ERH) predicts that the ability of species to become invasive is related to the scarcity of natural enemies, whose

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introduction is limited due to bottlenecks during the invasion process (Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003). Enemy release permits the invader to allocate more resources to growth and reproduction rather than to defence or regrowth after attack, thereby gaining a competitive advantage over native species (Keane and Crawley 2002, Wolfe 2002). Herein, I define 'host' to include prey, and 'enemy' to describe parasites (and parasitoids), pathogens, competitors or predators.

Given the rising popularity of the ERH (Chew and Laubichler 2003), I felt it prudent to identify and assess some of the assumptions implicit to this hypothesis. I identify four key assumptions of the ERH as a predictive hypothesis and evaluate each using a combination of case studies and theoretical background. I also explore potential biases that could confound attempts to test these assumptions. Finally, I explore the implications of the process underlying enemy release (i.e., bottlenecks during the invasion process; Mitchell and Power 2003) to identify alternative scenarios that may be important in shaping patterns of the success and impact of NIS.

Importance of enemies

Strong evidence for the effect of some enemies on host fitness can be found among many case studies, particularly in the parasitological literature (Hoffman and Schubert 1984, Hudson et al. 1998, Torchin et al. 2001). Likewise, the overwhelming success of several biological control (biocontrol) agents lends evidence to the importance of particular enemies in controlling the population dynamics of their host (e.g., see McFadyen 1998). The success of biocontrol has often been cited as evidence for the ERH (DeLoach 1995). However, non-target effects are rarely explored (Louda et al. 2003) and biocontrol agents often fail to effectively control their target (OTA 1995, Williamson 1996). Even where

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successful, modern biocontrol agents are almost always specialist enemies that are chosen for introduction non-randomly (McFadyen 1998, Louda et al. 2003).

Inherent assumptions of the ERH

Assumption #1: Fewer co-introduced enemies

Owing to the limited number of propagules typically associated with introduction events, their transportation to novel environments effectively results in a sub-sampling of source populations, reducing the likelihood of co-introduced enemies (i.e., a founder effect; see colonist subsample filter, Fig. 1). The number of transported individuals that become introduced may be further constrained by differential mortality of infected or parasitized propagules (Mitchell and Power 2003, Torchin et al. 2003) and by harsh conditions during transport (Lavoie et al. 1999; see transport survival filter, Fig. 1). Furthermore, transport vectors may predispose an invader to arrive without its enemies; for example, invertebrate, planktonic larval stages may lack parasites associated with adults (e.g., zebra mussels; Molloy et al. 1997; see transport uptake filter, Fig. 1). To complete their life cycle, many parasites (e.g., trematodes; Combes and Le Brun 1990) require multiple host species, and therefore would not establish in novel habitats without alternative hosts (see establishment filter, Fig. 1). Finally, human selection could influence the number of parasites available for transfer to the new habitat. It is well established that female birds may preferentially select mates with low parasite burdens based on appearance (e.g., plumage colour). If human importers of plants or animals select colonists that are relatively free of parasites, then the number available for transfer to the new ecosystem will be correspondingly lower (see transport uptake filter, Fig. 1). Despite the intuitive appeal of these arguments, empirical evidence for a reduction in the number of co-

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introduced enemies was rare until recently (Dobson and May 1986, Mitchell and Power 2003, Torchin et al. 2003). Nevertheless, empirical demonstrations of enemy release using measurements of parasitism, infection or predation in introduced populations should be viewed cautiously because patterns of enemy release may be confounded by biases in research effort or by the contrast group selected from the source region (see Poulin and Mouillot 2003).

Potential NIS and their enemies may be better studied in their native than in their nonindigenous ranges, and as such, more enemies would be expected in native populations simply due to sampling effort (Mitchell and Power 2003, Torchin et al. 2003). For example, of 26 randomly selected studies that addressed parasites of three globally invasive vertebrate species (i.e., rat, mosquitofish and rabbit), only 5 dealt with parasites found in the nonindigenous ranges (Torchin et al. 2003). Research effort and the likelihood of discovering parasites may, therefore, differ between native and introduced ranges of these species.

More importantly, accurate tests of the ERH require knowledge of the number of enemies in the source region. Studies that have explicitly compared range sizes with the number of co-occurring enemies for both nonindigenous and native populations of plant species have concluded that the best predictor of enemy diversity is host range (Southwood et al. 1982, Clay 1995). Thus, spatial variation in enemy occurrence within the source range may be pronounced. Since invading propagules are often drawn from a constrained area within their native range (Cristescu et al. 2001, Grant et al. 2001, Hänfling et al. 2002), the number of enemies available to be introduced to a new area with their hosts will be much lower than that represented by the total number available from across the realm (i.e., source region filter in Fig. 1). The use of cumulative numbers

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drawn from across an entire source biogeographic realm could therefore substantially overestimate the number of enemies available for transport to a new region. A more appropriate contrast would consider only those enemies found in the region from which the colonist population was likely drawn. Identification of invasion pathways should help clarify the region(s) to be considered in developing candidate lists of enemies available for transport to new areas (MacIsaac et al. 2001, Hänfling et al. 2002, Pollux et al. 2003).

A second sampling error derives from the limited number of founder colonists that are introduced. Since the initial colonists represent a subsample of the regional source population, a number of enemies are likely to be lost (Mitchell and Power 2003; i.e., colonist subsample filter, Fig. 1). Both of these cases represent a subsampling error that can lead to an 'apparent' enemy release, even if the 'realized' release (i.e., the parasite burden on any individual) is unchanged.

Assumption #2: Limited target-switching by native enemies

In order to gain an advantage over resident native species, NIS should be less prone to native enemies in the invaded region than are native species. These effects are often difficult to quantify, although some evidence exists in support of this assumption (see Keane and Crawley 2002); it is, however, by no means a universal 'rule of thumb', as numerous examples exist of host-switching by native enemies (Maron and Vilà 2001, Keane and Crawley 2002). In a study of native and invasive grasses, for example, host-switching resulted in more pathogens on NIS than on resident native species, in direct contradiction to the ERH (Clay 1995). Similarly, Agrawal and Kotanen (2003) found that nonindigenous species were no more resistant to a native herbivore than were native species.

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Assumption #3: Predictable behaviour from introduced natural enemies

Another fundamental assumption of the ERH is that co-introduced enemies will behave similarly in the invaded region as in their source region. However, introduced enemies might not focus exclusively on their co-evolved hosts. Resident native species, lacking adaptive experience with the introduced enemy, could be subjected to greater predation pressure than the NIS (see "Enemy of My Enemy" hypothesis below). Alternatively, co-introduced enemies could have a larger effect on nonindigenous populations owing to a loss of defences during introduction bottlenecks (see "Increased Susceptibility" hypothesis below). Finally, the effect of co-introduced enemies may be reduced or even reversed owing to biotic or abiotic differences between the native and introduced ranges (see "Enemy Inversion" hypothesis below).

Assumption #4: Increased fitness

Perhaps most importantly, the ERH assumes an inherent energetic cost to defending against enemies, and predicts that invasive species with fewer enemies grow larger or experience higher fitness in their nonindigenous ranges. Resources available to a plant are divided among growth, metabolism, reproduction, and herbivory. In the absence of herbivores, more resources can be directed to growth and reproduction, thereby bestowing apparent advantages to nonindigenous populations. Introduced individuals are often larger than their native counterparts (Crawley 1987, Grosholz and Ruiz 2003; but see Thébaud and Simberloff 2001), and there exist several reports of increased survival or vigour of NIS following release from some enemies (Wolfe 2002, Leger and Rice 2003, Mitchell and Power 2003, Torcin et al. 2003). For example, green crabs (*Carcinus*

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maenus) introduced to coastal habitats in North America lack parasitic castrators prevalent in native European habitats, and may grow to much larger size in consequence (Torchin et al. 2001). However, enemies also vary widely in their effects on co-evolved hosts (e.g., Hawkins et al. 1997, Keane and Crawley 2002), such that the loss of some enemies may not have appreciable effects.

Problems with proportionality

An overall pattern consistent with enemy release may instead be an artefact of 'propagule bias'. That is, apparent patterns of enemy release may result from filters acting at early stages of the invasion process that reduce the number of enemy propagules introduced (see assumption #1; also Fig. 1). To better test the ERH, an empirical relationship should be evident between some measure of 'invasiveness' (e.g., effect, distribution or abundance) of a species, and its release from enemies (Mitchell and Power 2003). However, inferring enemy release as a cause for such a relationship could prove difficult because qualitative and quantitative criteria for terms like 'invasive' and 'nuisance' are inadequately defined and may be applied disproportionately to populations of NIS than to native ones (Richardson et al. 2000a). Thus, a species that has the same effect on or propensity to invade habitats in both its native and nonindigenous range may be considered 'invasive' only among the latter. Taken with the patterns of enemy release expected from 'propagule biases' (see assumption #1 above), the most widespread NIS would be expected to have the greatest levels of enemy release, even though their success would be independent of this pattern. For example, studies of bird introductions have shown that species with larger native geographic range sizes are more likely to achieve

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larger range sizes at the location of introduction (Duncan et al. 1999, 2001, Williamson 2001).

A second confounding factor arises because species with more enemies are also more likely to have one or a few enemies with strong impacts. The remaining enemies may have very low impacts such that the statistical relationship is driven by the likelihood of having particular species of enemies rather than the number of co-occurring enemies *per se*. Similar arguments have been advanced to explain the relationship between species diversity and habitat productivity (Huston et al. 2000). A review by Denoth et al. (2002) concluded that the release of multiple biocontrol agents usually did not produce a cumulative effect, but increased the likelihood of introducing the 'right' control species.

To better explore the possibility of propagule biases, I examined nine recent (≥1995) studies that directly tested assumptions of the ERH (Table 1). Four of these studies contrasted populations of NIS in their native and introduced ranges, and thus represent a biogeographical-level analysis of NIS populations. Consistent with the ERH, each study found a significant reduction in either attack intensity (Wolfe 2002), or number of enemies (Fenner and Lee 2001, Mitchell and Power 2003, Torchin et al. 2003). Conversely, five studies examined resident native and nonindigenous species within a given region and thus represent a community-level analysis. These studies examined either the number of enemy species (Clay 1995) or the level of attack by enemies (Blaney and Kotanen 2001a, 2001b, 2002, Agrawal and Kotanen 2003). Contrary to the ERH, none of the community-level studies found any difference in the level of attack by or number of co-occurring enemies. Thus the ERH is supported at a biogeographical but not at a community level. This pattern is consistent with propagule biases on the number of enemies. Alternatively, nonindigenous species may have fewer co-introduced enemies at

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a biogeographical level, but without any translated release from attack at the community level. Either way, these results underscore the importance of understanding the complexity of interactions that can occur as a species leaves one community and becomes incorporated into another.

Alternative invasion scenarios

The process by which introduced species lose their enemies (i.e., bottlenecks during the invasion process) has other important implications at the community level for the success or failure of NIS. Below, I explore six alternative hypotheses expected to result from such bottlenecks (summarized in Table 2 and Fig. 2). It should be noted that of these hypotheses, only the EEH, EIH and EICAH (below) are truly alternate hypotheses to the ERH, though EICAH might also be considered a special case of the ERH.

Enemy of my Enemy Hypothesis (EEH)

The EEH takes its name from the proverb "the enemy of my enemy is a friend of mine" and predicts the converse effect of enemies on co-occurring NIS. Contrary to the ERH, nonindigenous enemies co-introduced with their hosts could have greater effects on native hosts in the introduced habitat. The introduction of more enemies could, therefore, increase the success of the original hosts by differentially affecting native species through apparent competition (Hoffman and Schubert 1984, Juliano 1998, Lafferty and Gerber 2002, Louda and O'Brien 2002; see Fig. 2). For example, introduced American crayfish (*Pacifastacus leniusculus*) carried a fungal parasite (*Aphanomyces astaci*) that wiped out most native crayfish populations in Europe (Reynolds 1988). Similarly, the on-going replacement of native red squirrels (*Sciurus vulgaris*) in the United Kingdom by

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introduced grey squirrels (*Sciurus carolinensis*) may be the result of enhanced vulnerability of the former to parapoxvirus introduced with the latter (Tompkins et al. 2003).

Through a special form of apparent competition, termed hyperpredation (Courchamp et al. 1999), a well-adapted prey might sustain an introduced predator population as the latter exerts pressure on naïve native species, potentially driving them to extinction. Such was the case when successive invasions of Guam brought the brown tree snake (*Boiga irregularis*) into contact with its co-evolved lizard prey, which facilitated the elimination of over a dozen endemic species of birds, reptiles and bats through intense predation (Fritts and Rodda 1998).

Facilitator Loss Hypothesis (FLH)

The FLH is based on a growing body of evidence linking mutualistic and commensalistic interactions with the success of NIS. Recent reviews indicate that positive interactions among NIS may be as or more important in determining invasion outcome than are classic biotic resistance mechanisms of the recipient community (Simberloff and von Holle 1999, Ricciardi 2001, Bruno et al. 2003). Additionally, Richardson et al. (2000b) stressed the importance of pollinators, seed dispersers, mycorrhizal fungi, and nitrogen-fixing bacteria to the invasion success of plants. Mechanisms responsible for introduction of fewer co-introduced enemies can, at the same time, result in fewer co-introduced facilitators. The overall success of NIS will depend on the trade-off between the positive effects of losing enemies versus the negative effects of losing facilitators.

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Enemy Inversion Hypothesis (EIH)

Having been released from many of the complex, multi-species interactions from their native region, the inversion hypotheses predict that co-introduced species (i.e., enemies or facilitators) will have an opposite net effect on their host species between its native and introduced ranges. Such an effect might arise through subtle, indirect pathways owing to complex species interactions in the new community. In one spectacular case, Pearson et al. (2000) found that larvae of two gall flies (*Urophora affinis and U. quadrifasciata*), introduced to control spotted knapweed (*Centaurea maculosa*), became a favoured meal of native deer mice (*Peromyscus maniculatus*), accounting for up to 84-86% of their diet. Mice consumed *Urophora*, reducing their effect to a level insufficient to adequately control *Centaurea*. Furthermore, because *Urophora* larvae inhabit *Centaurea* flower heads, *Peromyscus* inadvertently consumed fair numbers of *Centaurea* seeds, providing a novel mechanism of local dispersal by the invasive plant (Pearson et al. 2000). Amazingly, Pearson and Ortega (2001) later found viable *Centaurea* seeds in the pellets of Great Horned Owls (*Bubo virginianus*) that had apparently preyed upon *Peromyscus*, thereby providing a novel mechanism for long-distance dispersal by *Centaurea*. Although *Peromyscus* in this example acts as a facilitator, it can still be argued that the *Urophora* species have an indirect, but net positive effect on *Centaurea* in the introduced range, despite being a "well-behaved" biocontol agent (Pearson et al. 2000).

Facilitator Inversion Hypothesis (FIH)

The FIH predicts that invasive species fail because facilitators reverse their effects on their co-introduced hosts. I know of no studies to support the FIH, but it is essentially the reverse situation of the EIH. Moreover, examples supporting the FIH would be expected

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primarily where a nonindigenous population was less successful (i.e., had lower fitness) than its native source, thereby decreasing the chance of establishment. Since populations that fail to establish are rarely studied (Kolar and Lodge 2001), failure to find evidence for the FIH may not be surprising. Given the complexity associated with species interactions, such as the EIH example above, patterns of facilitator inversion are expected.

Increased Susceptibility Hypothesis (ISH)

The ISH predicts that when invasion bottlenecks limit the genetic diversity of polymorphic defences (e.g., recognition sites of the major histocompatibility complex), enemies will have disproportionate effects on introduced populations as compared to more genetically diverse native ones. Thus, factors reducing the number of co-evolved enemy species could also result in higher prevalence of enemies that are successfully co-introduced. Genetic bottlenecks due to founder effects have been identified in some NIS (Tsutsui et al. 2000, Grant et al. 2001), but not others (Holland 2001). Additionally, under a mechanism similar to the EEH (above), NIS represent naïve hosts to native enemies, which can result in profound effects from native enemies, that could be further confounded by the loss of polymorphic defences (e.g., Creed and Sheldon 1995). Nonindigenous populations would therefore be subjected to greater enemy effects than the source population even though it would involve a smaller complement of enemy species. I am not aware of any studies that have looked at the possibility of increased susceptibility. However, Torchin et al. (2003) noted that several NIS had higher prevalence levels for enemies found in both native and nonindigenous ranges, although this difference varied by host.

Evolution of Increased Competitive Ability Hypothesis (EICAH)

The EICAH is quite similar to the ERH but argues for an evolutionary rather than phenotypic response to enemy release (Blossey and Nötzold 1995). In plants, the EICAH has been favoured over the ERH for purple loosestrife (*Lythrum salicaria*) based on growth comparisons for native and nonindigenous populations grown under comparable conditions (Blossey and Nötzold 1995). However, similar experiments found little or no evidence for a number of other plant species (Willis et al. 2000, Leger and Rice 2003). The patterns consistent with the EICAH (e.g., size increase) may be further complicated by propagule biases during introduction. If introduced genotypes are chosen non-randomly or are imported from one or a few populations with divergent phenotypes, then introduced populations may be phenotypically different from native populations, independent of competitive interactions or other evolutionary mechanisms. For example, increased height among some nonindigenous plants may owe more to deliberate or inadvertent importation of large phenotypes – and presumably genotypes – than to the evolution of better competitive ability. If this were the case, increased size of individuals in nonindigenous relative to native populations would result from propagule bias rather than enemy release. Thébaud and Simberloff (2001) found that some species tended to be larger in their introduced ranges, while others were smaller, with no trend either way. Grosholz and Ruiz (2003) found evidence for a trend towards increased size in marine and estuarine invertebrate invaders, but were unable to identify the mechanism responsible for the pattern. However, enhanced size could represent a plastic response to enemy release (i.e., as predicted by the ERH). Identification of invasion pathways

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(MacIsaac et al. 2001) could help to identify source populations to allow for tests of propagule biases.

Conclusion

The idea that invasive species have few or no enemies, thereby granting NIS an "unfair advantage" over native species, is so intuitively appealing that it has flooded the popular media (Chew and Laubichler 2003). As I have shown, numerous examples exist to support the assertion that enemies can have profound effects on the populations of their hosts. Despite the growing popularity of the enemy release hypothesis, potential biases in apparent patterns of enemy release, combined with myriad possible species interactions, suggest a complex relationship between the number of enemies and the invasiveness of their hosts. Therefore, I caution against acceptance of the ERH without consideration of the entire invasion process and analysis of the mechanisms underlying invasion success. Even if NIS lose enemies during colonization events, a number of alternative scenarios, including the loss of co-evolved facilitators, of enemies that have greater effects on competing species, of species that switch allegiance, and of genetic diversity and its associated immunological response capability, render the balance unpredictable given our current knowledge.

TABLE 1. A list of recent studies that test assumptions of the Enemy Release Hypothesis (ERH).

Reference	Contrast Type	Characteristic Examined
Support the ERH		
Fenner and Lee 2001	Biogeographical	Diversity of seed predators on *Asteraceae*
Mitchell and Power 2003	Biogeographical	Diversity of viral and fungal pathogens on plant species
Torchin et al. 2003	Biogeographical	Diversity of parasites on animal species
Wolfe 2002	Biogeographical	Attack by aphids, fungal pathogens, herbivores and fruit predators on *Silene latifolia*
Do not support ERH		
Clay 1995	Community	Diversity of fungal pathogens on grass species
Blaney and Kotanen 2001a	Community	Attack by fungal pathogens on plant species
Blaney and Kotanen 2001b	Community	Attack by seed predators on plant species
Blaney and Kotanen 2002	Community	Attack by seed predators and fungal pathogens on plant species
Agrawal and Kotanen 2003	Community	Attack by leaf herbivores on plant species

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TABLE 2. Scenarios resulting from bottlenecks during the invasion process. Hypotheses predict either positive (+) or negative (-) effects on nonindigenous relative to native host populations. Some references relevant to each hypothesis are given.

Hypothesis	Effect	References
ERH (Enemy Release Hypothesis)	+	Hoffman and Schubert 1984, Hudson et al. 1998, Fenner and Lee 2001, Torchin et al. 2001, Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003; but see Clay 1995, Blaney and Kotanen 2001a, 2001b, 2002, Agrawal and Kotanen 2003, Poulin and Mouillot 2003
EEH (Enemy of my Enemy Hypothesis)	+	Hoffman and Schubert 1984, Reynolds 1988, Juliano 1998, Lafferty and Gerber 2002, Louda and O'Brien 2002, Tompkins et al. 2003
FLH (Facilitator Loss Hypothesis)	-	no direct tests; but see Simberloff and von Holle 1999, Richardson et al. 2000b, Ricciardi 2001, Bruno et al. 2003
EIH (Enemy Inversion Hypothesis)	+	Pearson et al. 2000
FIH (Facilitator Inversion Hypothesis)	-	no direct tests; feasible given EIH

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TABLE 2 (continued)

ISH (Increased Susceptibility Hypothesis)	–	only some species in Torchin et al. 2003; circumstantial evidence from host-switching: Clay 1995, Creed and Sheldon 1995, Maron and Vilà 2001, Agrawal and Kotanen 2003, Keane and Crawley 2002
EICAH (Evolution of Increased Competitive Ability Hypothesis)	+	Blossey and Nötzold 1995; but see Willis et al. 2000, Leger and Rice 2003

FIGURE. 1. Mechanisms of apparent and realized enemy release. From right to left,

subsampling of the biogeographic region (source region filter), and of the actual

source population (colonist subsample filter) result in an 'apparent' reduction in

enemies (E_{1-40}) with no effect on host fitness. Transport of a subsample of enemies

(transport uptake filter) that may experience mortality during transport (transport

survival filter) or establishment (establishment filter) results in a 'realized' reduction

in enemies that does lead to increased fitness. Host switching by native enemies (N_{E1-12})

in the introduced range can counteract the effects of 'realized' enemy release,

while still maintaining a pattern of 'apparent' release.
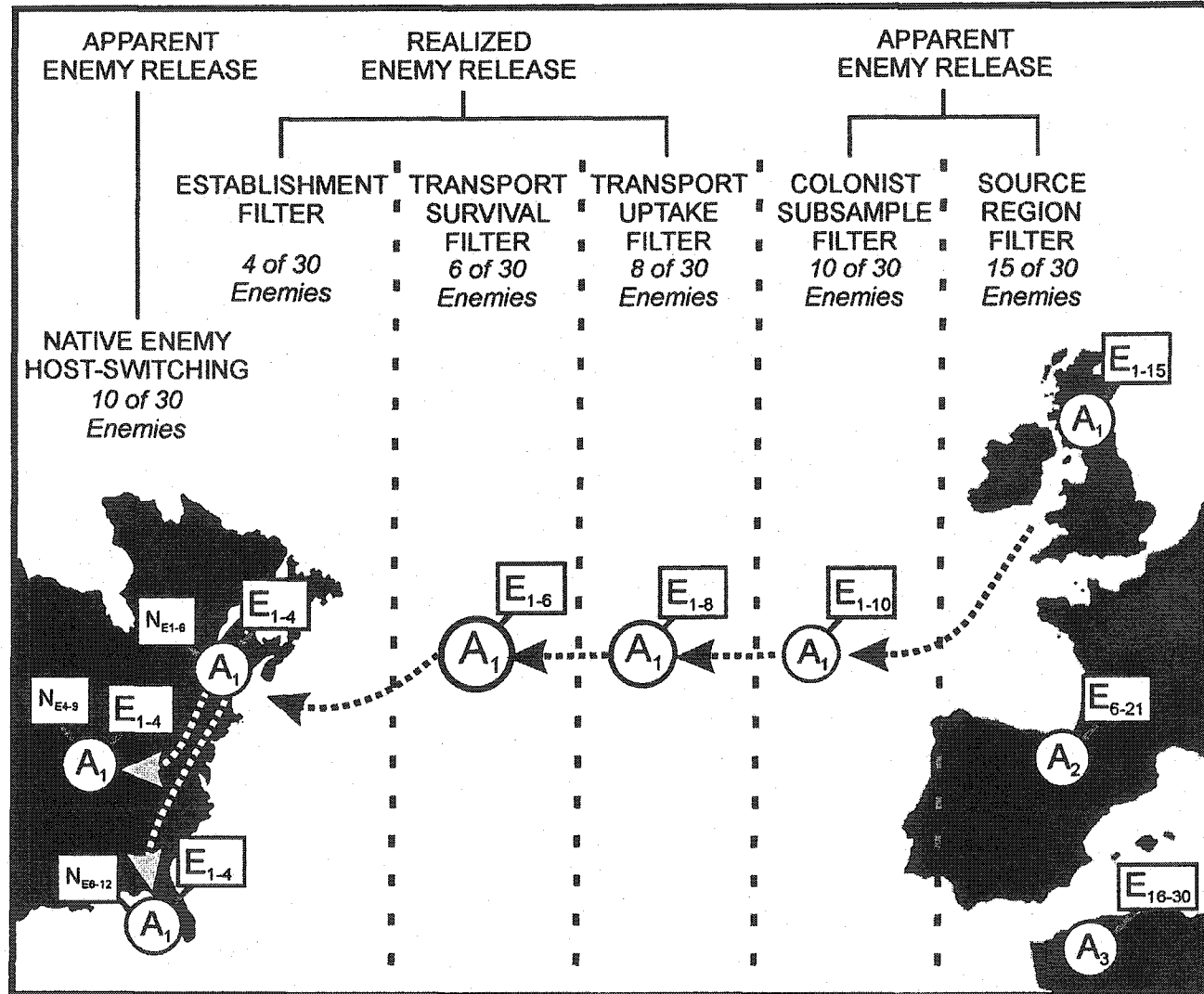
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FIGURE 1

FIGURE. 2. Alternative scenarios for the success or failure of nonindigenous species (NIS). Filters acting during the invasion process reduces the number of species of natural enemies (E_{1-40}) and facilitators (F) available to colonize a new area with host species A (right side). These bottlenecks may result in one of six scenarios for introduced populations (left side): ERH/EICAH – a reduction in the number of enemies leads to increased fitness of A; EEH – host switching by introduced enemies results in decreased vigour of native competitors (N) and proliferation of A; EIH – disruption of complex species interactions reverses the role of enemies, possibly through interactions with native species (N); FLH – loss of facilitators decreases the vigour of A; FIH – disruption of complex species interactions reverses the role of facilitators, possibly through interactions with native species (N); ISH – strong effects by a few introduced enemies (E_{1-2}) and by some of those already present (N_E) decreases the vigour of A. Relative population responses by invading species A and native species N are denoted by size of the corresponding circles. Strength of negative (-) and positive (+) species interactions are indicated by size of the interaction circles. See text for definitions and examples of interaction acronyms.

FIGURE 2
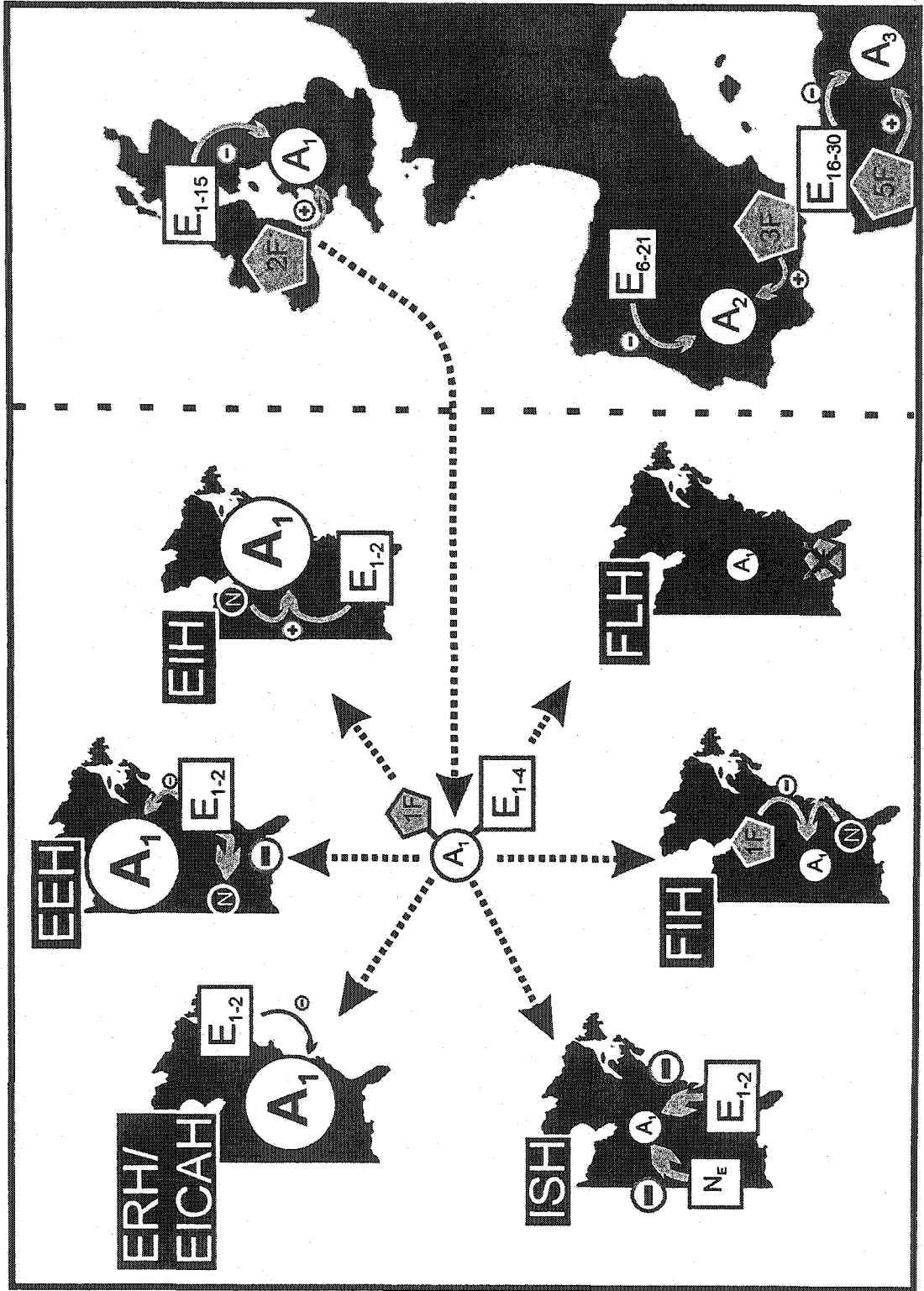
Chapter 5

Microsatellite loci reveal genetic paucity in the invasive Onychopod

Bythotrephes longimanus (Leydig)

Abstract

The Eurasian spiny waterflea (*Bythotrephes longimanus*) is a prolific, voracious zooplankter that is rapidly invading inland waterbodies throughout the Laurentian Great Lakes region. I isolated microsatellite DNA loci to discriminate among nonindigenous populations of *Bythotrephes* in North America. I screened a total of 78 primers from 24 loci, none of which showed polymorphisms among 18 individuals from nine populations, including one population from its native range in Eurasia. These results, combined with previous allozyme and mitochondrial DNA research suggest that *Bythotrephes* may represent a genetically depauperate, yet highly successful invader. If so, this species' invasion pattern in the Great Lakes and in inland lakes in Ontario illustrate that high genetic diversity is not a prerequisite for successful invasion. It remains unclear whether low genetic diversity is a cause or consequence of successful biological invasions in Bythotrephes.

Introduction

The predatory Onychopod *Bythotrephes longimanus* is a widespread Palearctic species with an invasion history in Western Europe (Ketelaars and Gille 1994). A *cederstromi* form of *B. longimanus* has also been described, and is easily identified by a kink in the caudal process. The *cederstromi* form was initially considered as a distinct species, although it is found in sympatry with the *longimanus* form (see Grigorovich et al. 1998). However, recent genetic evidence supports a view that the two forms represent phenotypes of a single species, *Bythotrephes longimanus* (Berg et al. 2001, Therriault et al. 2002). *Bythotrephes* likely established in Great Lakes around 1982 (Johannsson et al. 1991), and has since spread to 55 lakes in Ontario, Canada (Therriault et al. 2002;

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MacIsaac et al. 2003). To date only the *cederstromi* form of *B. longimanus* occurs regularly in North America, although some animals lacking caudal process kinks are found occasionally.

The rapid spread of *Bythotrephes* throughout inland lakes in Ontario owes partly to three key life history characteristics. First, *Bythotrephes* reproduces parthenogenetically, allowing for rapid proliferation at low population density. Second, a long, barbed caudal process tends to get snagged on fishing tackle and boat equipment, resulting in dense clusters of organisms that may be moved among lakes. Finally, dormant resting eggs are produced as a result of sexual reproduction. These resting eggs are able to survive extended periods of desiccation or ingestion by fish or birds (Grigorovich et al. 1998, Jarnagin et al. 2000), thereby facilitating the long distance survival of propagules fouled on fish lines or other boat-related equipment.

The close association between recreational watercraft movement and *Bythotrephes* invasions in Ontario was demonstrated by MacIsaac et al. (2003). Using gravity models of boater movement, the authors were able to significantly predict the likelihood of invasion for several lakes in Ontario (Fig. 1). Based on the 'propagule pressure' paradigm outlined in chapter 2, the model by MacIsaac et al. (2003) should represent a null model for the invasion of Bythotrephes. My intention here is to use genetic markers to assess the relatedness of *Bythotrephes* populations in different Ontario lakes, and to compare these patterns with inter-lake movement of boaters developed in the MacIsaac et al. (2003) study. Having such a detailed, independent model of colonization could greatly improve our understanding of population-level genetic processes in natural systems, and allow a direct test of the vector-based (i.e. 'propagule pressure') dispersal model.

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Microsatellite DNA markers are non-coding regions of DNA containing a number of repeating motifs of 2 to 6 base pairs (bp) in length. They have been found in every organism examined thus far (Zane et al. 2002), and occur throughout the eukaryotic genome in humans and mice (Dib et al. 1996, Dietrich et al. 1996). Mutations occur often as replication slippage in the duplication of microsatellite DNA, thereby adding or deleting one or more repeat segments (Schlötterer and Tautz 1992). The resulting polymorphisms can be easily separated for identification using gel electrophoresis. Microsatellite loci require a great deal of effort to develop, but hold a number of advantages over other markers: First, they are generally non-coding and are thus less likely prone to direct selection than are mitochondrial DNA or allozyme loci (Wright and Bentzen 1994). Second, microsatellite analysis is a PCR-based procedure, thereby requiring only the minute amounts of DNA available from small organisms like *Bythotrephes*. Third, microsatellite markers are co-dominant, allowing for greater statistical resolution than dominant markers such as random amplified polymorphic DNA (RAPD) or amplified fragment length polymorphisms (AFLPs). Finally, their high mutation rate results in high levels of polymorphism that can be used to discriminate between closely related populations (Beaumont and Bruford 1999). My goal is to develop a number of microsatellite loci for *Bythotrephes* to allow for the resolution of genetic substructure among North American populations.

Methods

Whole genome DNA was extracted from eight individual *Bythotrephes* from Shebandowan Lake, Ontario, using Promega's Wizard Kit®. The microsatellite isolation protocols that I used followed Hamilton et al. (1999), with modifications from O'Reilly et

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al. (2000). These protocols require approximately 16ug of genomic DNA, so DNA extracted from all eight individuals was combined and precipitated using a standard salt precipitation procedure (60% NaOAc + 110% Isopropanol, see Sambrook et al. 1989). I conducted separate enrichment procedures using $(GACA)_4$, $(AAAT)_4$, $(AGAT)_4$, $(AC)_8$, $(ATT)_4$, and $(AGC)_4$ probes. After running a double-stranding PCR on these tubes, I eliminated the AAAT- and ATT-enriched tubes because DNA enriched with these probes failed to amplify the desirable size range of DNA fragments. Enriched DNA was purified using micron PCR centrifugal filter tubes (Millipore), and transformed it into One Shot® *E. coli* cells using a TOPO TA Cloning® Kit (Invitrogen) or using a Promega® pGEM-T Vector System I with Promega®'s competent cells.

All *E. coli* were plated on LB agar plates prepared using protocols from Sambrook et al. (1989), containing 100ug/ml ampicillin, and covered with 100µl of 100mM IPTG and 20µl of 50mg/ml X-Gal. Plasmids from the transformed colonies were sub-cloned, isolated using an alkaline-lysis extraction protocol (Sambrook et al. 1989) and sequenced using a Beckman Coulter CEQ 8000 Genetic Analysis System. To increase signal strength, I sequenced PCR product from plasmids that had been amplified (30 cycles with a 58°C annealing temperature) using M13 F (5'-TTG TAA AAC GAC GGC CAG T-3') and R (5'-GGA AAC AGC TAT GAC CAT G-3') primers. To reduce stutter caused by the amplification of repetitive DNA, I included 1mM Betaine (Promega) in each reaction. Sequencing reactions were generally done using M13 F except where ambiguity was encountered, in which case clones were again amplified using M13 F and R, but sequenced using M13 R. All sequencing was performed according to protocols provided by Beckman Coulter, using 1/2, 1/4 or 1/6 reactions.

Primer design and testing

Primers for the inserted DNA were designed using the internet-based software Primer3 (Whitehead Institute for Biomedical Research) and NetPrimer (Premier Biosoft®). The inserted DNA, minus the SNX primers were analyzed for repeats, either visually, or using Alex Dong Li's RepeatFinder (http:// www.genet.sickkids.on.ca/ ~ali/ repeatfinder.html). Inserts with more than three repeats of two to eight base pairs were copied into Primer3 to create forward and reverse primers flanking the repeating region of interest. Suggested primers were then evaluated with NetPrimer for secondary structure and formation of primer-dimer. Primers with little internal structure and low propensity to form dimers were ordered from IDT® or Sigma-Aldrich®.

Each primer pair was first tested with DNA from four or eight individuals in addition to negative (no DNA) and positive (clone plasmid DNA) controls. I used a PCR gradient (PTC-225, MJ Research) of four to six temperatures ranging from 12°C below to 5°C above the calculated primer melting temperature (as calculated by the primer manufacturer). In this way, an optimal annealing temperature was determined for each primer pair. If primers did not amplify the positive control, either one, or two new primers were ordered. Primers that successfully amplified were used in a second PCR using DNA from 18 individuals from nine different populations (including one population from the Rybinsk Reservoir, Russia). Limited material precluded the testing of primers on more than two individuals from its native range. Reactions were run on either a PTC-225 or PTC-100 (MJ Research) PCR machine with the following program: 94°C for 2 minutes, followed by 35 cycles of 94°C for 1 minute, optimal melting temperature for the particular primer for 1 minute, and 72°C for 90 seconds. These 35 cycles were followed

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by a final 5-minute step at 72°C and stored at 4°C. From this product, 10 μl were run on a 2% high-resolution agarose gel with EtBr for 90-120 minutes to look for polymorphisms.

Results

A total of 204 transformed colonies were subcloned, of which 23 failed to amplify a single band with M13 F and R (likely owing to an error during plasmid isolation) and were discarded. Of the 181 fragments that amplified, 37 contained inserts <150 bp and were thus not retained for sequencing. Only 7 sequences contained no 'useful' repeating sequences (i.e., at least three consecutive copies of a two to eight base-pair motif).

Primer design and testing

A total of 82 primers from 24 clones were developed and tested for polymorphisms, but 4 of these did not produce at least one band, and one pair was redundant (Table 1). Not a single heterozygote was observed for any of the 24 loci. Some primers produced multiple bands at some temperatures, but these bands were likely due to mispriming or pseudo-genes, as they did not consistently produce 1 or 2 clear bands at any temperature (Table 1). Some primers that amplified products <200 bp were prone to contamination (i.e., bands of equal size appeared in the negative control).

Discussion

The lack of polymorphism among the 24 microsatellite loci examined in this study precludes a test of the 'propagule pressure'-based model by MacIsaac et al. (2003). However, these findings suggest a dearth of genetic variability in introduced populations of *Bythotrephes*. For example, several of the isolated loci, particularly Blo 4, 25, 26, 31,

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33, 65, 115, and 158 (Table 1), contain repeat numbers similar to microsatellite loci that have been found to be variable in *Daphnia* (Ender et al. 1996), but smaller than those reported for *Farfantenaeus notialis* (Robainas et al. 2002). Given that mutation rate, and therefore the expected level of polymorphism, increases with repeat size (Schlötterer and Tautz 1992), failure to find variation at even one of these six loci suggests a genetic bottleneck for this species.

Only four studies have examined the genetics of *Bythotrephes*, all of which include populations in North America. Of 18 allozyme loci sampled in Weider (1991), Berg and Garton (1994), and Berg et al. (2001), only four were polymorphic (i.e., occurrence of the most common allele was <0.95): phosphoglucomutase (PGM), peptidase-1 (PEP-1), malic enzyme (ME), phosphoglucose isomerase (PGI). Of these, PGI and ME were polymorphic in one study (Berg and Garton 1994) but not another (Berg et al. 2001). Thus it is appears that the heretofore examined populations of *Bythotrephes* are genetically depauperate, at least with respect to nuclear markers. Unfortunately, all of these studies examined populations from North America or areas adjacent to the Baltic Sea -- the putative source of North American populations (Berg and Garton 1994, Berg et al. 2001).

Therriault et al. (2002) found multiple mitochondrial DNA haplotypes at the COI region in samples of *Bythotrephes* from more eastern and southern locations in Europe. Only a single haplotype was identified in five individuals from Lake Ontario and Lake Simcoe, however this haplotype was shared with two individuals from Lake Puruvesi, Finland. Other European populations of *Bythotrephes* showed deeper divergence of COI haplotypes. However, no studies have examined nuclear markers for *Bythotrephes* from more isolated areas of Eurasia. It is not known whether this pattern holds across the rest

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of *Bythotrephes'* native range. It is possible, for example, that populations near the Baltic Sea may themselves be nonindigenous, even though they have been historically present (Ketelaars and Gille 1994). Alternatively, genetic paucity at nuclear loci may be characteristic of this species, with polymorphic mtDNA haplotypes representing ancestral variation. Testing of the microsatellite loci published here on more isolated, native populations will allow for discrimination between these two hypotheses. However, low genetic diversity of introduced populations is consistent with the pattern of mtDNA seen in *Bythotrephes'* closest relative, *Cercopagis pengoi* (Cristescu et al. 2001). Populations of this species in North American and the Baltic Sea contain only a single COI haplotype, even though 7 haplotypes are found near the Black Sea.

It is interesting to contrast the patterns of genetic paucity observed in introduced populations of *Bythotrephes* and *Cercopagis* with the high genetic diversity found in Great Lakes' populations of *Dreissena* species (Marsden et al. 1996, Stepien et al. 2002) and *Neogobius melanostomus* (Dillon and Stepien 2001). Both *Dreissena* and *N. melanostomus* were likely established in the Great Lakes several years after *Bythotrephes*. All species represent rapidly spreading, prolific invaders in the Great Lakes, yet the genetic architecture (i.e., additive genetic variance) available for selection in these species represents two surprising extremes.

Genetic bottlenecks have been found in many successful invaders (Tsutsui et al. 2000, Cristescu et al. 2001, De Meester et al. 2002, Hänfling et al. 2002, Müller et al. 2002; but see Holland 2001, Stepien et al. 2002). Although genetic bottlenecks are likely the result of circumstances underlying invasions (e.g., founder effects, selection for particular genotypes, etc.), reduction in genetic variability can have important consequences. For example, reduced genetic variability has been implicated in the

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success of the highly invasive Argentine ant *Linepithema humile*. The rapid spread and numerical dominance by this species has been related to a reduction in inter-colonial aggression as a result of the genetic similarity among introduced populations (Tsutsui et al. 2000). Thus, reduced genetic variability may be a cause of invasion success as well as a consequence of invasion circumstance.

It is not known whether the genetic paucity seen in introduced populations of *Bythotrephes* and *Cercopagis* is at least partially responsible for their success in the Great Lakes. One possibility is an invasion by particular genotypes that are somehow well adapted to spread to, and/or establish in, novel habitats (i.e., an 'invasive genotype'). Saltonstall (2002) found evidence for a cryptic invasion by an invasive genotype of *Phragmites australis* across North America. Invasion by *Bythotrephes* may likewise represent colonisation by an invasive genotype. Alternatively, founder effects during *Bythotrephes* invasion could represent a propagule bias, such that low genetic diversity is merely a consequence, not a cause of invasion. Nevertheless, understanding the consequences of genetic bottlenecks on invasion success remains an important avenue for future research.

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TABLE 1. Characterization of microsatellite primers screened for variability among 16 individuals. Four primers that did not amplify any product are excluded. (*) Blo 22 was a redundant locus with Blo 33. (†) Primers amplified more than two bands at some temperatures, likely due to mispriming or pseudogenes.

Manufacturer	Primer Name	Sequence (5'-3')	Tm	Repeat Motif
Sigma	Blo 4-F	CGC ACG TCT GTC TGT CTT TC	63.7	$(GTCT)_3(N)_2(CTGT)_6(N)_{56}(TG)_7$
Sigma	Blo 4-R	GGC GGA AAT ATG CAA ATC AT	63.4	$(GTCT)_3(N)_2(CTGT)_6(N)_{56}(TG)_7$
Sigma	Blo 7-F[†]	AGC GAG CGT ACG CAG ACA	66.1	$(CAGA)_3(N)_{12}(GACA)_5$
Sigma	Blo 7-R[†]	GCT ATC ACA TTC GGG GTG AG	64.3	$(CAGA)_3(N)_{12}(GACA)_5$
IDT	Blo14 Di/Tetra-F	GAA GGC CCG ACG GTT GA	57.9	$(CA)_3(N)_{12}(CA)_3(N)_{26}(CAGA)_4CA(CAGA)_3$
IDT	Blo14 Di/Tetra-R	AGG ATG TGC TGT GAT TGT GC	56.9	$(CA)_3(N)_{12}(CA)_3(N)_{26}(CAGA)_4CA(CAGA)_3$
IDT	Blo14-F di	CAA TGC GGT TTG AAG TGG	52.7	$(CA)_3(N)_{12}(CA)_3$
IDT	Blo14-R di	CCC GAC GGT TGA TTA AAC A	53.6	$(CA)_3(N)_{12}(CA)_3$
IDT	Blo14b-F[†]	GGA TGT GCT GTG ATT GTG C	55.3	$(CAGA)_4CA(CAGA)_3$
IDT	Blo14b-R[†]	TCA AAC CGC ATT GAT ATT CA	51.3	$(CAGA)_4CA(CAGA)_3$
IDT	Blo20 Tetra-F	TTC CAA ATT TCT TTC CGA GGT	53.8	$GTCTGTTT(GTCT)_3$
IDT	Blo20 Tetra-R	CCT TAG CTC AAT CAA TTG CT	51.7	$GTCTGTTT(GTCT)_3$
Sigma	Blo21-F	GGC AAA TTC AAG TTG GCA CT	63.9	$(AGAC)_5$

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TABLE 1 (continued)

Sigma	Blo21-R*	AAC ACT CGG TCG AAC ATT CC	63.9	$(AGAC)_5$
IDT	Blo22-F*	GAG CCT GGG AGG AGG TTG A	61.6	$(GACA)_{10}GATAATAAGAGAGT(GA)_{10}$
IDT	Blo22-R*	GCA CAA GCC CAT AGC CTC TC	59	$(GACA)_{10}GATAATAAGAGAGT(GA)_{10}$
IDT	Blo22-R*	TCT CTC TCT TAT TAT CTG	41.8	$(GACA)_{10}$
IDT	Blo24-F	CTA GCA GAA GCA TCG ACG AAC	56.7	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo24-F	CGA CGA ACA GGC AGA CTG A	57.8	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo24-F tetra	TTG CTA GCA GAA GCA TCG AC	56.2	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo24-R	TTG TCA TCT GTC TGT CTG CCT G	58.2	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo24-R	GCT TGT TTG TCT GTC ATC TGT G	55.6	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo24-R tetra	TCT TCT GCC TGT TTG TCG TC	56.1	$(CAGA)_3/(N)_{18}/(AGAC)_2$
IDT	Blo25 150-F	ACA GTG AAA CAA GCA CGT TG	55.2	$(CTGT)_{11}$
IDT	Blo25 150-R	TGT TCT CCG ACC GAC TCT TC	57.1	$(CTGT)_{11}$
IDT	Blo25 220-F	ACA GTG AAA CAA GCA CGT TG	55.2	$(CTGT)_{11}$
IDT	Blo25 220-R	TGC ACC ACT TTA TTC CCA TGT	56.1	$(CTGT)_{11}$
IDT	Blo25 290-F[†]	ACA GTG AAA CAA GCA CGT TG	55.2	$(CTGT)_{11}$
IDT	Blo25 290-R[†]	GCT AGC AGA AGC GCA AAG AT	56.9	$(CTGT)_{11}$
IDT	Blo26-F	CTT GAT GTG AGC CCA TTG A	53.5	$(CTGT)_7$

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TABLE 1 (continued)

IDT	Blo26-F	TGT ACA TTC ATG CAA TTT TTA TTC A	52	$(CTGT)_7$
IDT	Blo26-R	ATG TTT CCC TGT TAT CTT GAA GT	53.8	$(CTGT)_7$
IDT	Blo26-R	CAT GTT TCC CTG TTA TCT TGA AGT	54.8	$(CTGT)_7$
IDT	Blo29 111-F	AGC TTA TTA CGG TCT TTA ATT ATT ACT	52.4	$(TGTCTGCC)_6$
IDT	Blo29 129-F	AGC AAT AGC AAA CAC TCT AGC	54.2	$(TGTCTGCC)_6$
IDT	Blo29-F	GAA GCA GCA ATA GCA AAC AC	53.6	$(TGTCTGCC)_6$
IDT	Blo29-R	GCA GAA GCA GAC AGA CAG AC	56.4	$(TGTCTGCC)_6$
IDT	Blo29-R	AGA CAG ACA GAC AGG CAG	54.3	$(TGTCTGCC)_6$
Sigma	Blo31 105-F	TGA AGT ATC ACC TGA AAG ACT TG	53.9	$(TCTG)_4(N)_{35}(CTGT)_5$
IDT	Blo31 120-F	CCT GCA TTC ACT AAC TGA AGT ATC A	56.4	$(TCTG)_4(N)_{35}(CTGT)_5$
IDT	Blo31-F	GTG TCT GTC TTT ATT TCT CTC TG	52.2	$(TCTG)_4(N)_{35}(CTGT)_5$
IDT	Blo31-R	TGA GAC GAG TAG GCA AGA CA	56.3	$(TCTG)_4(N)_{35}(CTGT)_5$
Sigma	Blo31-R	AGA GGC AGA CAG AGA GAA ATA AA	54.9	$(TCTG)_4(N)_{35}(CTGT)_5$
IDT	Blo33 100-R*	CGA CTC ATC CAG CGT GTG	56.2	$(GACA)_9(N)_{16}(GA)_{10}$
IDT	Blo33 125-R*	CCT AAA CCA TCC TCT TCG TG	53.5	$(GACA)_9(N)_{16}(GA)_{10}$
IDT	Blo33-F*	CAG AAG CCC ATA GGC TCA TA	54.8	$(GACA)_9(N)_{16}(GA)_{10}$
IDT	Blo33-F*	AGT AAG CGC ACA AGC CCA TA	58	$(GACA)_9(N)_{16}(GA)_{10}$

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TABLE 1 (continued)

IDT	Blo33-R*	ACC TAA ACC ATC CTC TTC GTG	55.4	$(GACA)_9(N)_{16}(GA)_{10}$
IDT	Blo34 b-F	CAA CGC TGG CGG TAA TTG	55.2	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo34 b-R	TCC CTT TAA ATA GCC CGA ATG	53.8	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo34-F	GTA ATT GGA CCG TGA ATG ACA	54.1	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo34-F	GGT AAT TGG ACC GTG AAT GA	53.5	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo34-R	GCC CGA ATG TAT CAA CTG G	54.1	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo34-R	CTT CCC TTT AAA TAG CCC GAA T	54.1	$GTTT(GTCT)_3(GTTT)_2$
IDT	Blo35 Tetra-F	CTT CCC TTT AAA TAG CCC GAA T	54.1	$(CAAA)_3(CAGA)_3CAAACAGA$
IDT	Blo35 Tetra-R	CGG TAA TTG GAC CGT GAA TG	54.7	$(CAAA)_3(CAGA)_3CAAACAGA$
Sigma	Blo38-F	TGA TGT GGA TGG CAT GTT TT	63.8	$(GACACACA)_2(N)_{17}(GACA)_2$
Sigma	Blo38-R	TCT GTC TAT ACT GTC TGC TTG TCA G	61.4	$(GACACACA)_2(N)_{17}(GACA)_2$
IDT	Blo42-F	CCG CTA GGA CAA CAG AAC AA	55.9	$(CTGT)_9$
IDT	Blo42-R	ATC TGT CCG TCC GTT CGT	56.7	$(CTGT)_9$
IDT	Blo58 119-F[†]	GAG AAG TAG CAG CGG CAT C	56.4	minisat? - $(TCAACAGCAGCAGCA)_3$
IDT	Blo58 119-R[†]	GCA CTG CTG TTG CTG ACG	57.7	minisat? - $(TCAACAGCAGCAGCA)_3$
IDT	Blo58 143-F	ACA GCA GTA TTA CCA GTC CCT GA	59	minisat? - $(TCAACAGCAGCAGCA)_3$
IDT	Blo58 143-R	TAG CCT GCT GTT GCT GAC G	58.5	minisat? - $(TCAACAGCAGCAGCA)_3$

TABLE 1 (continued)

Sigma	Blo65-F	CAC GAC ACG ACG CGA CAC G	67.7	$(GACAG)_{10}$
Sigma	Blo65-R	CTG GCT AGC AGA GGC TG	63.9	$(GACAG)_{10}$
IDT	Blo75 57-R	TCC GTT TGA TCC TGT TGT TG	54.3	$(AGC)_5$
IDT	Blo75-F	GCA GTA GCA GCA GCA GTA GC	59.3	$(AGC)_5$
IDT	Blo90 216-F[†]	GTT GCC TGA TAC CGA CGA AG	56.5	$(GTT)_3(GCT)_8(GTT)_3(GCT)_5T(GTT)_2(GCT)_3GTT$ $(GCT)_3(GTT)_3GCT$
IDT	Blo90 216-R[†]	AAT CGG AAT CAG CAG CAA GT	56.1	$(GTT)_3(GCT)_8(GTT)_3(GCT)_5T(GTT)_2(GCT)_3GTT$ $(GCT)_3(GTT)_3GCT$
Sigma	Blo115-F	CTCCATCTTCCATCCATCCAT	65.9	$(CATC)11$
Sigma	Blo115-R	GGATGGATGGATGGAGGATAG	64.2	$(CATC)11$
IDT	Blo121 234-R[†]	CCA CCA CAA CGG ATG G	53	$(GCAACA)7GTAACA(GCAACA)4GCGACA$ $(GCAACA)8$
IDT	Blo121-F[†]	CAG CAG CAG CAA CAG CAA C	58.6	$(GCAACA)7GTAACA(GCAACA)4GCGACA$ $(GCAACA)8$
IDT	Blo158 118-F	GCC AGG GCG TAG GAA TTA TG	56.3	$(GTT)4(GGT)7(GCT)4(GGT)2(GCT)4$
IDT	Blo158 118-R	AGC ACC TTC ATC ACC AGC A	57.9	$(GTT)4(GGT)7(GCT)4(GGT)2(GCT)4$

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Figure 1. Putative sequence and sources of Ontario inland lake invasions by *Bythotrephes*

longimanus between 1989 (left side) and 2001 (right side) taken from MacIsaac et al.

(2003). The magnitude of an invasion vector is directly related to arrow thickness.

This vector-based model represents measurements of migration that could be

contrasted with genetic calculations of gene flow.

Figure 1
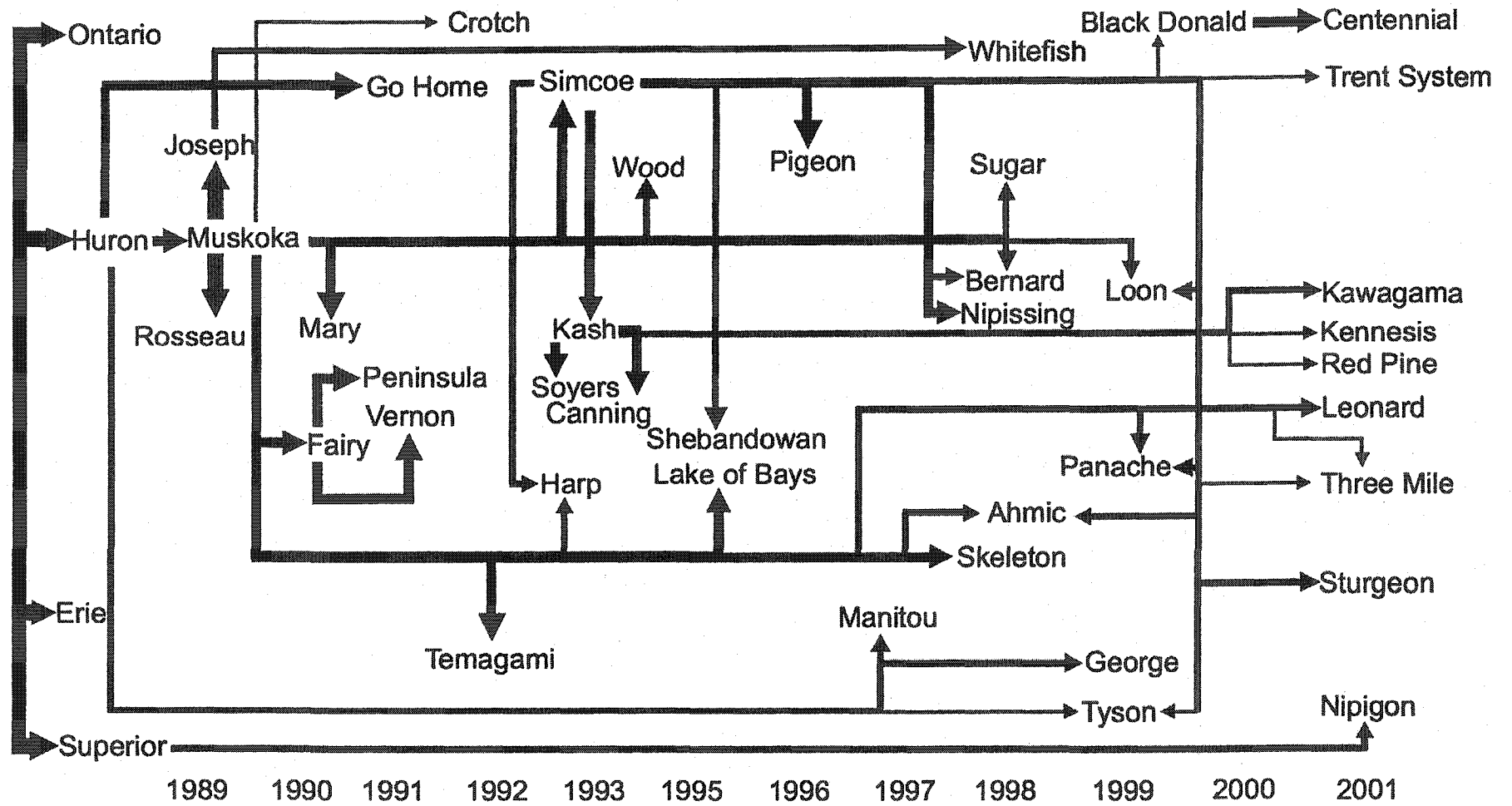
Conclusion

The present thesis is grounded in the premise that 'propagule pressure' is a poorly explored paradigm with a potential to confound current patterns and paradigms in invasion biology (e.g., the widespread success of some species, the 'enemy release hypothesis', etc.). As such, it should act as a basis for a reformulation of the protocols and procedures by which scientists investigate determinants of invasion success. Such an approach could produce new insights, and might help to disentangle some of the contradictory patterns reported in the literature (reviewed in chapter 2). At the very least, an explicit examination of propagule pressure-based hypotheses will help to identify potentially confounding factors such as the 'apparent' vs. 'realized' patterns of enemy release identified in chapter 4. Beyond a propagule pressure-based framework, a clearly defined, universally excepted lexicon like the one proposed in chapter 3 would also greatly improve our ability to generalize invasion phenomena. Finally, a shift in current thinking is needed – one that focuses on invasions as a biogeographical, rather than a taxonomic, phenomenon. A universal understanding of the circumstances underlying anthropogenic movement of species across historical barriers, and of the interactions between species and human activity in general, could go a long way toward improving our management and understanding of 'invasive' species.

Perhaps there is a lesson for all of ecology in the flaws of invasion biology. Instead of trekking tens of thousands of kilometres to study pristine ecosystems that have been largely inaccessible to man, we should focus heavily on the science of interaction between natural processes and human activities. Instead of seeking simple relationships in the isolated, equilibrial systems constructed largely in the mind's eye, we should explore the non-linearity of ecosystems, and the effect of constant human perturbation. In

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short, ecology should become the study of ecosystems and ecological processes in the context of an interactive biosphere in which humans are participants, not passive observers. Of course, modern ecology has come a long way in this respect; disciplines like ecotoxicology are integrations of ecological processes with human activities. However, the fundamental paradigms of ecology – theories like the niche, optimality, biotic resistance and facilitation, even island biogeography – all remain largely mired in the equilibrial assumptions of ecology past. Given the current rates of human over-consumption, and its resulting stress on natural resources, ecology will likely become the most important science discipline of the 21st century. I hope the time has come to transform ecology into a science that provides useful solutions to the problems of the future, rather than remaining a discipline that describes, in painstaking detail, the phenomena of the past.

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Appendix 1. Search string, and list of journals searched for characteristics of invaders and habitats susceptible to invasions.

Keywords: (NIS or invasive species or nonindigenous species or alien species or exotic species or non-native species or introduced species or invasiveness or invasibility) or invaded and (habitat* or communit* or ecosystem*)

Journals Searched:

AMERICAN MIDLAND NATURALIST

THE AMERICAN NATURALIST

ANIMAL BEHAVIOUR

ANIMAL CONSERVATION

ANNALS OF THE MISSOURI BOTANICAL GARDEN

ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS

ANNUAL REVIEW OF ENTOMOLOGY

AUSTRAL ECOLOGY

AUSTRALIAN JOURNAL OF BOTANY

AUSTRALIAN JOURNAL OF ECOLOGY

AUSTRALIAN JOURNAL OF ENTOMOLOGY

BIOLOGICAL CONSERVATION

BIOLOGICAL JOURNAL OF THE LINNEAN SOCIETY

BIOLOGICAL REVIEWS OF THE CAMBRIDGE PHILOSOPHICAL SOCIETY

BIOSCIENCE

CANADIAN JOURNAL OF ANIMAL SCIENCE

CANADIAN JOURNAL OF FISHERIES AND AQUATIC SCIENCES

CONSERVATION BIOLOGY

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ECOLOGICAL APPLICATIONS

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ECOLOGICAL MONOGRAPHS

ECOLOGICAL RESEARCH

ECOLOGICAL STUDIES

ECOLOGIST

ECOLOGY

ECOLOGY LETTERS

ECOLOGY OF FRESHWATER FISH

ECONOMIC BOTANY

ENVIRONMENTAL AND ECOLOGICAL STATISTICS

ENVIRONMENTAL AND EXPERIMENTAL BOTANY

ENVIRONMENTAL BIOLOGY OF FISHES

ENVIRONMENTAL CONSERVATION

ENVIRONMENTAL ENTOMOLOGY

EVOLUTION

EVOLUTIONARY BIOLOGY

EVOLUTIONARY ECOLOGY

EVOLUTIONARY ECOLOGY RESEARCH

EVOLUTIONARY TRENDS IN PLANTS

FRESHWATER BIOLOGY

GLOBAL ECOLOGY AND BIOGEOGRAPHY

IBIS

INTERNATIONAL JOURNAL OF PLANT SCIENCES

JOURNAL OF ANIMAL ECOLOGY

JOURNAL OF BIOGEOGRAPHY

JOURNAL OF GREAT LAKES RESEARCH

JOURNAL OF TROPICAL ECOLOGY

LIMNOLOGY AND OCEANOGRAPHY

NEW ZEALAND JOURNAL OF BOTANY

NEW ZEALAND JOURNAL OF ECOLOGY

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NORTHEASTERN NATURALIST

OECOLOGIA

OIKOS

SOUTH AFRICAN JOURNAL OF SCIENCE

TRENDS IN ECOLOGY & EVOLUTION

Appendix 2A. Summary of studies reporting characteristics of invasiveness. Characteristics identified: 0 – propagule pressure, 1 – taxonomic over-representation, 2 – physiological tolerance, 3 – body size, 4 – growth rate, 5 – generation time, 6 – invasion history/widespread, 7 – germination/hatch success or rate, 8 – seed/egg size, 9 – reproductive output, 10 – consumption efficiency, 11 – length of growing/breeding season, 12 – hermaphroditic/asexual reproduction

Comparison type	Authors	0	1	2	3	4	5	6	7	8	9	10	11	12
Plants														
established/introduced	Reichard and Hamilton 1997							+	+					+
established/introduced	Rejmánek and Richardson 1996		+				-			-				
established/introduced	Fine 2002			-										
invasive/non-invasive	Perrins et al 1993			+							+			
invasive/non-invasive	Thébaud et al 1996											+		
invasive/non-invasive	Richardson 1998	+					-			-				
invasive/non-invasive	Gerlach and Rice 2003								n.d.				+	-
invasive/non-invasive	Smith and Knapp 2001													
NIS/native	Smith and Knapp 2001											+		

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NIS/native	Mesleard et al 1993		-						
NIS/native	Baruch and Goldstein 1999							+	
NIS/native	Cadotte and Lovett-Doust 2002	+			-			+	+
NIS/native	Daehler 2001	n.d.							
NIS/native	Luken et al 1997		+						
NIS/native	Noe 2002		+			+			
NIS/native	Radford and Cousens 2000				-	+	+	+	
NIS/native	Radho-Toly et al 2001		n.d.						
NIS/native	Schierenbeck et al 1994		+						
NIS/native	Smith et al 1999		-			+			
NIS/native	Weber 1997	+							
NIS/native	Williamson and Fitter 1996					+	+		+
NIS/native	van Clef and Stiles 2001					+			
NIS/native	Vilà and D'Antonio 1998			+		+			
NIS/native	Horvitz et al 1998				+				
NIS/native	Levine 2001								
NIS/native	Craine and Lee 2003							-	
NIS/native	Leger and Rice 2003			+			+		

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		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
NIS/native	Allcock 2002										+	
NIS/native	Morris et al 2002										+	
NIS/native source	Goodwin et al 1999						+	n.d.				n.d.
NIS/native source	Grotkopp et al 2002				+	-			-			
NIS/native source	McDowell and Turner 2002										+	
established/introduced	Prinzing et al 2002	+					+					

Invertebrates

		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
established/introduced	Berggren 2001	+										
NIS/native	McGlynn 1999a			-								
NIS/native	Byers 2000										+	
NIS/native	McMahon 2002		-			-				+		
NIS/native worldwide	McGlynn1999b						+					

Fish

		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
established/introduced	Wonham et al 2000	+										
established/introduced	Kolar and Lodge 2002		+		+		+					
invasive/non-invasive	Kolar and Lodge 2002		+		-							

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invasive/non-invasive	Rosecchi et al 2001		+	n.d.	n.d.			n.d.	n.d.

Birds

established/introduced	Blackburn and Duncan 2001		+			+			
established/introduced	Cassey 2001a			-/+					
established/introduced	Cassey 2001b	+		+	+				
established/introduced	Moulton et al 2001								
established/introduced	Sol et al 2002	+							
established/introduced	Sol and Lefebvre 2000	+							
established/introduced	Duncan et al 2001			+		+			
established/introduced	Sorci et al 1998	+							
established/introduced	Veltman et al 1996	+							
NIS/native worldwide	Lockwood	+	+						
invasive/noninvasive	Duncan et al 2001			-		-	+		

Mammals

established/introduced	Forsyth and Duncan 2001	+			-				

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Appendix 2B. Summary of studies reporting characteristics of invasibility. Characteristics identified: 0 - propagule pressure, 0/1 - anthropogenic activity, 1 – disturbance, 2 – nutrient levels, 3 – resident species diversity, 4 – resident species abundance/density.

		Trait					
Authors	NIS comparison	0	0/1	1	2	3	4

Terrestrial Plants

Authors	NIS comparison	0	0/1	1	2	3	4
Anderson and Inouye 2001	Abundance						-
Davis et al 2000	Abundance			+	+		
Dukes 2002	Abundance					n.d.	-
Horvitz et al 1998	Abundance			+			
Hutchinson and Vankat 1997	Abundance		+			-	-
Parker et al1993	Abundance						-
Prieur-Richard et al 2000	Abundance					-	
Rose et al 1998	Abundance				-		
Prieur-Richard et al. 2002	Abundance						+
Wilsey and Polley 2002	Abundance					+	
Davis and Pelsor 2001	Abundance and Survivorship			+			
Brothers and Spingarn 1992	Diversity		+				
Burke and Grime 1996	Diversity			+	+		
Cabin et al 2002	Diversity						
Cadotte and Lovett-Doust 2002	Diversity			+			
Corlett 1992	Diversity		+	+			
Curnutt 2000	Diversity						
Fensham and Cowie 1998	Diversity		+	+	+	-	
Harrison 1999	Diversity				+		

Reference	Type						
Higgins et al 1999	Diversity					+	
King and Buckney 2002	Diversity				+		
Knops et al 1995	Diversity		+				
Larson et al 2001	Diversity			+			
Lonsdale 1999	Diversity		+			+	
McIntyre 1994	Diversity			+	+		
McIntyre 2001	Diversity			+/n.d	+/n.d.		
Parendes and Jones 2000	Diversity		+				
Pyšek et al 2002	Diversity		+				
Roy et al 1999	Diversity		+				
Safford and Harrison 2001	Diversity			-		-	
Smith and Haukos 2002	Diversity					+	
Stadler et al 2000	Diversity					+	
Stohlgren et al 1999a	Diversity				+	-/+	-/+
Stohlgren et al 1999b	Diversity			+	+	+	
Symstad 2000	Diversity					-	
Vilà and Pujadas 2001	Diversity		+				
Williamson and Harrison 2002	Diversity	+		+			
PlantyTabacchi et al 1996	Diversity		+	+		+	
Lonsdale and Lane 1994	Diversity	+					
Frenot et al 2001	Diversity		+				
Harrison et al 2003	Diversity			+			
Teo et al. 2003	Diversity			+		n.d.	
Levine and D'Antonio 2003	Diversity	+					
Brown and Peet 2003	Diversity					+/-	
Bowles et al. 2003	Diversity		+	-			
Foster et al. 2002	Diversity			+		n.d.	
Gabriel et al 2001	Diversity and		+	+		n.d	n.d

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	Abundance						
Harrison et al 2001	Diversity and Abundance	+	+	+			
McIvor 1998	Diversity and Abundance	+		-			+
Richardson and Bond 1991	Diversity and Abundance	+	+				
Gelbard and Harrison 2003	Diversity and Abundance		+				
Watkins et al. 2003	Diversity and Abundance		+				
Gelbard and Belnap 2003	Diversity and Abundance		+	+			
Troumbis et al 2002	Diversity and Abundance				n.d.	-	-
Allen and Ramcharan 2001	Presence	+					
Gilfedder and Kirkpatrick 1998	Presence	+	+	+			
Walker and Wilson 2002	Presence			+			
Wilson et al 1992	Presence						
Zalba et al 2000	Presence						
Forys et al 2002	Presence		+				
King and Buckney 2001	Presence and Abundance	n.d.					
Lindenmayer and McCarthy 2001	Presence and Abundance		+	+			
Jesson et al 2000	Survivorship		+				
Robinson et al 1995	Survivorship			+			+
Appleby 1998	Seed Diversity	+					

Aquatic plants

Study	Measure						
Buchan and Padilla 2000	Presence	n.d.		+	+		

Birds

Study	Measure						
Blair 1996	Diversity		+				
Case 1996	Diversity	+			+	-	
Sol 2000	Presence						

Fishes

Study	Measure						
Baltz and Moyle 1993	Diversity					- /n.d.	
Fausch et al 2001	Abundance						
Marchetti and Moyle 2001	Diversity and Abundance			-			
Feyrer and Healey 2003	Diversity						

Invertebrates/microorganisms

Study	Measure						
Holway et al 2002	Survivorship				+	n.d.	
Miller et al 2002	Survivorship				+	-	
Stachowicz et al 2002	Survivorship and Abundance					-	n.d.
Drake et al 1993	Order of Establishment						
Shurin 2000 -moved from plants	Diversity and Abundance					-	

Multiple fauna

Study	Measure						
McKinney 2001	Diversity		+p,f			+p	-f

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Chown et al 1998	Diversity	+b	+s		+b	+s
Smallwood 1994	Diversity		+b,m		-m	
Rivard et al 2000	Diversity	+s	+s		-s	

p – plants, b – birds, f – fishes, m – mammals, s – multiple species

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