Ecology Letters, (2005) **8**: 715–721 doi: 10.1111/j.1461-0248.2005.00774.x

LETTER

Studying invasion: have we missed the boat?

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Abstract

Invasive species, and the ensuing homogenization of the world's biota, form a global problem with consequences ranging from the decline and extirpation of native species to threats to human health. The magnitude of this issue demands a thorough understanding of the invasion process, which consists of three main stages: initial dispersal, establishment of self-sustaining populations, and spread. To assess the relative distribution of research effort among these stages, we conducted a literature review using 873 articles published in 23 major journals over the past 10 years. Of the 873 papers, only 96 (11.0%) studied initial dispersal, and only half of these (6.2% of the total) were empirical. As the first stage in a contingent process, we argue that initial dispersal is the best stage during which to direct management efforts. In addition, initial dispersal has direct relevance for fundamental ecological questions regarding community assembly and metacommunity dynamics. In so far that answering these questions and preventing invasion are goals of ecologists, the disparity in research effort noted here suggests that ecologists need to expand their efforts to include more research on initial dispersal.

Keywords

Colonization, community assembly, establishment, exotic species, initial dispersal, invasion, invasive species, metacommunity, metapopulation, research effort, spread.

Ecology Letters (2005) 8: 715–721

INTRODUCTION

Following a long period of neglect since Charles Elton's seminal work on invasion in 1958 (Elton 1958), invasive species have recently re-emerged as an important focus of ecological study, with studies of the invasion process and exotic species increasing considerably in the past decade (Williamson 1996) (Fig. 1a). Invasion is a multi-step process (Williamson 1996; Kolar & Lodge 2001; Leung *et al.* 2002) comprised of three phases: initial dispersal (where an organism moves from its native habitat, often over long distances, to a new habitat outside of its home range), establishment of self-sustaining populations within the new habitat, and spread of the organism to nearby habitats. While successful invasions, comprised of those species that establish populations and spread, receive the greatest attention, the contingent nature of the invasion process makes initial dispersal the stage with the greatest effects on other, later stages.

The process of invasion is fundamentally important for understanding community assembly (Diamond 1975; Webb *et al.* 2002) and metapopulation and metacommunity dynamics (Leibold *et al.* 2004), as well as for managing the unwanted colonization and spread of exotic species. The contingent nature of both invasion and community assembly render the first stage, initial dispersal, the fundamental stage upon which all other stages rest. At long temporal scales, the initial dispersal stage of the invasion process is the essential first filter upon which all other community assembly processes operate, including subsequent diversification (Webb *et al.* 2002). Therefore, initial dispersal is essential to understanding the response or recovery of communities to environmental perturbations, including climate change (Clark *et al.* 2003) and post-glacial retreat (Williams *et al.* 2001). At shorter temporal scales, dispersal of native species is of fundamental importance to metapopulations because it mediates the dynamic balance between extinction and colonization (Hanski 1999). Dispersal also is central to growing research on metacommunities because it is the mechanism that links local and regional community dynamics (Leibold *et al.* 2004) and because tradeoffs between dispersal and competitive abilities mediate local community structure (Abrams & Wilson 2004; Kneitel & Chase 2004).

In a management context, it is during the initial dispersal stage that management efforts can prevent the establishment and subsequent, often detrimental impacts of invasive species (Mills *et al.* 1993; Hobbs & Humphries 1995;

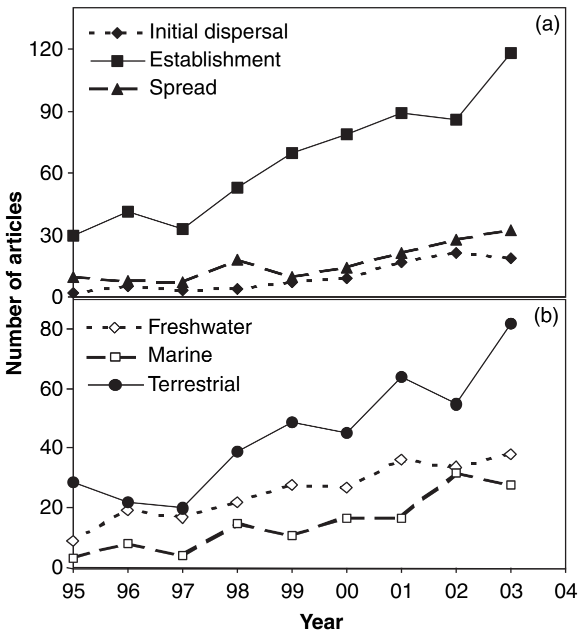

Figure 1 (a) Number of papers in the period 1995–2003 found in a literature search on ISI Web of Science using the search terms invasion, invasive species and exotic species. Numbers are broken down by stage of invasion process they describe. (b) From the same literature search, but removing all articles from study-system-specific journals, the number of papers studying initial dispersal, distinguished by study system.

Pimentel *et al.* 2000; Leung *et al.* 2002; Simberloff 2003). Typically, only a small percentage of colonists survive the initial dispersal stage (Lodge 1993; Kolar & Lodge 2001). While some non-indigenous species may have neutral or even beneficial impacts on native biota and ecosystems (e.g. crop species and pollinators), others will become invasive (species that establish populations and spread). The eradication of invasive species can be extremely costly, involve potentially harmful chemicals (Myers *et al.* 2000), and is rarely accomplished, except on small islands, in isolated areas, or before species have spread widely (Myers *et al.* 2000; Zavaleta *et al.* 2001; Simberloff 2003). Even when eradication is successful, invasive species may have caused long-lasting changes in community structure and ecosystem function (Zavaleta *et al.* 2001). Thus, preventing unintentional introductions by targeting the initial dispersal stage is likely to be the most effective management option.

Because community assembly, metacommunity dynamics, and the management of invasive species depend so critically upon our understanding initial dispersal, the earliest stage of the invasion process, we have been surprised by the lack of research on this topic. Thus, we raise the question: are ecologists studying the invasion process (for management or understanding community assembly) focusing their resources effectively? Here, we report on a literature review to answer this question using 873 studies published in 25 major journals over the past 10 years in two stages of literature searches.

MATERIALS AND METHODS

We searched ISI Web of Science in 2004 for the time period 1995–2004 in 25 sources that we considered general science and ecological journals. We included five journals focusing exclusively on freshwater and/or marine systems to attempt to counter potential terrestrial biases in the more general literature. Therefore, for the rest of the article, we will refer to two searches: one based on all 25 journals (ALL) and one based on these 25 journals minus the five freshwater and/or marine journals (GENERAL). For both searches we used the key words invasion OR invasive species OR exotic species. We chose these three key words to effectively survey the literature without unduly biasing our results. For example, using the key words 'dispersal' or 'spread' might have biased our results and overestimated studies of either initial dispersal or spread, respectively. Other key words such as 'noxious species' or 'colonization' connote established exotic species and could have biased our results against finding studies of initial dispersal, while the term 'transport' would limit our study to those organisms carried by vectors. Searching with these terms garnered papers addressing both basic and applied ecological issues, including the assembly process, metapopulation and metacommunity dynamics, the effects of new species on community structure and ecosystem function and the management of invasive species. The articles included empirical studies, theoretical papers, reviews, and opinion pieces. We included in our search the journals *Science*, *Nature*, *The American Naturalist*, *Ecology*, *Ecology Letters*, *Ecological Applications*, *Ecological Entomology*, *Ecological Monographs*, *Ecological Modeling*, *Conservation Biology*, *Oecologia*, *Oikos*, *Landscape Ecology*, *TREE*, *Journal of Ecology*, *Journal of Animal Ecology*, *Proceedings of the National Academy of Sciences*, *The Journal of Biogeography*, *Diversity and Distributions*, *Journal of Experimental Marine Biology and Ecology*, *Marine Ecology Progress Series*, *Limnology and Oceanography*, *Canadian Journal of Fisheries and Aquatic Sciences and Hydrobiologia*. We included strictly freshwater and marine journals to account for a perceived terrestrial bias in more general journals. This search (ALL) yielded 942 studies, of which 69 were excluded as being exclusively molecular, medical, or biogeochemical in nature, and so not pertinent for this exercise.

After reading the abstracts, we classified each article according to the stage of invasion it considered (initial dispersal, establishment, spread), whether it was empirical, and the study system considered (terrestrial, freshwater aquatic or marine). Where any of these categories were

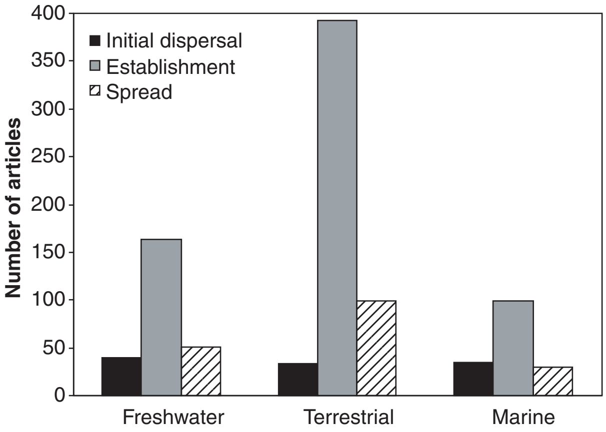

Figure 2 Number of papers in the period 1995–2003 found in a literature search on ISI Web of Science using the search terms invasion, invasive species and exotic species, broken down by both study system and stage of invasion process.

unclear from the abstract, the article itself was consulted. Some articles did not fit neatly into a single category (e.g. marine and freshwater), and were assigned to multiple categories. Journals studying the effects of exotic species on native biota or ecosystems were classified as considering establishment. For analysis of the distribution of research effort by study system, we looked at both all journals (Fig. 2) and a subset of these journals that excluded articles from system-specific journals (Fig. 1b). The total number of articles published on invasion per year increased by nearly fourfold over this time period (Fig. 1a).

RESULTS

Of the 873 papers, only 96 (11.0%) considered the initial stage of invasion (Fig. 1a). Roughly half of those papers (43 or 4.8% of the total) were theoretical or synthetic, leaving an extremely small number of empirical studies of initial dispersal – just 6.2% of all papers published on invasion in the past decade. 169 (25.7%) of the 873 papers discussed the subsequent spread of organisms once they had arrived in their new habitats. Of these, 115 were empirical, vs. 54 theoretical or synthetic articles. Despite the fundamental nature of initial dispersal and spread for invasion (Mills *et al.* 1993; Hobbs & Humphries 1995; Clark *et al.* 1998; Simberloff 2003), and community assembly (Diamond 1975; Webb *et al.* 2002), very little of this research effort in the past decade has focused on understanding how these species move. The vast majority of the research effort, 639 or 73.1% of 873 papers, only addressed the establishment stage of invasion.

These papers also reveal an inequality in the study systems and the number of species considered (Figs 1b and 2). Of all 873 articles (all), 440 (50.4%) focused on terrestrial systems, 240 (27.5%) were freshwater studies, and 154 (17.6%) concentrated on marine systems (Fig. 2). When purely marine and/or freshwater journal articles were excluded, 434 (66.1%) were terrestrial studies, 119 (18.1%) concentrated on freshwater systems, 53 (8.3%) targeted marine systems (Fig. 1b), and 68 (10.4%) were not system-specific because they were theoretical or synthetic (numbers do not sum to 100% because some papers were classified in two or more categories; e.g. aquatic and terrestrial). Of this subset of papers (general), 276 articles discussed a single species, while 381 articles discussed multiple species, although often only two species. Of the 26 empirical studies from this subset (general) focusing on initial dispersal, six (23.1%) were conducted in freshwater systems, five (19.2%) in marine systems, and 15 (57.7%) in terrestrial systems.

DISCUSSION

Our results show a strong disparity in the research effort allotted to the different stages of invasion (Figs 1a and 2), with the bulk of the research effort directed at establishment, and a much smaller portion of the effort directed at initial dispersal and spread. While the overall effort directed at invasion over the past decade has increased greatly (Fig. 1a), its proportional division according to invasion stage has remained relatively steady. Invasion research has grown most rapidly among terrestrial study systems (Fig. 1b), with lesser gains in marine and freshwater systems. The division of research according to stage is not equal among the three types of study systems, either, with a greater proportion of effort allotted to initial dispersal for freshwater and marine studies (16.7% of freshwater, 25.7% of marine and 7.5% of terrestrial studies, respectively) and a greater proportion directed at establishment for terrestrial studies (67.9% of freshwater, 73.0% of marine and 89.5% of terrestrial studies, respectively; Fig. 2).

The difference in research effort allotted to the different study systems is only partially accounted for by potential system bias in the journals we surveyed. When comparing the general journals to all journals surveyed, the proportional effort increases from 8.3 to 17.6% and from 18.1 to 27.5% of articles surveyed, respectively, for marine and freshwater systems, while that for terrestrial studies decreases from 66.1 to 50.4%. Despite the changes in effort, this pattern still highlights a strong emphasis on terrestrial systems (Figs 1a and 2). Terrestrial systems are the most visible and accessible habitats for humans and, as such, receive the preponderance of ecological attention. Freshwater and marine systems, however, are vital as sources of drinking water, seafood, transportation, and recreation opportunities, and can be highly vulnerable to the effects of exotic species (Mills *et al.* 1993; Chapman *et al.* 2003).

Marine systems are often the first point of contact for trade shipments arriving in a country, and so may be more vulnerable to invasion than terrestrial systems. In addition, many aquatic systems are fairly isolated and contain many endemics. In isolated aquatic ecosystems, as on islands, the effect of exotic species is often manifest in remarkably high extinction rates of endemic species (Lodge 1993).

The disparity in effort allotted to empirical vs. theoretical work highlights the differences in the difficulty of addressing the separate stages of invasion using theoretical or empirical approaches [with empirical articles representing 56.2, 77.6, and 62.8%, respectively, of the total number of journal articles (all) for that stage for initial dispersal, establishment, and spread]. For example, our results suggest it may be easier to deal with spread theoretically rather than empirically. We found that 20.8% of non-empirical initial dispersal papers included mathematical models, compared with 80.0% of non-empirical spread articles. One reason for this greater ease of modelling of spread is that exponential dispersal functions can reasonably capture much of the dynamics (Williamson 1996; Shigesada & Kawasaki 1997). Furthermore, the rare, long distance dispersal events typical of initial dispersal can be hard to model (Clark *et al.* 2003) and detect empirically, and it is typically not ethical to experimentally manipulate the introduction of exotic species. In contrast to initial dispersal, the vast number of potential interactions involved with establishment, and the consequences of establishment, make considerable grist for the empirical research mill, but provide little generality for theoretical models. Balancing these disparities should be a high priority.

Initial dispersal vs. spread

It is important to note that the difference between initial dispersal and spread varies according to whether one considers the stages in a functional or temporal sense. Functionally, there is often little difference between the two stages, as they both indicate movement of organisms to new habitats, although they may vary in the relative importance of human vectors vs. organismal dispersal for this movement (e.g. Hrabik & Magnuson 1999; Puth & Allen in press). This difference may become even more blurred in the case of well-bounded habitat patches, such as lakes, islands or forest fragments, where new colonists must necessarily cross unfavourable habitat. In such cases, spread would look similar to initial dispersal. Temporally, however, there is a substantial difference between the two stages, and hence, a difference in opportunities for both management and research. The contingent nature of the stages of invasion makes initial dispersal the best opportunity for halting invasions. The smaller numbers of organisms at this stage, however, along with the isolated nature of the first colonized patches, make this stage fundamentally different from spread, when patches within a region can re-supply patches where initial colonists do not survive and reproduce. In addition, because patches are less isolated during spread, movement of organisms may be able to occur from more directions than during initial dispersal, with consequences for the probability of arrival and for modelling methods. Organismal movement during spread may fit metapopulation or metacommunity models much better than that occurring during initial dispersal. Finally, the decision of whether an organism is moving from its native range or from an adopted one is, to some extent, a human decision of what temporal scale is important (e.g. at what time did the organism need to exist in a given location to be considered native).

Broader implications

All three stages of the invasion process (initial dispersal, establishment and spread) are important for understanding community assembly and addressing invasive species, but initial dispersal deserves special attention because the other stages are contingent upon it (Mills *et al.* 1993; Webb *et al.* 2002). If initial dispersal is interrupted, establishment and spread do not occur. Likewise, initial dispersal strongly affects the regional species pool from which communities develop, either through the local sorting process or through subsequent evolution (McCune & Allen 1985; Webb *et al.* 2002). Dispersal ability and dispersal limitation, both related to initial colonization, are essential for understanding large-scale biogeographic patterns (Wiens & Donoghue 2004). The absence of a species or an entire clade from a region suitable for establishment (e.g. within the species or clade's fundamental niche) could result from strong interspecific interaction (e.g. limitation of the realized niche) or from dispersal limitation (Webb *et al.* 2002; Wiens & Donoghue 2004). For example, the absence of snakes from New Zealand likely represents their inability to reach the islands rather than their inability to withstand competition once there. A complete understanding of the processes regulating community structure requires full consideration of all stages of assembly, including initial dispersal.

Initial dispersal strongly influences community structure at a variety of temporal scales. At long time scales, it determines the regional species pool from which local community membership and community interactions emerge. At intermediate and shorter time scales, initial dispersal regulates the dynamics of metacommunities (Warren 1996) and invasive species. For metacommunities, the balance between initial dispersal and local extinction determines which species survive in a community (Gilpin & Hanski 1991; Mouquet & Loreau 2002; Leibold *et al.* 2004), although different paradigms within the metacommunity perspective place different emphasis on the importance and effects of initial dispersal (Leibold *et al.* 2004). This process is mimicked by the invasion of exotic species, although the source of the species involved may be more distant. Many ecologists assume that, because of high dispersal rates for many species, initial dispersal plays a minor role in structuring communities (e.g. Shurin 2000); however, even in communities of species assumed to spread rapidly, this is not always the case (e.g. Cáceres & Soluk 2002).

The importance of the initial stage of invasion does not, however, suggest that ecologists should stop studying establishment. Rather, we maintain that studying establishment at the cost of studying initial dispersal limits management options and hinders overall understanding of the invasion process. In order to understand the effects of exotic species once they have invaded, we must study establishment and spread. However, where the effects of exotic species are negative and prevention of arrival and establishment is desirable, studies of the initial dispersal stage should be a higher priority.

Ecological studies of establishment remain important both because the invasion of new species can never be completely prevented, and because many exotic species that have few or no negative impacts (Williamson 1996). Studies of establishment are required to identify which species are likely to have harmful impacts. Such studies often parallel central questions in ecology more closely than do issues of initial dispersal or spread, and can be conducted at time scales appropriate for ecological funding cycles, while many studies of initial dispersal require decades for trends to appear. Studying initial dispersal often requires knowledge outside the traditional realm of ecology (e.g. international trade, geomorphology, climate change, plate tectonics, etc.), which may discourage researchers from tackling these issues, but that does not detract from the importance of this first stage for the overall process of invasion and assembly. Furthermore, because there are potential interactions between initial dispersal and establishment (e.g. dispersal ability and invasiveness may be correlated in some groups of organisms), it is crucial to study the multiple stages of invasion together. In the articles surveyed for this paper, only 37 papers addressed both initial dispersal and establishment (with or without spread), of which only 22 were empirical.

Implications for management and research

There have been some important management successes based on studies of initial dispersal. In many states, there are restrictions on the use of live bait by anglers, and boaters are required to remove vegetation from boats and trailers to prevent the initial dispersal and spread of potentially invasive species. With the adoption of The International Convention for the Control and Management of Ships' Ballast Water and Sediments, ships will be required to dump and reacquire ballast water at least 50 nautical miles from shore, which should help prevent the initial cross-oceanic transport of species (Drake & Lodge 2004; IMO 2004). Such efforts have targeted relatively easy and obvious vectors of exotic species, but may miss the more cryptic or diffuse sources of invasion (Kay & Hoyle 2001; Chapman *et al.* 2003).

Given this large gap in understanding the initial dispersal and spread of most exotic species, we need to fund and conduct vastly more research on the patterns and mechanisms of this critical initial stage of species invasions and community assembly. This stage of invasion is crucial for the understanding of several ecological issues. Major questions to address include linking species' traits to movement ability, exploring the impacts of landscape heterogeneity on dispersal success, studying differences in human-mediated vs. 'natural' movement, and comparing dispersal ability to competitive ability. As we mentioned above, understanding initial dispersal will not be easy, both because it is composed of rare events that are hard to detect and because these often occur over large spatial and temporal scales. One solution to these difficulties would be to infer likely invasion patterns from the colonization of new habitats by native species in field experiments. Such dispersal studies will be most informative when they compare across multiple species (e.g. Cáceres & Soluk 2002), rather than focusing on a single species, and when they focus on species that can colonize rapidly. From an experimental point of view, this approach avoids the ethical problems of unintentional release of exotic species contributing to the homogenization of the earth's biota while allowing ecologists to investigate patterns and processes of invasion and community assembly of new systems. While dispersal studies of this type do exist, they typically have not placed their results in the context of invasion, but have focused exclusively on community assembly (e.g. Jenkins & Buikema 1998; Cáceres & Soluk 2002; Havel *et al.* 2002). Conversely, direct monitoring of the initial stage of invasion is useful because it allows the detection of exotic species before they can affect community structure and ecosystem function, and allows the study of community assembly at ecologically relevant scales.

This matching of ecologically relevant scales to initial dispersal is not a trivial empirical problem because of the rare, long-distance nature of initial dispersal. In addition to theoretical approaches, ecologists might address the issue empirically through direct contemporary monitoring of exotic species or by using paleoecological and molecular genetic methods to infer historical patterns of initial dispersal and colonization. A monitoring programme might be accomplished through more single PI research, but because of the spatially and temporally sporadic nature of initial dispersal, the initial stage of invasion might be most strongly addressed through coordinated regional monitoring efforts that operate at long temporal or large spatial scales (e.g. NSF's NEON programme, the Smithsonian's National Ballast Information Clearinghouse and Marine Invasions Research Laboratory, Sea Grant's Nonindigenous Species Program, USDA's Vectors and Pathways Program). Paleoecological and molecular genetic techniques have been instrumental in addressing a historical questions about initial dispersal and community assembly at multiple temporal scales (e.g. Hairston *et al.* 1999; Bohonak & Roderick 2001; Williams *et al.* 2001; Ackerly 2003). Although paleoecological and molecular genetic techniques cannot detect initial dispersal events where establishment fails, their ability to evaluate past events makes the combination of paleoecological and molecular genetic techniques particularly powerful for understanding the importance of initial dispersal for community assembly (Williams *et al.* 2001; Webb *et al.* 2002; Ackerly 2003).

CONCLUSIONS

Our results highlight the need for more research on initial dispersal, the first stage in the invasion process. We suggest addressing this priority using a multifaceted research programme that includes modelling, direct monitoring of exotic species, and field and laboratory studies of community assembly. A more thorough grasp of the factors regulating initial dispersal will facilitate better informed and effective management of the spread of exotic species and is fundamental to the understanding of metacommunity dynamics and community assembly.

ACKNOWLEDGEMENTS

We thank D. Skelly, M. Smith, D. Sax, J. Gurevitch and two anonymous referees for helpful comments on the manuscript.

REFERENCES

Abrams P.A. & Wilson W.G. (2004). Coexistence of competitors in metacommunities due to spatial variation in resource growth rates; does R*predict the outcome of competition? *Ecol. Lett.*, 7, 929–940.

Ackerly D.D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.*, 164, S165–S184.

Bohonak A.J. & Roderick G.K. (2001). Dispersal of invertebrates among temporary ponds: are genetic estimates accurate? *Israel J. Zool.*, 47, 367–386.

Cáceres C.E. & Soluk D.A. (2002). Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia*, 131, 402–408.

Chapman J.W., Miller T.W. & Coan E.V. (2003). Live seafood species as recipes for invasion. *Conserv. Biol.*, 17, 1386–1395.

Clark J.S., Fastie C., Hurtt G., Jackson S.T., Johnson C., King G.A. *et al.* (1998). Reid's paradox of rapid plant migration. *BioScience*, 48, 13–24.

Clark J.S., Lewis M., McLachlan J.S. & HilleRisLambers J. (2003). Estimating population spread: what can we forecast and how well? *Ecology*, 84, 1979–1988.

Diamond J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of Communities* (eds Cody M.L. & Diamond J.M.). Harvard University Press, Cambridge, MA, pp. 342–444.

Drake J.M. & Lodge D.M. (2004). Global hot spots of biological invasions: evaluating options for ballast-water management. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 271, 575–580.

Elton C.S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Gilpin M.E. & Hanski I.A. (1991). *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, San Diego, CA.

Hairston N.G., Perry L.J., Bohonak A.J., Fellows M.Q., Kearns C.M. & Engstrom D.R. (1999). Population biology of a failed invasion: Paleolimnology of Daphnia exilis in upstate New York. *Limnol. Oceanogr.*, 44, 477–486.

Hanski I.A. (1999). *Metapopulation Ecology*. Oxford University Press, Oxford, England.

Havel J.E., Shurin J.B. & Jones J.R. (2002). Estimating dispersal from patterns of spread: spatial and local control of lake invasions. *Ecology*, 83, 3306–3318.

Hobbs R.J. & Humphries S.E. (1995). An integrated approach to the ecology and management of plant invasions. *Conserv. Biol.*, 9, 761–770.

Hrabik T.R. & Magnuson J.J. (1999). Simulated dispersal of exotic rainbow smelt (Osmerus mordax) in a northern Wisconsin lake district and implications for management. *Can. J. Fish. Aquatic Sci.*, 56 (Suppl. 1), 35–42.

IMO (2004). Alien invaders in ballast water – new convention adopted at IMO, available at: URL http://www.imo.org/newsroom/mainframe.asp?topic_id=848&doc_id=3475

Jenkins D.G. & Buikema A.L. Jr (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol. Monogr.*, 68, 421–443.

Kay S.H. & Hoyle S.T. (2001). Mail order, the Internet, and invasive aquatic weeds. *J. Aquatic Plant Manage.*, 39, 88–91.

Kneitel J.M. & Chase J.M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, 7, 69–80.

Kolar C.S. & Lodge D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199–204.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.

Leung B., Lodge D.M., Finnoff D., Shogren J.F., Lewis M.A. & Lamberti G. (2002). An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 269, 2407–2413.

Lodge D.M. (1993). Biological invasions: lessons for ecology. *Trends Ecol. Evol.*, 8, 133–137.

McCune B. & Allen T.F.H. (1985). Will similar forests develop on similar sites? *Can. J. Bot.*, 63, 367–376.

Mills E.L., Leach J.H., Secor C.L. & Carlton J.T. (1993) What's next? The prediction and management of exotic species in the Great Lakes. In: *Great Lakes Fishery Commission*, Ann Arbor, MI.
Mouquet N. & Loreau M. (2002). Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.*, 159, 420–426.
Myers J.H., Simberloff D., Kuris A.M. & Carey J.R. (2000). Eradication revisited: dealing with exotic species. *Trends Ecol. Evol.*, 15, 316–320.
Pimentel D., Lach L., Zuniga R. & Morrison D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50, 53–65.
Puth L.M. & Allen T.F.H. (in press). Potential corridors for the rusty crayfish, Orconectes rusticus, in northern Wisconsin (USA) lakes: lessons for exotic invasions. *Landscape Ecol.*.
Shigesada N. & Kawasaki K. (1997). *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, UK.
Shurin J.B. (2000). Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology*, 81, 3074–3086.
Simberloff D. (2003). How much information on population biology is needed to manage introduced species? *Conserv. Biol.*, 17, 83–92.
Warren P.H. (1996). The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia*, 105, 132–140.
Webb C.O., Ackerly D.D., McPeek M.A. & Donoghue M.J. (2002). Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.*, 33, 475–505.
Wiens J.J. & Donoghue M.J. (2004). Historical biogeography, ecology and species richness. *Trends Ecol. Evol.*, 19, 639–644.
Williams J.W., Shuman B.N. & Webb T. (2001). Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology*, 82, 3346–3362.
Williamson M.H. (1996). *Biological Invasions*. Chapman & Hall, London, UK.
Zavaleta E.S., Hobbs R.J. & Mooney H.A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.*, 16, 454–459.

Editor, Jessica Gurevitch
Manuscript received 11 October 2004
First decision made 3 November 2004
Second decision made 26 December 2004
Manuscript accepted 4 April 2005