Chapter 20

RESEARCHING INVASIVE SPECIES 50 YEARS AFTER ELTON: A CAUTIONARY TALE

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20.1 INTRODUCTION

Rather surprisingly, the publication of Elton's book in 1958 did not instigate a flood of research on species introductions (Simberloff, this volume). There had been a trickle of articles on introduced species before Elton's book (for example Allan 1936; Egler 1942; Baker 1948), which continued during the 1960s and 1970s (for example Sukopp (1962); Jehlík & Slavík (1968); Moyle 1973; Burdon & Chilvers (1977)). However, it was not until the initiation of the SCOPE (Scientific Committee on Problems of the Environment) in 1983, 25 years after the publication of Elton's book, that the modern field of invasion biology really began to take shape (Richardson & Pysek 2006; Simberloff, this volume).

During the past quarter of a century or so, the field has grown enormously (MacIsaac et al., this volume). What had begun as a small group of committed researchers in the 1980s is now a prominent and multi-facetted research field within ecology. Researchers from throughout the world are currently focusing their research on biological invasions and thousands of papers on species introductions, and their spread, impact and management, have been published in the past decade. The result has been a considerable increase in our knowledge in all these areas. At the same time, as is the case with any initiative or organization that grows very quickly, the field has experienced some growing pains. Certain obstacles and pitfalls may have impeded the field's progress. Some of these obstacles are of our own making and can be remedied. Others relate to the inherent properties and dynamics of species introductions and spread and will likely remain as challenges in the future. In this chapter, I briefly describe what I believe have been two missteps by the field: reliance for too long on a niche-based approach to understanding invasions and a tendency to overstate certain conclusions and claims.

20.2 THE NICHE-BASED APPROACH TO UNDERSTANDING INVASIONS: MORE A HINDRANCE THAN A HELP?

Scientific disciplines, like populations, can experience a founder effect. If one looks at the scientists who played a leading role in inaugurating invasion biology through SCOPE in the 1980s, one sees that most were ecologists, particularly community ecologists. As a result, in many ways, invasion biology emerged as a disciplinary offspring of community ecology. At this time, the early 1980s, the field of community ecology was still largely dominated by the niche-based theories of MacArthur and Hutchinson. It is not surprising, then, that the early years of invasion biology were shaped by a perspective that emphasized determinism and local processes. For example, the first two questions originally articulated by the 1983 SCOPE scientific advisory committee on biological invasions, which were intended to focus subsequent research, focused on species traits and local processes.

In invasion biology, the niche-based approach is probably most obvious in the diversity–invasibility hypothesis, which holds that species diverse environments should be more resistant to invasion than species-poor environments (see Fridley, this volume). The essence of this argument has changed little in the 50 years since Elton articulated this line of reasoning, which bore some similarity to Darwin's naturalization hypothesis. Those who have promoted the diversity–invasibility hypothesis, whether invoking species diversity or functional diversity, typically have specifically articulated a niche-limitation argument (see, for example, Fargione & Tilman 2005; Fridley, this volume).

Following in the wake of a larger ship works well as long as the large ship is seaworthy and headed in the right direction. However, in the eyes of many, the ship of community ecology has been foundering, or at least not making much progress, for some time. There has been increasing discontent within community ecology in recent years. Frustrated by what he believed to be lack of progress in community ecology, Lawton (1999) referred to the state of community ecology at that time as 'a mess' and questioned whether community ecology even had a future. Lawton (2000) particularly criticized the localized approach to understanding communities, noting that 'the details and many of the key drivers appear to be different from system to system in virtually every published study … and we have no means of predicting which processes will be important in which types of system'. Lawton is hardly alone in raising concerns over the lack of progress in the field of community ecology (see, for example, Cuddington & Beisner 2005; Ricklefs 2006). Castle (2005) acknowledged the abundant discussions in community ecology over theory during the past 50 years, but questioned how much new knowledge actually has been acquired.

This general disappointment in progress made in community ecology is mirrored by the souring on the niche-based approach that has been taking place in invasion biology. For example, Williamson (1996) did not believe a niche-based approach to studying invasions held much promise, bluntly concluding, ‘it looks as if models of invasion based on niches will be as disappointing as other community studies of niches’. More recently, the use of niche theory in invasion biology has been criticized by Bruno et al. (2005), who charged the field with uncritically accepting the niche-based competition paradigm for several decades. Although small-scale experiments involving constructed environments and communities have often found the invasibility of environments to be inversely correlated with the environment’s species richness (see, for example, Naeem et al. 2000; Fargione & Tilman 2005; Stachowicz et al. 2002), most larger-scale studies have found little support for a biotic-resistance model based on species diversity, (see, for example, Stohlgren et al. 1999; Levine et al. 2004; Richardson et al. 2005). In fact, more typically, among naturally occurring environments, species-rich communities have been found to accommodate more introduced species than species-poor communities (see, for example, Stohlgren et al. 2003; Wiser & Allen 2006; Belote et al. 2008).

Certainly, if the impacts of biotic interactions on community assembly are very weak, whether because species respond similarly to one another and to the environment, and/or because regional and stochastic processes normally overwhelm the effects of biotic interactions, then it would seem a niche-based model would be a poor choice to represent community assembly involving recently introduced species. Nevertheless, despite increasing reservations by many about the use of a niche-based and competition approach to understanding invasions, and despite the fact that most data do not support the diversity–invasibility hypothesis, or the related notion of species saturation (Stohlgren et al. 2008), niche-based invasion models have continued to play a major role in invasion theory (see, for example, Shea & Chesson 2002; Fargione et al. 2003; Tilman 2004; Melbourne et al. 2007). Are these models contributing positively to our understanding of invasion dynamics, or are they an example of how some approaches and ideas are able to persist in ecology without strong empirical support, perhaps, as suggested by Graham & Dayton (2002), owing more to other factors, such as the prominence of some of those advocating the ideas?

Levins (1966) observed that good theory rests on three pillars: generality, precision and realism. For biological invasions, niche theory may score high on the first pillar but low on the other two. A question worthy of discussion is whether the localized and niche-based approach to invasions, embodied most clearly in the diversity–invasibility hypothesis, has hindered more than it has helped progress in the field of invasion biology. The localized and niche-based perspective, which, in the early 1980s, likely led the emerging field of invasion biology to focus attention on species traits and local processes, may have delayed the development and emergence of the contemporary view of invasions, which emphasizes history, fluctuating environmental conditions and regional factors (particularly propagule pressure), as well as local processes, in the invasion process (Davis et al. 2000; Lockwood et al. 2005; Rejmánek et al. 2005a; Colautti et al. 2006).

In community ecology in general, and in invasion ecology in particular, it has often seemed difficult for discovery to resolve debates about competing hypotheses and theories. In an unpublished presentation to the British Biological Society in 2004, Peter Grubb expressed this concern, citing the failure of ecologists to reject wrong ideas and faulty interpretations (cited in Grime 2007). Similar concerns were raised by Craine (2005), who noted that some theories in community ecology have persisted in the face of empirical data that have contradicted them. A similar point was made a few years earlier by Graham and Dayton (2002), who argued that without the clarity provided by empirical discovery, some ideas, theories and approaches have dominated the field of ecology despite being supported by little empirical data.

As pointed out by Richardson and Pyšek (2008), although the field of invasion biology has proved itself very prolific in generating new hypotheses and theories, it seems much less inclined, or able, to reject them. This has resulted in a field characterized more by theory accumulation than theory discrimination. This is not a call to halt the formulation of new theory. In fact, recent efforts to develop more overarching and integrative theories (see, for example, Moles et al. 2008; Barney & Whitlow 2008; Catford et al. 2009) are exactly what the field needs. Rather, this is a call to recognize that some theories and hypotheses simply have found little support from empirical data and that, in these instances, it might be best to take these theories off the table. For some reason, this seems a challenge for the field, as illustrated by the Rasputin-like persistence of the diversity–invasibility hypothesis. There is an overwhelming lack of supporting evidence for this hypothesis, beyond support provided from some small-scale constructed communities. In fact, most data from natural systems have shown that increased invasibility tends to be associated with species-rich, not species-poor, communities. Nevertheless, this hypothesis still exhibits considerable vitality in the field, and there is little sign that it is about to be retired any time soon. Why has the field of invasion biology been so hesitant, unwilling or unable to reject this hypothesis?

20.3 THE PROBLEM OF OVERSTATING CLAIMS AND CONCLUSIONS

In any discipline, it is important that preliminary ideas, or tentative conclusions made on the basis of one or a few studies, do not acquire a life of their own, eventually assuming a level of validity and generality that is unjustified on the basis of the actual data. Unfortunately, with common citation practices, it is very easy for this to happen. Lamenting the vitality and longevity of many inflated scientific claims, Gitzen (2007) observed, ‘Once bold claims about ... a weak result are published, their sins are forgiven and they can be worked into future introductions and discussions at will’.

The process by which preliminary conclusions become inflated generalizations often involves a series of small missteps, each one of which might be regarded as mostly innocuous. For example, when citing a particular finding or conclusion for the first time, authors often take the time to describe the particular context in which the specific finding or conclusion was made. At a later time, the same author may then cite this same finding in another manuscript, or other researchers, without having actually read the original source, may use the information provided by a secondary reference to cite the original work. In both cases, it is common for these subsequent references to leave out the details needed to assess the reliability and generality of the original finding or conclusion. As time goes on, it is not uncommon for the finding or conclusion to be simply stated as fact, with a perfunctory citation of the original author. By now, the original findings or conclusions are often included as boilerplate in introductions and conclusions of articles and proposals. After enough of these iterations, the original finding can become such an integral part of accepted ecological wisdom that many authors feel comfortable in reporting it without citing any source at all. The general problem is that the more often that preliminary ideas and tentative conclusions are presented as an axiomatic starting point for further discussion and research, the more likely it is that practitioners, particularly young practitioners, begin to regard the statements as factual, believing that they have having been thoroughly and comprehensively empirically confirmed.

A particular striking example of this phenomenon in invasion biology is the conclusion by Wilcove et al. (1998) that non-native species are the second greatest threat to the survival of species in peril. This statement was cited more than 700 times in the decade after its publication, and, no doubt, in many research proposals, management documents and college classes. By the early 2000s, this statement had become common, boilerplate for invasion literature, the conclusion often presented as fact. Given the limitations and some biases in the information used by Wilcove et al. to come to their conclusion, it is difficult to believe that all those who have cited this article actually have read it. First, as the authors were careful to make very clear, little of the information used to support the claim that non-native species were the second greatest extinction threat involved actual data:

> ‘We emphasize at the outset that there are some important limitations to the data we used. The attribution of a specific threat to a species is usually based on the judgment of an expert source, such as a USFWS employee who prepares a listing notice or a state Fish and Game employee who monitors endangered species in a given region. Their evaluation of the threats facing that species may not be based on experimental evidence or even on quantitative data. Indeed, such data often do not exist. With respect to species listed under the ESA [(Element Stewardship Abstract, prepared by The Nature Conservancy)], Easter-Pilcher (1996) has shown that many listing notices lack important biological information, including data on past and possible future impacts of habitat destruction, pesticides, and alien species. Depending on the species in question, the absence of information may reflect a lack

> of data, an oversight, or a determination by USFWS that a particular threat is not harming the species. The extent to which such limitations on the data influence our results is unknown.'

Second, despite the fact that the article is commonly cited as support for a global claim of extinction threat by non-native species, Wilcove et al. only addressed threats to species in the USA. Third, Wilcove et al.'s findings are dramatically affected by the inclusion of Hawaii, which, although of course part of the USA, clearly has a dramatically different invasion history than does the continental, and substantially majority, portion of the country.

A similar review of extinction threats in Canada found introduced species to be the *least* important of the six categories analysed (habitat loss, overexploitation, pollution, native species interactions, introduced species and natural causes, the last including stochastic events such as storms) (Venter et al. 2006). Venter et al. (2006) reanalysed Wilcove et al.'s data excluding Hawaii and found that the USA and Canada did not differ in the threats posed by introduced species, meaning that the high ranking of non-native species as an extinction threat was due almost entirely to the inclusion of Hawaii. Other studies that have examined species threats over a much larger global area have come to similar conclusions. For example, in their analysis of the causes of species depletions and extinctions in estuaries and coastal marine waters, Lotze et al. (2006) concluded that the threat of non-native species was negligible compared with exploitation and habitat destruction. In Australia, non-native species have been reported to have contributed to the extinctions of some native mammals (see Finlayson 1961; Kinnear et al. 1998). However, the fact that declines in the native species typically began decades before the introductions of species such as cats and foxes (often reputed to be the causes of the extinctions), and the fact that species introductions are usually associated with other types of anthropegenic change that are believed to have contributed to the declines (for example land use change), it is difficult to ascribe extinctions of Australian mammals exclusively to non-native species (Abbott 2002; McKenzie et al. 2007). At the same time, it is likely that non-native species have contributed to some of the Australian extinctions, for example by causing local extinctions of small remnant populations created by drought or land use change (Morton 1990; McKenzie et al. 2007). I am not arguing that non-native species never cause extinctions on continents, just that they are rare and that, on a global scale, they are certainly not the second greatest extinction threat.

Wilcove et al. (1998) cannot be singled out as solely responsible for their preliminary and region-specific conclusion ascending to the status of ecological canon. After all, as shown above, they were careful to describe the limitations of their data. And the title of the article makes it clear that their focus was just regional (the USA), not global. However, the authors must shoulder part of the responsibility. For example, they concluded that 57% of imperilled US plants were threatened by predation or competition from alien species. Because predation is unlikely to be a common threat to plants, one must assume the authors meant to imply that most of the threat to native plants came from non-native plant species. However, it is widely known that the impacts of non-native plants on biodiversity are much less than those of non-native pathogens, herbivores and predators (Rejmánek et al. 2005b). Moreover, when the paper was written there was no evidence that a single native North American plant species had been driven to extinction, or even extirpated within a single US state, by competition from an introduced plant species (John T. Kartesz, Biota of North America Program, University of North Carolina, personal communication). Therefore, concluding, or implying, that non-native plant species threaten a large portion of the US flora with extinction seems quite unjustified. Moreover, the authors certainly would have known that the inclusion of Hawaii in their analyses significantly influenced the results.

Although Wilcove et al. should be held partly accountable for framing their conclusions as they did, the primary responsibility for their conclusion's ascendancy to boilerplate must lie with those who continued to cite the article's region-specific conclusion as a generally accepted global fact, even in the face of considerable and increasing evidence showing that non-native species do not represent a major extinction threat to most species in most environments, with the exception of islands and other insular environments (for example lakes and other freshwater systems), where there are many examples of introduced species causing extinctions. Even in some recent and prominent publications, Wilcove et al. (1998) has been cited as justification for making global statements about non-native species being one of the top two extinction threats, (see, for example, Perrings et al. 2005). In some cases, the statement that non-native species are the second most important cause of species extinctions is made without any citation at all, but simply stated as fact (see, for example, Shine et al. 2005).

There are many documented instances of non-native species causing extinctions in insular environments, particularly oceanic islands and freshwater lakes (Blackburn et al. 2004; Cox & Lima 2006; Sax & Gaines 2008). However, the data collected for terrestrial continental environments and marine systems overwhelmingly show that introduced species seldom drive native species to extinction. Without question, some introduced species in marine and continental terrestrial environments produce other sorts of consequences that may be deemed undesirable, including seriously disrupting ecological services and dramatically reducing the population sizes of some native species. These, and any other impacts that are well documented by actual data, are the effects that should be emphasized. It is time the field puts to rest once and for all any and all general claims that introduced invasive species represent the second greatest global extinction threat to imperilled native species, and instead focuses on the many other sorts of effects that non-native species are having, including impacts on biodiversity that do not involve actual extinctions (Gaertner et al. 2009; Davis 2009).

20.4 CONCLUSIONS

It is the nature of scientific disciplines to face challenges. Disciplines will be most successful if the primary challenges and obstacles they face are those complexities inherent of their subject of study. Disciplines become less effective if they are sidetracked or impeded by obstacles of their own making. The field's very close ties to community ecology when the modern field was emerging in the early 1980s provided opportunities and obstacles. Given the focus of community ecology at that time, the field of invasion biology focused considerable attention on species traits and local and deterministic factors. In particular, a niche-based approach guided much of the field's initial efforts to understand invasion establishment and what makes some environments more invasible than others. Although data frequently have not supported niche-based theories, and despite the fact that Williamson (1996) concluded in his comprehensive review of the field that a niche-based approach to understanding invasions seemed unlikely to offer much of value, this approach has continued to play a prominent role within the field. Unfortunately, this emphasis was, to some extent, at the expense of attention paid to the importance of regional and historical factors in the invasion process, which may have impeded the field's growth. Fortunately, the importance of historical and regional factors has been widely recognized in recent years and invasion biology of the future should be characterized by a more integrated approach, one that recognizes the importance of both local and regional processes.

The problem of preliminary conclusions and tentative statements being transformed into invasion gospel is a challenge the field of invasion biology needs to work hard at preventing. If invasion biology is to be a highly regarded scientific discipline, its primary assertions and conclusions need to be based on comprehensive and thoroughly vetted data sets. When conclusions are preliminary or based on data from a particular region, ecosystem or type of organism, they need to be presented as such, and those that cite these preliminary or limited conclusions need to portray them accurately as such. It is vitally important scientists police themselves in this regard. If we do not, then eventually others will, with a much greater negative and long-lasting impact on the field's credibility.

Fifty years after Elton's book, I believe that the field of invasion biology is undergoing considerable change as it develops into a more nuanced and less intellectually isolated discipline. This is partly due to the influx of many young investigators, who have been attracted to the intellectually rich and socially relevant field developed during the 1980s and 1990s. This bodes very well for the field's future. Disciplines begin to stagnate in the absence of new participants and perspectives (Reiners & Lockwood 2010). The influx of new minds and perspectives into the field is exactly what will ensure the field's vitality in the coming decades. The new investigators and new ideas represent opportunities, not unlike the way that introductions of species can provide the long-term residents with new ecological and evolutionary prospects.

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