Chapter three

Invasion biology 1958-2005: the pursuit of science and conservation

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INTRODUCTION

The history of invasion biology would be a dream dissertation topic for some history of science graduate student. The list of researchers who have weighed in on the topic at one time or another reads like a Who's Who of late 20th century ecology. Controversy and disagreements, occasionally resulting in lively exchanges among researchers, have created an intellectually dynamic and sometimes emotionally charged atmosphere in recent years. Authors of both technical and popular articles have often used evocative language and imagery in their writing. Some of the issues have attracted the interests of scholars outside the biological sciences, particularly philosophers. And, for the past several decades, invasion ecology research has been conducted within a larger social milieu of contentious environmental values and politics. No doubt for all these reasons, invasion ecology has captured the attention of national and international media outlets, which, having their own agendas, have emphasized and presented particular research findings and perspectives for their audiences.

However, an examination of the field's history should be of interest not just to historians of science but to ecologists as well. After all, a look backwards is

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almost always a good idea before charting new paths. How have research questions changed over time? What have we learned? What continues to challenge our understanding? If we can answer these questions, we can more effectively formulate future priorities. A historical review cannot guarantee answers to these questions, but neither can the answers be obtained without such a review. In researching and writing this chapter, I have strived to provide a historical review of invasion biology since 1958 (the publication date Charles Elton's invasion classic, *The Ecology of Invasions by Animals and Plants*) in order to answer the above questions, and, based on whatever insights could be gained from these efforts, to offer a few suggestions as to how invasion biology might profitably proceed from this point forward.

THE 1960S

In 1964, The International Union of Biological Sciences held its first Biological Sciences Symposium, part of what was to be a series of such meetings designed to focus attention on biological topics having international significance. The objective of the first symposium (held in Asilomar, California) was to bring together geneticists, ecologists, taxonomists, and applied scientists working in the area of pest control and to present and discuss facts and ideas "about the kinds of evolutionary change which take place when organisms are introduced into new territories" (Waddington 1965). The proceedings were published in a *The Genetics of Colonizing Species* (Baker and Stebbins 1965) now regarded as a classic. As would be expected given the organizing group, the book represented a distinctly international initiative, consisting of 27 authors representing 11 countries. The range of topics considered in this volume was broader than the title suggests, and included discussions on the nature of the colonized environments as well as the attributes and genetics of colonizing species. Chapters addressed a broad range of taxa, including plants, insects, birds, mammals, and microbes. The symposium and the book were defined by a strong evolutionary emphasis and participants included many of the prominent evolutionary biologists of the time, including Mayr, Stebbins, Dobzhansky, Wilson (E. O.), Carson, Lewontin, and Waddington. Significantly, authors considered colonists broadly, discussing colonizations that occurred during succession, colonizations of widespread species that had occurred without human assistance, colonizations of native weeds, as well as colonizations of species into new regions occurring as a direct result of human activity. Although the latter group did receive the most attention, participants recognized that common ecological and evolutionary processes underlay the different types of colonizations.

One noteworthy aspect of the book is the striking contrast between the language used by the authors and that commonly used by invasion ecologists today. A careful search of the book's text is necessary to find terms such as 'alien', 'exotic', 'invader', and 'invasion'. Most authors never used these words. A few,

such as Wilson (E. O.), Mayr, and Wodzicki used them occasionally, but the articles and discussions were overwhelmingly guided by nouns, verbs, and adjectives, such as, 'colonizers', 'founding populations', 'introduced', 'non-native', 'new arrivals', 'migration', 'spread', 'geographically widespread'. Thus, participants did not adopt the effusive style used by Elton in his 1958 book, characterized by the frequent use of metaphor and analogy, often with explicit militaristic references. The one exception was Elton's colleague, John Harper, who usually did refer to the new species as 'aliens' and 'invaders' and whose chapter, *Establishment, Aggression, and Cohabitation in Weedy Species,* exhibited some of the same evocative language that Elton used in his book. The opening sentence of Harper's chapter is so reminiscent of the language used by Elton that the latter's influence on Harper can hardly be denied. Harper (1965) began, "The movements of man and his goods have resulted in a bombardment of areas of land and sea by alien species, both by chance and by the deliberate introduction of cultivated plants of the farm and garden."

In the preface to his book, Elton (1958) said his goal was to bring together three streams of thought — faunal history, ecology, particularly population ecology, and conservation. But the conservation theme dominated the book. He opened his book with graphic battlefield examples of invasions and ended the book with two chapters on the need for conservation. In contrast, the Asilomar participants did not consider conservation implications of species colonizations whatsoever (E. O. Wilson, personal communication). The clearly defined agenda of the 1964 Asilomar symposium was the search for generalizations regarding the evolutionary and ecological processes involved in species colonizations. In the 27 chapters and 562 pages of the symposium proceedings, Elton's 1958 invasion classic was cited only three times, once each by Birch, Mayr, and Wilson (E. O.).

As a publication focusing on introduced species, *The Genetics of Colonizing Species* stands starkly alone during this time period. Perhaps it was because the book focused more on evolutionary issues than ecological theory, but the symposium and companion volume elicited almost no response from the ecological community. Despite the publication of this volume and Elton's book seven years earlier, biological invasions did not attract the interest of many ecologists during the 1960s, at least from ecologists whose primary interests and objectives involved the development of theory and generalizations that transcend particular organisms and habitats. It is certainly true that with the development and dissemination of island biogeography theory (MacArthur and Wilson 1963, 1967; Simberloff and Wilson 1969), considerable attention was given to how arriving species would fit into resident communities. However, few ecologists at this time connected their research with the sort of invasion literature and issues summarized and presented by Elton (Simberloff, personal communication).

It must be pointed out that, during this time, some ecologists outside of North America were actively researching and publishing in the area of introduced species. Sukopp (1962) addressed both theory and terminology in his report on introduced species in the natural plant associations of central Europe. Holub

and Jirásek (1967) and Schroeder (1969) presented classification schemes for non-native species (based on the mode of introduction, time of introduction, and degree of naturalization). Faliński (1966) wrote his dissertation on the distribution of introduced species in Poland's Bialowieza Primeval Forest) and Faliński (1968, 1969) and Kornas (1968a, 1968b) published a number of subsequent articles during the 1960s on the ecology of introduced species in natural and semi-natural communities in Poland. Hungarian ecologist Pal Juhasz-Nagy (1964) conducted field experiments in his studies of 'ecesis resistance' (invasibility) and used the term 'ecological homeostasis' to describe communities that were resistant to invasion. Hejný and Lhotská (1964) and Jehlík and Slavík (1968) described the ecology and distribution and spread in natural environments of several introduced species in the Czech Republic. Kohler and Sukopp (1964) studied the ecology of introduced species in cities, part of a long-standing interest among European plant ecologists. (One of the more memorable findings of Kohler and Sukopp was that *Robinia pseudoacacia* had spread spontaneously on the rubble of cities bombed during WWII.) Except for the abstracts, none of the above articles was published in English, and most English-speaking ecologists were probably not well aware of this research during the sixties.

Although biological invasions received little attention from ecologists during the 1960s, particularly in North America, this does not mean that research was not being conducted on introduced species and their impacts. In fact, considerable research on this topic was being conducted in Australia, New Zealand, South Africa, Europe, as well as North America. It was simply being conducted by biologists whose interests and priorities were more applied in nature, involving fisheries (e.g., Albrect 1964), wildlife (e.g., Bump and Bohl 1964, TCWF 1967, Warner 1968), forestry (e.g., Nichols 1961, Taylor 1969) and agriculture (e.g., Salisbury 1961, Metcalf *et al.* 1962, DeBach 1964). The applied and pest-control research conducted in during the 1960s did not represent any new initiative, and very little, if any, of it was inspired by Elton's book. Rather it was a continuation of extensive applied research in this area extending back to the beginning of the 20th century (e.g., Little 1916, Bailey 1924, Bryant 1927, Sim 1927, Wicht 1945), and even earlier (e.g., Merriam 1889, Palmer 1899).

From an historical perspective, a 1966 book by George Laycock was a noteworthy publication during this time. Titled, *The Alien Animals: The Story of Imported Wildlife*, the book was published by The American Museum of Natural History. Well researched, it contained nearly 200 references from the scientific literature. Like Elton's 1958 classic, this book was written from a conservation, and distinctly value-based, perspective, as well as for a larger public audience. On the opening page, Laycock (1966) refers to "man" as "the supreme meddler"; on the book's final page he warns of natural communities being "polluted" by alien species; and titles of his chapters included *Stangers in the Southwest*, *How the Gray Squirrels Invaded England*, and *The Conquering Mongoose*. In the book, Laycock presents twenty case studies of animal introductions around the world that had caused great economic and conservation harm. The book's language, tone, and

series of case studies is very similar to Elton's 1958 book, although, rather inexplicably, Elton was not one of the nearly 200 references listed in the bibliography. However, unlike Elton, Laycock was not a scientist. He was a freelance writer, who, during his career, authored more than twenty books on animals and nature, many of them written for children and young adults. Nevertheless, Laycock's characterization of introduced species seems to have portended the perspective adopted in a large number of invasion ecology literature, both popular and scientific, later in the century, more so than has the Asilomar publication, *The Genetics of Colonizing Species*.

THE 1970S

On April 22, 1970, hundreds of thousands of students and others across the United States celebrated the first Earth Day, an event conceived and organized by Gaylord Nelson, then Senator of Wisconsin. Although Nelson, Rachel Carson, and others had been trying to raise environmental consciousness within the United States during the sixties, the 1970s is when the environmental movement finally captured the public's attention, in the US and throughout the world. SCOPE (Scientific Committee on Problems of the Environment, a committee established by the International Council of Scientific Unions) published the first of its SCOPE Series titles (now numbering more than sixty) in 1971. The 1970s is when conservation biology began to emerge as a discipline and ecologists worldwide began to study introduced species from a conservation perspective. In the early 1970s, the new journal *Biological Conservation* began publishing articles describing the threats posed by introduced species (e.g., Campbell and Ormond 1970, Schofield 1973).

Applied ecologists who had been studying introduced species and their ecological effects in the sixties and earlier, continued to do so in the seventies, publishing primarily in taxonomic-specific journals as they had previously. For example, Owre (1973) described the extent of introduced avifauna in southeastern Florida and raised the possibility of competition between the native and new species (in the conservation section of The Wilson Bulletin). Christie (1972) described the effects of species introductions on salmonid communities (Journal of the Fisheries Board of Canada), and Moyle (1973) reported on the effects on the native frogs of the introduced bullfrogs in California (Copeia). In a *Bioscience* review paper, Courtenay and Robins (1975) summarized the conservation problems (primarily in North America) created by the introduction of "exotic" animals by fish and game agencies and the pet trade. The European ecologists who had been studying introduced species and their ecological effects in the sixties also continued their research in the seventies, publishing hundreds of papers on this topic. For example, Faliński (1971) and Sukopp (1971) continued their work on the urban introduced and adventitious flora and Jehlík and Hejný (1974) continued their research in the Czech Republic, describing migration routes of introduced species

and making what perhaps were the first predictions of when plant invasions would occur in particular locations (Hejný *et al.* 1973). Although this floristic approach to introduced species was not as common in the United States at this time, occasional studies of this type were undertaken, e.g., Muehlenbach's (1977) detailed account the adventive flora along railroads around Saint Louis, Missouri.

Occasional papers on biological invasions can be found in the ecological literature well before the 1970s (e.g., Egler 1942). However, the seventies was the first time since Elton that biological invasions began to appear in mainstream ecology literature with any frequency. In his review of the ecology of weeds, published in *Annual Review of Ecology and Systematics*, Baker (1974) explicitly extended the discussion of weeds beyond the disciplinary boundaries of horticulture and agriculture to include ecology. Other examples include Burdon and Chilver's 1977 *Oecologia* article on the impact of introduced pine species on Australia's eucalyptus forests, and Embree's (1979) chapter on the ecology of animal invaders in the book, *An Analysis of Ecological Systems* (Horn *et al.* 1979).

Although some ecologists were beginning to think about biological invasions during the seventies, there was still little coordination and communication among investigators. And, there was no formal infrastructure to support efforts to develop a theory of biological invasions. Ecology meetings at that time did not devote special symposia or paper sections to biological invasions, which would have served as important communication hubs for this topic. Thus, although scattered papers on biological invasions were appearing in the ecological literature, invasion ecology had not yet emerged as its own research specialty area.

1980-1984

The number of published studies on biological invasions increased dramatically during the 1980s, especially in particular taxa, such as plants (see review by Pyšek 1995). The emphasis on floristics that characterized much of the work in previous decades began to give way to the increasing interest on species biology and ecological interactions (Pyšek 1995). Due to the proliferation of invasion publications during this time, the historical account of this decade has been split into two periods.

Many of the European ecologists who had been studying introduced and adventive flora in prior decades continued to do so in the eighties, particularly focusing on the ecology of urban flora (e.g., Sukopp and Werner 1983, Kowarik 1984). In the United States, Richard Mack published his first article on biological invasions in 1981, reporting on the ecological impact in western North America of *Bromus tectorum*. Mack took a conservation approach in his article, quoting Elton and emphasizing the decline of native grass species. He chose to submit his article to the more applied journal *Agroecosystems* because its scope encompassed the ecosystems that cheatgrass had invaded. In the same year, Dan Simberloff contributed a chapter to the book *Biotic Crises in Ecological and Evolutionary Time*

(Nitecki 1981). The title of the book suggests that Simberloff (1981) might also have emphasized the conservation aspects of biological invasions. In fact, he did not do this, but rather used biological invasions as a way to test ecological theory, e.g., island biogeography theory and models of limiting similarity. Thus, whereas Mack's (1981) article was more in the conservation tradition of Elton's 1958 book, Simberloff's chapter was more in keeping with the emphasis on ecological and evolutionary theory that distinguished *The Genetics of Colonizing Species*. In the same year, Brown and Marshall (1981) published an article even more reminiscent of the 1965 Asilomar proceedings, emphasizing the evolutionary changes accompanying the colonization of plants. Two years later, Moulton and Pimm (1983) examined the impacts of the introduced Hawaiian avifauna as a way to assess the importance of competition in community assembly. Like Simberloff and Brown and Marshall, they also emphasized theory, as evidenced by their choice of journal (American Naturalist). The tone and style used by Simberloff (1981), Brown and Marshall (1981), and Moulton and Pimm (1983) was consistent to that used by the contributors to *The Genetics of Colonizing Species* (other than Harper).

The connection between introduced species and conservation continued to grow during the 1981. *Immigrant Killers* (King 1984), described the impact of introduced predators on native birds in New Zealand. Although written for a popular audience, King's book was well researched and referenced, and it represented an important scientific contribution as well.

In 1981, William Jordan III and the University of Wisconsin Arboretum published the first issue of *Restoration and Management Notes* (now published under the name of *Ecological Restoration*), an event that signified the beginning of an organized interest in habitat restoration in North America. Land managers had been thinking about restoration in the 1970s. For example, NATO sponsored a 1976 conference in Reykjavik, Iceland that resulted in the publication of *The Breakdown and Restoration of Ecosystems* (Holdgate and Woodman 1978). Europeans constituted the majority of participants at the Reykjavik conference and the interest at the meeting was more in "rehabilitating" the landscape rather than trying to restore the habitat to some prior native condition, as illustrated by a statement by Bradshaw *et al.* (1978), "from the point of view of nature conservation, rehabilitation should not necessarily mean restoration of the original, often uninteresting, ecosystem". This perspective contrasted greatly with the emerging interest in ecological restoration in the United States. In his opening editorial of the first volume of *Restoration and Management Notes*, William Jordan III (1981) stated that the new journal "will deal only with the development and management of communities that are native or at least ecologically appropriate to their site." The stated focus of the journal was to be the restoration and management of ecological communities for scientific and aesthetic purposes, e.g., prairies, wetlands, and forests, but not for range or timber management, and not for "reclamation efforts aimed solely at land stabilization." The subsequent development of the field of restoration ecology in future years was to have a major impact on

invasion ecology, particularly in North America, through its emphasis on native environments and native species.

By the mid-1980s, more and more ecologists were beginning to think about invasions from an ecological perspective. However, what was still lacking was a synthesis of this thinking that would help define a field of invasion ecology. In fact, the groundwork for such an effort was already underway. In 1980, the Third International Conference on Mediterranean Ecosystems was held in Stellenbosch, South Africa, and interest in biological invasions at the meeting led to a proposal to the SCOPE general assembly in Ottawa in 1982. This proposal resulted in the creation in 1983 of a scientific advisory committee that was to encourage and facilitate focus on the impacts of biological invasions on natural ecosystems. The advisory committee articulated three questions to guide the SCOPE invasion program: 1) what factors determine whether a species will be an invader or not? 2) what are the characteristics of the environment that make it either vulnerable to or resistant to invasions? 3) how can the knowledge gained from answering the first two questions be used to develop effective management strategies? Developed with the intent of "building on the considerable knowledge base available on invaders of agricultural systems", the SCOPE program on biological invasions was clearly conceived in the conservation tradition of Elton. It is no coincidence that scientists from South Africa, Australia, New Zealand, and the United States contributed so significantly to the SCOPE initiative. The natural environments in these countries had been experiencing recent and substantial introductions of new species from other regions of the world and considerable conservation concerns were being raised in these countries regarding the impacts of these species.

1985-1989

South African scientists had been among the leaders in recognizing the conservation implications of introduced species (e.g., Wicht 1945, Taylor 1969) and they published the first SCOPE volume in 1984 (Macdonald and Jarman 1984). However, it was not until the latter half of the decade that most of the SCOPE regional workshops began publishing their proceedings. The North American contingent published *Ecology of Biological Invasions of North America and Hawaii* (Mooney and Drake 1986). The book was organized around various patterns of invasions, including associations with different taxonomic groups, attributes of invaders, and site characteristics promoting invasions. In addition a variety of case studies were provided. This publication was entirely a United States initiative, with both editors and all the contributors being from US universities. That biological invasions had finally captured the interest of prominent North American ecologists is evidenced by the contributors to the book, e.g., Simberloff, Ehrlich, Bazazz, Regal, Orians, Vitousek, Roughgarden, Ewel, Pimm, and Mooney.

Coincidentally, the symposium that led to this volume took place in Asilomar, California, the same site of the symposium on the genetics of colonizing species

held twenty years earlier. The 1986 volume contains an interesting mixture of chapters. Most were clearly conceived and written with a conservation and environmental perspective, as would be expected given the nature of the SCOPE program. However, some chapters were written more in the spirit of the 1964 Asilomar symposium and focused more on ecological theory. Simberloff's (1986) chapter on the biogeography of insect introductions examined topics such as island-mainland patterns and issues of biotic resistance primarily from a theoretical perspective. Although he did cite Elton, Simberloff did not take a strongly conservation approach in his chapter, referring primarily to 'introduced' species and 'colonizers' rather than 'invaders' and 'exotics' and specifically recommended the "refinement of the approach of many of the papers in *The Genetics of Colonizing Species*. Bazzaz (1986) organized his chapter on life histories around the concept of 'colonizing species' and also made explicit references to the 1965 book. Moulton and Pimm (1986) expanded on their 1983 paper and showed how biological invasions can be used to test ecological theory.

Additional proceedings were published from SCOPE workshops held in South Africa, Australia, and Great Britain (e.g., Macdonald *et al.* 1986, Groves and Burdon 1986, Kornberg and Williamson 1987). Being SCOPE initiatives, these publications were also written from a conservation perspective. However, comments by the editors of the Australian proceedings indicate that they recognized an emerging tension that was developing in invasion ecology as some ecologists embraced the conservation and strong environmental emphasis articulated by Elton, while others expressed concern over the strong normative nature of this approach. In the Foreword to the 1986 publication (Groves and Burdon 1986), the editors stated that "the terminology associated with 'invasions' generally is unsatisfactory with its connotations of a military operation. .... Wherever possible we have tried to eliminate emotive terms such as 'weeds', 'pests', 'exotics', and 'aliens'." Instead, the editors strived to utilize the word 'introduced' as much as possible throughout the book.

Another important development that occurred during this time period was the founding in 1987 of the Society for Ecological Restoration (SER), now known as Society for Ecological Restoration International. SER emerged out of the rapidly developing interest in restoration by individuals and conservation groups interested in managing natural environments. Upon its founding, SER was primarily a North American initiative, and the restoration ecology movement that it represented and inspired sharply distinguished between species based on their geography of origin, with native species being desirable and non-natives being undesirable in natural environments. The stark dichotomy between native and non-native species particularly characterized conservation and restoration efforts in regions like North America, Hawaii, and New Zealand, which had experienced relatively few species introductions until the past few centuries. This distinction seemed to be less crucial among conservationists and restorationists in Europe where, as Usher (1988b) acknowledged, distinguishing between native and introduced species is often problematic due to the millennia of human movements and

species introductions across the continent. Restoration ecology and invasion ecology emerged at about the same time, and, in North America, they developed as sister disciplines during the latter1980s, and continued to reinforce one another in subsequent years.

The growing relationship between invasion ecology and conservation ecology during this time was illustrated by the decision of the editors of the journal *Biological Conservation* to devote a special issue to this topic. Titled, *Biological Invasions of Nature Reserves*, this publication (Usher 1988a) represented another SCOPE product. Although it was becoming increasingly common for ecologists to adopt the more explicit conservation perspective emphasized by the SCOPE program, not all ecologists were doing so. For example, in his article on invasion windows, Johnstone (1986) examined habitat invasibility mostly from a theoretical perspective, and he did not link his article to conservation concerns regarding invasions.

The decade ended with the publication of *Biological Invasions: A Global Perspective* (Drake *et al.* 1989), the synthesis report of the various regional SCOPE symposia and workshops. This publication represented the 37th publication in the SCOPE series. Twenty-nine ecologists, representing seven countries (USA, UK, Australia, South Africa, France, Denmark, India), many of whom had contributed to the 1986 volume, authored chapters for this publication. Some of the prominent non-American contributors, many of whom have continued to focus much of their research on biological invasions up to the present, included Francesco di Castri, Peter Ashton, David Richardson, Ian Macdonald, Michael Usher, Mark Williamson, Richard Hobbs, Michael Crawley, Richard Groves and Marcel Rejmanek. (Rejmanek had moved from Czechoslovakia to the United States by the time the book was published.). Individually focusing on different taxa or regions of the world, contributors tried to answer the three questions that had been posed by the SCOPE advisory committee in 1983. In the book's final chapter, Mooney and Drake (1989) concluded that although knowledge permitted "generic guidelines" for assessing the likelihood of biological invasions, e.g., disturbances normally increased invasibility, they concurred with the conclusions reached by most of the authors that it was not possible at that time to make accurate predictions about individual cases.

Although some of the North American ecologists continued to use the terms 'introduction' and 'introduced species' rather than 'invasions' and 'invaders' in the 1989 volume (e.g., Simberloff and Pimm), possibly indicating some resistance to adopting the more value-based conservation approach, it is interesting that the frequency with which American ecologists cited Elton's 1958 book continued to increase. In 1965, only three of the eleven (27%) US contributors to *the Genetics of Colonizing Species* cited *The Ecology of Invasions by Animals and Plants*. In the North American 1986 SCOPE volume, which was authored entirely by US ecologists, 56% of the chapters cited Elton's book. And in the 1989 SCOPE synthesis volume, 8 of the 9 (89%) US authored chapters cited Elton's book. By contrast, only 2 of 11 (18%) of the chapters in the 1989 SCOPE volume authored entirely by non-US ecologists cited Elton. (Two of the chapters were authored by at least

one US and one non-US author; one of these cited Elton and the other did not.) In the book's final chapter, Hal Mooney and James Drake (both US ecologists) specifically encouraged the readers to consult Elton's book: "Those wishing an in-depth treatment of the dynamics of biological invasions are referred to Elton's (1958) classic work, and to the publications which arose out of the program" [i.e., the SCOPE program].

The scattered ideas concerning biological invasions put forth by ecologists in the seventies and early eighties finally coalesced in the mid to late eighties, resulting in the publication of a number of important papers and edited volumes from 1986-1989. These publications reviewed knowledge and theory to that point, identified questions to be answered, and set much of the direction for future research of biological invasions. In short, invasion ecology emerged as a research specialty area during this time period as a direct result of these publications. Although, some investigators continued to pursue invasion ecology more in the tradition of the 1964 Asilomar symposium on colonization, i.e., focusing primarily on ecological and evolutionary theory, more and more ecologists, particularly North American ecologists, were presenting their writings in an explicitly environmental context, the path set forth by Elton in 1958.

1990-2005

Invasion ecology took the spotlight following the series of invasion books and articles published between 1986 and 1989. Biological invasions became a popular area of research and an increasingly controversial topic of debate during the 1990s resulting in a flood of publications, both scholarly and popular, that continues to this day. National and international ecology meetings, and some general science meetings (e.g., AAAS) began to regularly schedule symposia and paper sessions devoted to biological invasions and introduced species during the nineties. The first of seven international conferences on the ecology of alien plant invasions was held in Loughborough, UK in 1992, and the 7th conference was held in Fort Lauderdale, Florida, USA in 2003, and several of these conferences resulted in publications of the proceedings (e.g., Pyšek *et al.* 1995, Starfinger *et al.* 1998, Child *et al.* 2003). With the exception of the second and seventh conferences (held in Tempe, Arizona and Fort Lauderdale, Florida), the conferences took place in Europe, with European ecologists representing the majority of participants. Thus, this series provides an excellent overview of the research and ideas coming from Europe at this time, particularly from eastern European countries such as the Czech Republic, which, as stated above, have had a long tradition of studying invasions. Some of the prominent ecologists who played a significant role in these conferences and publications include Petr Pyšek and Karel Prach (Czech Republic), Ingo Kowarik and Uwe Starfinger (Germany), Mark Williamson, Max Wade, and Lois Child (UK), Giuseppi Brundu (Italy), and John Brock and Marcel Rejmanek (USA).

Unlike the time periods described above, the years 1990-2005 do not offer an obvious list of important publications, due to the sheer number of books and articles produced during this time. Thus, the publications briefly mentioned below constitute a very small representative subset of the large number of significant publications one could have included.

Lodge's 1993 TREE article provided a comprehensive overview and assessment of the field of invasion ecology to that point. Consistent with prior assessments, Lodge concluded that it was not yet possible to accurately predict the consequences of a single invasion event and that any hope of useful predictions could only emerge from focused studies on particular species and environments. Lodge's paper was distinctive because it contained well developed aspects of both the conceptual approaches to biological invasions that had developed during the preceding three decades. While Lodge began his paper emphasizing the environmental impacts of 'exotic' species, which have "serious consequences for both man and nature", he also stressed the scientific opportunity that invasions provide, "because the characteristics and ecological impact of exotic species may provide clues to longstanding issues in the study of community assembly". Consistent with this dual emphasis, Lodge cited both Elton (1958) and Baker and Stebbins (1965) in the same sentence, referring to them both as 'classics'. Williamson's 1996 book *Biological Invasions*, which reviewed and synthesized invasion research and theory conducted and developed during the prior several decades, made a very important contribution by providing investigators a comprehensive and up-to-date overview of the new and rapidly evolving field. Williamson's book primarily focused on the scientific aspects of species invasions, however he did set the book in a clear conservation context, emphasizing the management value of better scientific understanding of invasions. James Carlton's numerous publications on the impacts of invasions on marine ecosystems (e.g., Carlton 1996a, 1996b, 1999) prompted more marine ecologists to consider the importance of biological invasions. The publication of *Biological Invasions: Theory and Practice* by Japanese ecologists Shigesada and Kawasaki (1997), which reviewed mathematical models of species spread, illustrated the extent to which biological invasions had attracted the interests of ecologists from around the world.

The importance of understanding interactions with soil microbes (positive and negative) as part of the invasion process in plants was emphasized by Klironomos (2002) and Richardson *et al.* (2000) emphasized the role that mutualisms can play in the invasion process. The enemy-release hypothesis received considerable attention during this time, although studies produced conflicting results (Keane and Crawley 2002). Williamson (1993, 1996) proposed the since oft-cited 'tens rule' of biological invasions, which states that approximately 10% of imported species exist in some sense outside of captivity, 10% of these established self-sustaining populations, and 10% of these become pests. Reviving the emphasis on genetics of colonizing species that characterized the 1964 Asilomar symposium, many ecologists began focusing on the genetics of introduced species, recognizing

the importance that new genotypes might play in species spread (Ellstrand and Schierenbeck 2000, Vila *et al.* 2000, Daehler and Carino 2001, Pysěk *et al.* 2003). Ewel *et al.* (1999) reviewed the benefits and risks associated with deliberate species introductions and outlined the research needed to provide the information required to increase the former and lower the latter. As invasion ecology continued to develop during this period, several scientists expressed concern that the field was not well connected with other disciplines and that invasion ecology was not being informed by, nor informing, disciplines such as biogeography, evolutionary biology, and ecological subdisciplines, such as succession ecology and weed ecology (Vermeij 1996, Davis *et al.* 2001, Davis *et al.* 2005). At the same time, some conscious efforts were being made to bridge these gaps (e.g., Booth *et al.* 2003).

During the nineties, ecologists continued the several decades-long effort to determine whether invaders possessed distinctive traits. Many researchers concluded that there was little difference between the traits of invasive and non-invasive species (e.g., Thompson *et al.*, 1995, Goodwin *et al.* 1999, Williamson 1999), although some taxonomically-based comparative studies did show distinct differences between resident and spreading introduced species (e.g., Rejmanek and Richardson 1996). Kolar and Lodge (2001) were more optimistic that traits could be used as predictors of invasions, concluding that quantitative approaches (e.g., Daehler and Carino 2000) were making progress and that these approaches should "allow us to predict patterns of invading species more successfully." Unlike Lodge's 1993 paper which emphasized both the conservation and scientific implications of biological invasions, the 2001 TREE paper by Kolar and Lodge was much more strongly organized around the conservation and environmental concerns about species invasions.

Factors that contribute to an environment's susceptibility to invasion (invasibility), one of the other organizing themes of the SCOPE initiatives in the 80s, also continued to be a central focus of research and discussion during the 90s and the early years of the new century. In his book *Biological Diversity*, Huston (1994) addressed invasibility and emphasized the combined importance of disturbance and productivity. Lonsdale (1999) presented his findings of a comprehensive review of global patterns of plant invasions and found a positive correlation between native and exotic species at a site, although he concluded that it was difficult to discriminate between the relative importance of invasibility and propagule pressure. Davis *et al.* (2000) argued for a theory of invasibility based on resource availability, emphasizing that invasibility is not a constant characteristic of an environment but is an attribute that varies over time as resource availability fluctuates. Davis and Pelsor (2001) tested this theory in a field experiment based on the introduction of native species (prairie forbs) into a plant community dominated by introduced species (North American old field), showing that it is the ecological processes that matter, not the geographic origin of the species involved.

Although much of the progress in invasion ecology during the eighties and nineties involved moving beyond purely floristic studies of native and introduced

flora, more comprehensive efforts to describe and catalog flora were also undertaken during this time, providing valuable data bases for ongoing and future studies (e.g., Pyšek *et al.* 2003). The most comprehensive national or regional plant data bases at the current time are likely those of the United Kingdom (Clement and Foster 1994, Ryves *et al.* 1996), the Czech Republic (Pyšek *et al.* 2002), and Austria (Essl and Rabitsch 2002). Other excellent plant data bases include those in Germany (Klotz *et al.* 2003) and North America (Kartesz and Meacham 1999).

With the development of invasion ecology as a recognized research specialty area, two invasion related journals were established in the late nineties. *Diversity and Distributions* (Blackwell Publishing) was founded in 1998 (succeeding the journal *Biodiversity Letters*) with an emphasis on biological invasions and biodiversity. David Richardson has served as the journal's editor-in-chief from its outset. *Biological Invasions* (Kluwer) was founded in 1999 with James T. Carleton as the editor-in-chief, a position currently held by James A. Drake. The stated aims and scopes of both journals emphasize the science rather than the conservation aspects of biological invasions. However, it is not uncommon for authors to invoke conservation concerns in their articles, particularly in *Biological Invasions*.

Two developments in ecology during the 1990s particularly impacted invasion ecology — a renewed emphasis on the ecological effects of biodiversity and the increasing emphasis on global change. Research on the ecological impacts of biodiversity focused attention on Elton's (1958) hypothesis that species-rich communities should be more resistant to invasions than species-poor communities. A number of small-plot experimental studies involving constructed plant communities yielded results that supported Elton's diversity-invasibility hypothesis (Tilman 1997, Knops *et al.* 1999). However, these experiments were challenged on methodological grounds (Wardle 2001) and their relevancy was questioned since studies in natural communities often found that the most diverse environments were the most heavily invaded (Lonsdale 1999, Stohlgren *et al.* 1999). Efforts have been made to resolve this debate, e.g., emphasizing the role that spatial scale plays in interpreting the results and the fact that correlated environmental factors may affect both diversity and invasibity (Levine and D'Antonio 1999, Levine 2000, Shea and Chesson 2002). However, to date, these efforts have not quelled the controversy (Rejmanek 2003, Renne and Tracy 2003, Stohlgren 2003).

The interest in global change that developed in ecology in the nineties went beyond concerns involving increases in atmospheric CO_2 and climate change. Dukes and Mooney (1999) emphasized the global dimensions of biological invasions and researchers emphasized the cause and effect relationship that existed between biological invasions and other types of global change (Kowarik 2001). As a result of connections made between biological invasions and global change, the topic of biological invasion, historically a rather narrow and specialized area of research, has become part of a much larger and more prominent environmental agenda.

A number of books published during the 1990s and early 2000s, and, like Elton's 1958 book, were written from an explicit conservation and environmental perspective and aimed at the general public. Many of these books utilized similar evocative imagery to capture the public's attention. Examples of such books written or edited by ecologists, or science journalists, include *Life Out of Bounds: Bioinvasions in a Borderless World* (Bright and 1998), *Killer Algae* (Meinesz 1999), *Nature Out of Place: Biological Invasions in the Global Age* (Van Driesche and Van Driesche 2000), *Tinkering with Eden: A Natural History of Exotics in America* (Todd 2001), and *Plagues of Rats and Rubbervines* (Baskin 2002).

With their lamentation over the loss of native environments and decline of native species, the above books illustrate the increasingly strong synergy that had developed between restoration ecology and invasion ecology (particularly in North America) during the nineties, with the objectives of each reinforcing those of the other. Restoration ecology's emphasis on restoring environments with native species affirmed the importance of invasion ecology, and invasion ecology's emphasis on the harm caused by a small proportion of introduced species provided important justification for restoration ecology's preference for native species. However, by the end of the nineties and beginning of this century, more scientists were questioning the dichotomous and normative nature of a perspective that prefers some species over others on the basis of their geography of origin (Gould 1998, Slobodkin 2001), emphasizing the useful contributions that some introduced species might be able to make in restoration projects (D'Antonio and Meyerson 2002). Such objections were not new. In the SCOPE synthesis report (Drake *et al.* 1989), James Brown (1989) made the same arguments regarding the potentially positive value of some introduced species and expressed concern over "a kind of irrational xenophobia about invading animals and plants that resembles the inherent fear and intolerance of foreign races, cultures, and religions", an "attitude" he said he "detected" at the SCOPE conference. Actually, Egler (1942) raised these same concerns forty-seven years earlier. In his article in *Ecology*, he criticized the common resort to hyperbole and military imagery in discussions of alien species and warned against "anthropomorphic sentimentalism that breeds a spirit of defeat". During the nineties, writings of invasion biologists also attracted the attention of philosophers (Eser 1998, Sagoff 1999), who expressed similar concerns over the language and values they said permeated the writings of invasion ecology. Finally, although no ecologists questioned the fact that the earth's biota was becoming increasingly homogenized due to widespread species introductions, the common contention that species introductions lead to declines in regional and local biodiversity was challenged by several investigators (Rosenzweig 2001, Davis 2003, Sax and Gaines 2003), a point that had actually been made much earlier by Harper (1965).

By the end of the nineties, invasion biology was becoming increasingly institutionalized with the establishment of more national and international conservation and biodiversity initiatives relating to biological invasions. The United Nations sponsored conference on "invasive alien species" in Trondheim, Norway

in 1996 (Sandlund *et al.* 1999) led to the formation in the following year of the Global Invasive Species Programme (GISP). GISP was developed explicitly as a conservation and environmental initiative, as evidenced by its mission statement: 'to conserve biodiversity and sustain human livelihoods by minimizing the spread and impact of invasive alien species'. To date, the GISP program has resulted in 27 publications.

In 1998, the European Environment Agency (EEA) highlighted the introduction of alien species as one of the principal threats to Europe's biodiversity in its year-end report on the status of the European environment (EEA 1998). In 1999, President Clinton signed Executive Order 13112, which authorized US federal agencies to prevent the introduction of alien invasive species, control the spread of alien invasive species in the United States, and restore native species and habitats that had been invaded. In 2000, IUCN (The World Conservation Union) passed 'Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species' and published the guidelines on its website in 2001. In 2002, the Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States published its final report (National Research Council 2002). The final report of GISP's first phase was published in 2004 (Mooney *et al.*), and biological invasions was the theme of the 2004 annual meeting of AIBS (American Institute for Biological Sciences).

It is clear that forty-six years following the publication of Elton's 1958 classic, interest in biological invasions was stronger than ever both within and outside the scientific community, particularly with respect to the conservation and management aspects of introduced species.

LOOKING AHEAD: ANY LESSONS AND INSIGHTS FROM THE PAST?

Are there any lessons we can learn from this brief look over our shoulder? Can we gain any insights that might help us chart a productive path for the future? I think so. Of course, exactly what are those lessons and insights will likely be a matter of lively debate. Thus, the thoughts that follow are not intended to be prescriptive, but rather to focus discussion on how ecologists interested in biological invasions might best proceed from this point forward.

Two roads, one less traveled than the other

After the Asilomar conference in 1964, those interested in studying species introductions were presented with two distinct paths. They could take the strongly conservation and environmental approach advanced by Elton, or they could adopt the more value-neutral and more strictly scientific approach exhibited by *The Genetics of Colonizing Species*. The Eltonian path could be described as a top-down, deductive approach, in which an effort was made to apply general ecological theory and principles to biological invasions in order to help develop control management programs

for specific invasions. Conversely, the Asilomar path could be considered more of a bottom-up, inductive approach, in which individual colonizations/invasions are examined in an effort to better inform general ecological theory and understanding of communities and populations. Another way to contrast the two paths might be to characterize the Eltonian path as a Platonic approach and the Asilomar path as an Aristotelian approach (*sensu* Sagoff 1993).

Although there have been some exceptions and occasional resistance by some ecologists over the years, invasion ecology has become increasingly more allied with the Eltonian approach, particularly in the United States, during past few decades. There are probably many explanations for this. Ecologists such as Aldo Leopold, Rachel Carson, and Paul Ehrlich were instrumental in raising the public consciousness on environmental issues which resulted in the emergence of the environmental movement during the 1970s. This movement attracted the attention not only of the general public, but also of many other ecologists. Whereas much of the focus in ecology in the 1950s and 60s had been on theoretical issues involving population dynamics and community assembly, desire, even pressure, to apply ecological knowledge to environmental problems began to be expressed, both from within the discipline and from society at large. Society in the US and elsewhere had long applied an ecological approach to introduced pests of fisheries, forests, and agricultural systems. The Eltonian path extended this approach to natural systems that were not necessarily providing direct economic benefits. Without question, the founding of the SCOPE initiative on invasions in the early 1980s played a major role in defining the conservation focus of invasion biology from that point onward. During the 1980s and 90s, ESA began to advocate a more active public role in general for ecologists, and for itself as an organization. In many ways, what had been a fairly clear distinction between "pure" ecology and "applied" ecology in the 50s, and 60s, dissolved during the latter decades of the twentieth century.

During the eighties and nineties in the United States there was increasing pressure for ecologists to justify their research in a larger social context. This was felt at all levels. To justify its budget to Congress, The National Science Foundation needed to more clearly articulate how the research it funded benefited the public good. In turn, in order to get funded by NSF, individual researchers needed to provide increasing evidence not only of the scientific value of their research but also of its broader impacts, including benefits to society. In addition, irrespective of these infrastructure pressures, some ecologists may have wanted to seek a more public forum for personal reasons, whether out of a sense of social responsibility or simply an interest in participating in policy-making and policy discussions. Probably all these factors in varying degrees played a role in the development of the strong environmental emphasis that now characterizes invasion ecology. Today, invasion ecology has become nearly an equal sibling (at least a close cousin) to the explicitly applied fields of conservation ecology and restoration ecology. One might consider the three fields as constituting a kind of triumvirate, leading the efforts to preserve the earth's biodiversity.

Most major invasion publications and conferences, whether targeted to the general public or to a more strictly scientific audience, are now explicitly framed from a conservation perspective, usually emphasizing current biodiversity threats and potential impending ecological crises, often using language and imagery similar to that used by Elton in 1958. Elton was not the father of invasion ecology, but he might be considered the founder of one path of invasion ecology. This path, the conservation and environmental path, has been well traveled and maintained during past several decades. However, the alternative path, embodied by the 1964 Asilomar conference, while certainly not wholly rejected, has not been as well traveled (Vermeij 1996). The difference has probably been most apparent during the past 20 years, and particularly in the United States. No doubt part of the explanation for this difference is that a large number of ecologists are employed by conservation groups and governmental agencies where they work primarily on applied problems.

Progress vs. effort

If one takes the time to go back and read the invasion and colonization literature from twenty, thirty, and forty years ago, one is struck by how little the questions, and, unfortunately, often the answers, seem to have changed over time. It is not easy to find either questions or answers (generalizations and theory) made in recent years that are not in the literature of thirty or forty years ago, or even earlier than that. The mission of the SCOPE invasion program was to try to answer three questions: what factors determine whether or not a species will be an invader, what properties determine whether or not a particular environment will prone to invasion, and, how can the knowledge gained from answering these questions help management efforts. The first question was actually the organizing question of the 1964 Asimolar symposium, and the second was articulated by Elton himself.

There is no question that our understanding of the process of biological invasions has increased considerably during the past forty-six years, particularly our knowledge of the details involved in particular biological invasions. However, the extent to which this understanding has enhanced our ability to develop effective management strategies (the 3rd SCOPE objective), is less clear and depends on whom you ask. Some ecologists maintain that good progress is being made and that, with the application of new analysis tools and approaches such as species screening (Daehler *et al.* 2004) and the use of climatic envelopes (Peterson 2003), there is good reason to be optimistic about invasion ecologists' ability to effectively inform land managers. Others are not so sanguine, arguing that the type of knowledge and understanding gained so far are seldom useful in specific management efforts (Moyle and Light 1996, Simberloff and Stiling 1996), meaning that efforts by invasion ecologists to effectively inform land managers continue to be frustrated (Williamson 1999, Hulme 2003).

CONCLUSION
(WITH A FEW SUGGESTIONS TO CONSIDER)

Invasion ecology and conservation

All the evidence to date indicates that it is unlikely that ecologists will be able to develop a general theory of biological invasions that can be of significant practical value to land managers. Much research seems to have affirmed Asa Gray's observations of weeds more than a century ago. Trying to determine specific characteristics that make some plants weeds, Gray (1879) concluded that he "could discern nothing in the plant itself that would give it an advantage". Continuing, he wrote "the reasons for predominance may be almost as diverse as the weeds themselves".

With respect to its goal of assisting land managers in the control and management of introduced species, invasion ecology might consider emphasizing less the development of general theory and more the acquisition of system-specific knowledge. The fact that invasion ecology has consisted primarily as a series of case studies has generally been viewed as a weakness of the field (Williamson 1999). But, in reality, it may be very difficulty, perhaps even impossible, for the field to move much beyond this, at least at the level of providing useful management information. In this case, invasion ecologists might be better off viewing the "system specific" nature of the field's knowledge as a strength. Rather than lamenting the case-study nature of the field, ecologists might try to make increasing system-specific knowledge a primary objective (e.g., Rejmanek and Richardson 1996). While a land manager trying to manage the species composition of a grassland may not find invasion theory particularly helpful, the more system-specific knowledge that is available in his/her toolbox, the more successful the management efforts will be. To the extent that invasion ecology wants to inform conservation efforts, it may also make sense to for invasion ecologists to become more involved in developing formalized and comprehensive monitoring programs, which have the potential of greatly enhancing the effectiveness of management and control efforts (Lonsdale and Milton 2002).

Invasion ecology and science

The conservation and environmental emphasis in invasion ecology described above has been motivated by the conviction that ecological knowledge and theory can be used to better understand and predict biological invasions. The Asilomar approach was motivated by the opposite conviction — that biological colonizations/invasions can be viewed as natural experiments and used to inform more general ecological theory and understanding. Although there was some interest among ecologists in the early eighties to continue this emphasis (Brown and Marshall 1981, Simberloff 1981, Moulton and Pimm 1983), this approach has not been as well nurtured over the years by invasion ecology, compared to the

Eltonian conservation approach. The reinvigoration of a science of colonization and species spread as a way to study core concepts and theories of evolution and ecology would seem to be an exciting option for invasion ecology. Robert Frost's traveler could only choose one road, but there is no reason that invasion ecology couldn't embrace both a conservation and a more strictly scientific path. It has been forty years since the historic 1964 Asilomar symposium on colonization biology; perhaps it is time to organize another one.

Invasion ecology and language

High rates of species spread and introductions are here to stay. In some respects, one might question the sense of defining an ecological subdiscipline area around species introductions. Due to the abundance of introduced species in environments throughout the world, which is only going to increase in the future, it is becoming increasingly difficult to undertake any ecological study in which introduced species can be ignored. That biotic globalization is now the world in which we now live certainly does not mean we should cease efforts to control and manage the small number of introduced species that do cause great health, economic, and ecological harm (Ewel *et al.* 1999). However, it does raise questions as to the logic of dichotomously splitting species into natives and exotics, and even of using any terminology that singles out recently introduced species as a group (e.g., indigenous and non-indigenous) given that so few of these species are problematic. At the same time, particular research efforts will need to distinguish species that have been present in a region for a long time from those that have recently arrived through one means or another. Thus, from a practical perspective, categorizing species on their basis of geographic origin will be necessary in some cases (Webb 1985, Richardson *et al.* 2000, Colautti and MacIsaac 2004, Pyšek *et al.* 2004).

From a strictly scientific point of view, it would seem difficult to argue against the value of returning to the more value-neutral terminology used at the 1964 Asilomar symposium. If one is studying species introductions as a way illuminate basic ecological ideas and theory, then terms such as "introduced species", "colonizers", "new species", "new residents", and "geographic spread" seem more apt than the language often associated with the Eltonian path, e.g., "exotics", "aliens", and "invasions". Whether or not ecologists should modify their language when advocating environmental concerns will likely be a matter of disagreement within the field. Some will be concerned that, despite the best of intentions, the field's credibility and stature as a scientific discipline are being compromised when ecologists make their case to the public, and to one another, using value-laden terminology, an approach more typically associated with environmental-action groups. Those with this concern would probably be more comfortable if the field dropped the invasion/alien terminology altogether and replaced it with a terminology in which values were articulated more explicitly than implicitly. Using this approach, ecologists might refer to problem species such as zebra mussels

and Japanese knotweed as 'harmful new species' or 'harmful introduced species', as opposed to using a terminology in which values are more subtly implicated, e.g., 'invasive alien species'. Others will argue that metaphoric, and even at times, hyperbolic language, is needed to capture the attention of policy makers and the general public and to persuade them of the need to act, just as Elton (1958) did when he characterized the global spread of species as a "convulsion in the world's flora and fauna", and framed the challenge confronting us as a "battle" to "determine the fate of the world", the latter a quote from Conan Doyle's book, *The Lost World*.

Looking ahead

The past twenty years have seen extraordinary development in the field of invasion ecology. With numerous national and international initiatives, the creation of two new journals, and the countless number of symposia, conferences, and workshops devoted to biological invasions, not to mention the thousands of invasion papers published, there has been little time for participants to step back and reflect on the way that the field has developed. Perhaps now would be a good time to do this before moving ahead. To what extent is invasion ecology becoming largely an applied discipline like conservation biology and restoration ecology? To what extent should the field try to revitalize efforts to study species introductions as a way to illuminate more general ecological theory, *a la* the 1964 Asilomar symposium approach? (The current book, and one similar to it (Sax *et al.* in press), appear to illustrate a revived interest in this approach.) Is it possible for invasion ecology, and individual ecologists, to embrace both a strongly value-based environmental path and a more value-neutral scientific approach to species introductions? Should an effort be made to keep the paths separate, in the way that the news pages and editorial pages are kept separate in a newspaper, or should the two paths be integrated? What language and imagery should ecologists utilize in their discourse, among themselves and with the public? These are some of the questions that the field of invasion ecology might want to address way before moving ahead.

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