Part 2

Evolution and Current Dimensions of Invasion Ecology

 Fifty Years of Invasion Ecology: The Legacy of Charles Elton
 Edited by David M. Richardson

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PATTERNS AND Rate of growth of studies in Invasion ecology

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5.1 INTRODUCTION

Human activities are resulting in the spread of many non-indigenous species to habitats in which they are non-native. Introductions appear to be widespread and increasing in marine, freshwater and terrestrial ecosystems alike, with even remote Arctic and Antarctic ecosystems affected (Ruiz et al. 2000; Pyšek et al. 2006; Ricciardi 2006; Aronson et al. 2007). The association between climate change and species invasion suggests that the rising invasion rate will not abate anytime soon (Reid et al. 2007; Cheung et al. 2009). In addition, enhanced globalization of trade provides the means by which non-indigenous species may spread (Hulme 2009). The consequences of the increasing rate of invasion will include an array of ecological, economic and health impacts for invaded countries (Levine & D'Antonio 2003; Pimentel et al. 2005; Reaser et al. 2007; Perrings, this volume).

Charles Elton published his famous volume in 1958, yet more than two decades elapsed before biological invasions became a popular academic pursuit (Richardson & Pysek 2008; Simberloff, this volume). For example, we were able to tabulate publication of seven books on biological invasions between 1959 and 1979, and at least 20 more were published during the 1980s (H.J. MacIsaac, unpublished data). Simberloff (this volume) discusses the role of the Scientific Committee on Problems of the Environment (SCOPE) in raising interest in invasions. Journal publications on non-indigenous species began in earnest around 1990 (Davis et al. 2001; Lockwood et al. 2007). Elton's (1958) legacy to the field is a high citation rate (in more than 40% of papers) in current literature on papers addressing topics developed in his book, including the influence on invasion success of disturbance and native species diversity and stability, and on differences between islands and continents in their vulnerability to the occurrence and impacts of invasion (Richardson & Pyšek 2008; Ricciardi & MacIsaac 2008). Journal publications related to non-indigenous species increased dramatically during the early 1990s (Lockwood et al. 2007; Richardson & Pyšek 2008; Ricciardi & MacIsaac 2008), though it is not clear how this growth is distributed across taxonomic lines.

This chapter explores trends in the modern (since Elton 1958) growth of publications that address nonindigenous species, and tests three hypotheses:

1 Animals accumulate studies earlier than plants. Rationale: animals tend to have effects that are

more conspicuous, thus they are likely to be studied earlier.

2 Terrestrial species accumulated studies earlier than aquatic ones. Rationale: firstly, terrestrial organisms are more conspicuous and easier to detect than most aquatic NIS. Secondly, the relative importance of vectors transmitting these groups has changed. The rate of increase for aquatic animals is expected to initially lag behind that of terrestrial animals, consistent with the early historical prevalence of introductions of land mammals and birds, whereas the growing importance of ballast water has driven a rapid increase in aquatic invasions in recent years (see, for example, Ricciardi 2006). Finally, the perception of the consequences of intentional introductions has changed.

3 Aquatic invertebrates accumulate studies later than fishes. Rationale: both the relative importance of vectors transmitting these groups and the perception of consequences of intentional introductions have changed, resulting in especially lower numbers of fish introductions. Fishes have been stocked into systems well before invertebrates were introduced to systems in an attempt to enhance fisheries. Furthermore, documentation of widespread introductions of aquatic invertebrates appears to be driven partly by heightened interest in high-profile ballast-water mediated invasions after 1980 by species including the zebra mussel *Dreissena polymorpha* and comb jelly *Mnemiopsis leidyi*.

We address each of these hypotheses using the ISI Web of Science to track publications in the literature.

5.2 METHODS

We used Thomson's ISI (Institute for Science Information) Web of Knowledge 4.0 to search for and track publications in scientific literature for '100 of the World's Worst Invasive Alien Species' as determined by the World Conservation Union (IUCN; Lowe et al. 2004). We chose these 100 species in an attempt to explore objectively publication patterns for different taxonomic groups. As implied by the name, these species represent many of the most invasive (i.e. problematic) non-indigenous species found in a diversity of habitats around the world, and thus we expected that they would draw researchers' attention. It is important to note, however, that many other highly invasive non-indigenous species were not included on this list (e.g. spiny waterflea *Bythotrephes longimanus*). Species included on the IUCN list were selected based on two criteria: (i) the significance of invader impacts on either humans or biological diversity; and (ii) their illustration of important issues surrounding biological invasions (Lowe et al. 2004). The IUCN list includes a broad representation of biodiversity including three microorganisms, five macro-fungi, four aquatic plants, 30 terrestrial plants, nine aquatic invertebrates, 17 terrestrial invertebrates, three amphibians, eight fishes, three birds, two reptiles and 14 mammals (Lowe et al. 2004).

For all 100 species, we searched using common and scientific names in the topic box for the period 1965 to 2007 inclusive. We used the Scientific Citation Index Expanded (SCI-EXPANDED), and excluded the Social Sciences Citation Index and the Arts and Humanities Citation Index. ISI Web of Knowledge tracks journals that are written in English and certain principally northern hemisphere languages including Spanish, German, French, Portuguese, Czech, Dutch, Russian, Polish, Turkish, Japanese, Chinese, Swedish, Norwegian, Lithuanian, Slovak, Estonian, Finnish, Hungarian, Slovene, Korean and Serbian.

We conducted two sets of searches for all species in May 2008. The first set consisted of the species' scientific name or common name – as per the IUCN report (Lowe et al. 2004) – in the topic box. Search topics were then refined by subject area, and only field topics relevant to ecology, broadly-speaking, were used. These field topics included ecology, biodiversity conservation, environmental sciences, plant sciences, zoology, limnology and entomology; the same set of field topics were used for all species (Appendix 5.1). Biomedical fields that seemed unrelated to ecology – such as veterinary sciences and immunology - were excluded. Results were tabulated by year, publication count and cumulative numbers of publications for each species. Publication trends were analysed only if the species had accumulated at least one paper in each of a minimum of 6 years. We compared cumulative number of publications of animal versus plant species. of terrestrial versus aquatic species, and of aquatic invertebrates versus fishes, using *t*-tests and log(x + 1)data for the period 1965 to 2007. Amphibians were excluded from analysis of terrestrial versus aquatic species since they inhabit both habitats, and the redeared slider turtle was included with the aquatic group.

To assess only papers that explicitly considered the species as non-indigenous, a second set of searches was

conducted that combined the above species' scientific or common name with six additional synonyms (nonnative species, alien species, exotic species, introduced species, colonizing species, or exotic species). The same procedures and conditions that were applied for the first set of searches were applied to these combined searches.

We modelled the cumulative number of publications between 1965 and 2007 for each using nonlinear regression in Systat 12.0. Early studied species were considered those that accumulated at least 25% of total publications occurred before 1990. Cumulative growth was fitted as an exponential equation (cumulative publications = α year^{β}) where α and β were fitted variables and year is the Julian year with 1965 as year 1. The coefficient α and exponent β relate to how early the species was studied and how rapidly the species accumulated publications, respectively. Differences in mean $\log(\alpha + 1)$ and in β were assessed for plants versus animals, for terrestrial versus aquatic species, and for aquatic invertebrates versus fishes were assessed using *t*-tests. Again, we excluded amphibians from analyses, and the red-eared slider was considered aquatic. It is important to note that growth patterns for all species are assessed versus a 1965 starting point. This allowed us to determine temporal differences in accumulations of studies for different taxa. Taxa with the same relative growth of papers (as a function of the total for that species) could have different α and β values depending on when these publications first started appearing in the literature. Thus our analysis assesses comparative growth relative to 1965, and not whether individual species' accumulation curves differ after the species begins to appear in the literature. We also calculated the time from 1965 that was required to achieve the 25th percentiles for the total number of publications.

5.3 RESULTS AND DISCUSSION

The cumulative publication rate was readily fit using an exponential function for most species, which is not unexpected (Wonham & Pachepsky 2006). However, the Kaphra beetle, a pest species of stored grain, accumulated a relatively large number of papers between the late 1960s and mid-1970s followed by a much reduced rate in later years. This resulted in an asymptotic accumulation pattern and fitted function that had an extremely high α and very low β . Because of the

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unusual nature of this fitted function, we removed this beetle from further statistical analyses. In addition, curves could not be fit for the fishhook waterflea Cercopagis pengoi, Asian longhorn beetle Anoplophora glabripennis and yellow crazy ant Anoplolepis gracilipes. In each case, studies have been published so recently - mainly since 2000 - that exponential curves could not be fitted. Fishhook fleas originated in the Black Sea, but were first reported in the Baltic Sea and in the Great Lakes in the late 1990s (see Cristescu et al. 2001). The Asian longhorn beetle is a wood-boring insect of quarantine significance that has been found at a variety of North American (e.g. New York, Chicago, Toronto) and European (Braunau, Austria: Gien and Sainte-Anne-sur-Brivet, France; Neukirchen am Inn, Germany) cities (e.g. Haack 2006). The yellow crazy ant has been introduced to parts of Africa, Asia and to islands in the Pacific and Indian Oceans and the Caribbean Sea, where it may exert strong negative impacts on resident species (see, for example, O'Dowd et al. 2003).

Fifteen per cent of the species on the '100 of the World's Worst Invasive Alien Species' list were studied very early. These species include an array of notorious invaders including the common carp *Cyprinus carpio*, bullfrog Rana catesbeiana, cane toad Bufo marinus, ship rat Rattus rattus, starling Sturnus vulgaris, phytophthora root rot Phytophthora cinnamomi and Dutch elm disease Ophiostoma ulmi. Indeed, Dutch elm disease accumulated papers very quickly, recording the 25th and 50th percentiles of its total number between 1982 and 1992, respectively. A second group, constituting approximately half of the species on the list, were studied to some extent before 1990 but very well thereafter. This group includes infamous invaders including water hyacinth Eichhornia crassipes, Nile perch Lates niloticus, comb jelly Mnemiopsis leidyi, little fire ant Wasmannia auropunctata, gypsy moth Lymantria dispar, leucaena Leucaena leucocephala and avian malaria Plasmodium relictum. A third group of species were studied exclusively or almost so after 1990. These species include the zebra mussel, green alga Caulerpa taxifolia, brown tree snake Boiga irregularis, rosy wolf snail Euglandina rosea, fire tree Morella faya, kudzu Pueraria montana var. lobata, Brazilian pepper tree Schinus terebinthifolius and chestnut blight Cryphonectria parasitica. Species that have only recently been studied include the aforementioned fishhook waterflea, Asian longhorn beetle, and frog chytrid fungus Batrachochytrium dendrobatidis. Poorly studied species include the yellow crazy ant, Indian myna bird *Acridotheres tristis*, small Indian mongoose *Herpestes javanicus* and mile-a-minute weed *Mikania micrantha* (fewer than 50 papers each).

The nine species (and publication number) that were excluded from our analysis because they contained too few (no more than five) years of ISI records were mainly terrestrial plants. These species include the African tulip tree Spathodea campanulata (16), hiptage Hiptage benghalensis (12), Kahili ginger Hedychium qardnerianum (10), Koster's curse Clidemia hirta (24), quinine tree Cinchona pubescens (12), shoebutton ardisia Ardisia elliptica (12), yellow Himalayan raspberry Rubus ellipticus (13), cypress aphid Cinara cupressi (11) and red-vented bulbul Pycnonotus cafer (15). We were surprised that so many species from the 100 of the World's Worst Invasive Alien Species list were so poorly documented in the formal literature. Pyšek et al. (2008) noted that only 1.6% of 892 invasive species had more than 20 published studies. The dearth of ISI-tracked publications for many of these species may relate in part to their recent history of spread (e.g. fishhook waterflea, Asian longhorn beetle) or to our recent awareness of the species as a major conservation concern (e.g. rosy wolf snail). It is also possible that some of these species may have been problematic in their native region but were poorly documented as such, owing to a lack of publications in journals tracked by the ISI index. This problem would be particularly acute for invaders originating in, or spreading to, countries in the southern hemisphere or Asia, where invasive species generally receive much less attention - with the notable exceptions of New Zealand, Australia and South Africa. Pyšek et al. (2008) determined that the invasion literature tracked by Web of Science is dominated by studies from North America and Europe, whereas Asia and much of Africa appear vastly understudied.

The single best studied species were all animals: house mouse (*Mus musculus*; 92,221 studies), rainbow trout (*Oncorhynchus mykiss*; 21,584 studies), rabbit (*Oryctolagus cuniculus*; 13,480 studies), pig (*Sus scrofa*; 10,567 studies), and carp (8579 studies) (Fig. 5.1). The best studied plants included the fire tree (2214 studies) and leucaena (1311 studies). Because species are studied for many reasons other than their invasiveness, these values fall considerably when assessments are limited to studies in which the species is specifically identified as invasive by the original authors (see below).



Fig. 5.1 Number of papers published between 1965 and 2007 on non-indigenous species of plants and animals (a), aquatic invertebrates and fishes (b), and aquatic versus terrestrial species (c).

Number of papers published (since 1965)

Consistent with our first hypothesis, animals were significantly better studied than plants, in part reflecting the popularity of papers on numerous fishes (*t*-test, P < 0.001) (Fig. 5.1). However, this result was also contingent on inclusion of the house mouse, which had more than four times as many studies as any other species. Even with the elimination of obvious biomedical topic fields, some species accumulated large numbers publications that may or may not be related to invasion ecology (e.g. 7852 papers on genetics and heredity); because of our uncertainty on the nature of the individual papers, we retained them studies in our analysis. Overall, animals averaged 3604 studies

(median 658), versus only 374 for plants (median 194). Animals also accumulated studies earlier than plants. For example, the 25th percentile of all publications occurred in 1991 for animals and 1995 for plants.

The hypothesis that terrestrial species tend to be more conspicuous than aquatic species and therefore better studied was not supported. We found no difference (*t*-test, P = 0.210) in mean number of publications for aquatic versus terrestrial species (2144 versus 2687, respectively). The time required to achieve the 25th percentile of total publications was also very similar between aquatic (1992) and terrestrial (1993) species.

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Among aquatic animals, fishes tended to be better studied than aquatic invertebrates (average: 4782 versus 781 studies, respectively), although variation was pronounced in both groups and the difference was not significant (P = 0.064; Fig. 5.1). Consequently, our third hypothesis that the widespread stocking of fishes would result in more publications than for invertebrates was not supported. It should be noted that invertebrates were stocked extensively in the former USSR and Scandinavia to enhance fisheries, although none of the species uses for this purpose are included on the 100 worst invaders list. Furthermore, several of the invertebrate species on the list have been widely dispersed by shipping (e.g. European green crab Carcinus maenas, comb jelly, zebra mussel) and/or stocking (Chinese mitten crab Eriocheir sinensis, Mediterranean mussel Mytilus galloprovincialis), which contributed to enhanced numbers of publications particularly in recent years. Fishes achieved the 25th percentile of all publications slightly earlier than did aquatic invertebrates (1991 versus 1993, respectively).

In addition to rainbow trout and common carp, brown trout Salmo trutta (4661 studies) and Mozambique tilapia Oreochromis mossambicus (1144 studies) were early and well studied cases. By contrast, Nile perch was poorly studied (174 studies) despite its fundamental and perhaps unprecedented role in the collapse of cichlid fish diversity in Lake Victoria (see, for example, Goudswaard et al. 2008). Among aquatic invertebrates, the European green crab (2089 studies), Mediterranean mussel (1896 studies), and zebra mussel (1596 studies) were the best studied species. The former species has been introduced and is established in coastal marine habitats of all continents except Antarctica (Darling et al. 2008). Mytilus galloprovincialis has an extensive and lengthy record of introductions to marine coastal habitats globally (Carlton 1999). Dreissena polymorpha is native to fresh

and brackish waters of the Black, Caspian and Azov Seas (see May et al. 2006), though it has spread via canals and shipping beginning in the 18th century throughout much of western and eastern Europe; more recently the species has consolidated its range in Europe, with, for example, initial colonization of Spain and Ireland and enhanced distribution in Italy (Bij de Vaate et al. 2002; Lancioni & Gaino 2006; Rajagopal et al. 2009). The species colonized Lake Erie in the Laurentian Great Lakes no later than 1986 (Carlton 2008), and has since spread widely across eastern North America including most major river systems and hundreds of inland lakes (Drake & Bossenbroek 2004). In 2008, the species was found across the continental divide for the first time, with established populations in Colorado and California.

When names of species from the 100 of the World's Worst Invasive Alien Species were cross-referenced against the seven synonyms for 'invasive species', the number of publications recovered fell dramatically (see, for example, Fig. 5.2a,b). Overall publications for these averaged 2320 papers, though an average of only 55 (2.4%) specifically referenced the species as 'non-indigenous'. When we combined the two searches, 29 of the 91 profiled species had fewer than 20 publications in which they were identified as 'nonindigenous'. This group included all three microorganisms (Plasmodium relictum, Banana bunchy top virus, Rinderpest virus), and four of five macro-fungi (Cryphonectria parasitica, Ophiostoma ulmi, Batrachochytrium dendrobatidis, Phytophthora cinnamomi). Ten of 25 terrestrial plants were also represented by fewer than 20 papers in the literature in which they were identified as invasive. By contrast, all of the four aquatic plant species, seven of eight fishes and seven of nine aquatic invertebrates (marine and freshwater) were identified in more than 20 studies as 'nonindigenous'. Consistent with Pyšek et al. (2008), the

Fig. 5.2 Profiles of growth in number of publications for nine aquatic species (a) and nine terrestrial species (b) listed on the IUCN's 100 of the World's Worst Invasive Alien Species. Aquatic species include carp *Cyprinus carpio*, brown trout *Salmo trutta*, water hyacinth *Eichhornia crassipes*, zebra mussel *Dreissena polymorpha*, marine clam *Corbula amurensis* (previously *Potamocorbula amurensis*), caulerpa seaweed *Caulerpa taxifolia*, rainbow trout *Oncorhynchus mykiss*, Nile perch *Lates niloticus* and Mozambique tilapia *Oreochromis mossambicus*. Terrestrial species include cogon grass *Imperata cylindrica*, lantana *Lantana camara*, mimosa *Mimosa pigra*, brown tree snake *Boiga irregularis*, pig *Sus scrofa*, ship rat *Rattus rattus*, starling *Sturnus vulgaris*, cane toad *Bufo marinus* and gypsy moth *Lymantria dispar*. In all cases, the dashed line is a fitted exponential curve describing cumulative publications obtained by searching using species' common and scientific names only, whereas solid lines are fitted curves for species names cross-referenced with seven synonyms for non-indigenous species (i.e. only those papers where the species is viewed in a non-indigenous context).



Table 5.1 Mean (standard deviation (SD)) coefficient (α) and exponent (β) describing growth of publications for different taxonomic groups. Values were calculated as: EC = α (Year)^{β} where EC is the estimated cumulative number of publications based on nonlinear regression for the period 1965 to 2007. Non-indigenous Ratio is the mean percentage of studies in which the species were considered invasive (see Fig. 5.2 legend). All estimates use a starting point of 1965.

Group	α (SD)	β (SD)	Non-Indigenous ratio	N
Microbes	0.0001 (0.0002)	3.7449 (0.4046)	3.4	3
Macro-fungi	0.6797 (0.7885)	2.8023 (1.3229)	9.5	5
Aquatic plants	0.0372 (0.0742)	4.3442 (1.8666)	23.3	4
Land plants	0.0131 (0.0401)	4.2286 (1.3986)	17.8	25
Aquatic invertebrates	0.0070 (0.0188)	4.5096 (1.1442)	15.5	9
Land invertebrates	0.7774 (0.0188)	3.4550 (1.1442)	16.8	15
Amphibians	0.4358 (0.5199)	2.7066 (1.2290)	4.4	3
Fish	0.1288 (0.1893)	3.2059 (0.8317)	6.5	8
Birds	0.0360 (0.0394)	2.4461 (0.3355)	12.7	2
Reptiles	<0.0001 (<0.0001)	4.8710 (0.3099)	10.0	2
Mammals	0.4622 (1.4765)	3.13128 (0.6482)	6.0	14

zebra mussel was identified as 'non-indigenous' in more papers (261) than any other species on the list of 100 of the World's Worst Invasive Alien Species. The fishhook waterflea (62%) and yellow crazy ant (53%) had the highest percentage of studies published in which they were identified as 'non-indigenous', followed by Japanese knotweed Fallopia japonica and the green alga Caulerpa taxifolia (46%). Among fish, Nile perch had the highest ratio of 'non-indigenous' studies (26%), though surprisingly there is a relative paucity of studies for this invader (Fig. 5.2a). No other fish species had an 'non-indigenous ratio' greater than 10%, illustrating the benign attitude of many researchers to the impacts of introduced fishes as well as the predominantly positive attention given to stocked nonindigenous fishes. As a group, aquatic plants and terrestrial plants were the most likely to be viewed as 'non-indigenous' by the research community (Table 5.1).

We quantified whether growth of publications for the 100 of the World's Worst Invasive Alien Species began relatively early (i.e. around 1965; high α) or at a relatively high rate in recent years (high β). As a group, the highest values of α were observed for terrestrial invertebrates, macro-fungi, mammals and amphibians (Table 5.1). Reptiles, microbes and aquatic invertebrates had very low values of α , reflecting very low publication rates for member species in the 1960s. The greatest growth in publications in recent years occurred among reptiles, aquatic invertebrates, and aquatic and terrestrial plants (Table 5.1). Initial studies on plants and animals began about the same time, as differences in α were not significant (*t*-test, *P* = 0.107). However, plants apparently accumulated studies more rapidly in recent years (β ; *t*-test, *P* = 0.022).

The relatively low rate of identification of the 100 of the World's Worst Invasive Alien Species with seven terms commonly used by the academic community to identify taxa that pose problems may reflect changes in public attitudes or popular terminology in academia. Clearly, terms like 'alien', 'invasive' and the like are more popular (and controversial) today than in the past, whereas others, like 'colonizing' appear to be used less commonly today. However, it seems implausible that the widespread increase in scientific publications on non-indigenous species observed during the 1990s is related to popular terminology. Rather, it is more likely that the increase in publications in scholarly journals follows the pattern of landmark conferences and book publications launched during the 1980s.

Our results have several potential limitations that must be considered. The Web of Knowledge tracks mainly western journals published in 22 languages commonly used in the northern hemisphere. Journals published in other languages are not picked up by the ISI index, and studies on species reported in these outlets would be under-represented in consequence. Publications in the 'grey' literature (e.g. government reports) also are not tracked by the ISI index. The Nile perch has accumulated only 174 papers in our search of the tracked literature and 220 papers if all topics are considered (Fig. 5.2a). Given the importance of this

species to the unfolding biodiversity crisis and to African societies dependent on it as a fishery resource (Matsuishi et al. 2006), our analysis almost certainly underestimates the total research effort devoted to this species. Wilson et al. (2007) found that species with high societal importance tended to receive more scientific attention than species with little societal value. thus the comparatively small number of scientific publications uncovered in our search is puzzling. Finally, we assessed growth patterns (α and β) of publications using a common reference date (1965) for all species. Different patterns could be uncovered had we used the publication date when each species was first described as non-indigenous in scientific publications. Nevertheless, our analysis is consistent with our stated purpose of identifying temporal patterns of attention devoted to different introduced taxa.

Publication histories indicate that studies on most of the species that we investigated have increased dramatically since 1990. This can be due to a general surge of interest in invasion ecology because of increased funding available to sponsor these studies, or it may simply reflect a general increase in the volume of scientific literature published. Some of the species on the 100 World's Worst Invasive Alien Species list have been studied for a long time (e.g. water hyacinth, common carp), though for many others (e.g. fishhook waterflea, comb jelly, zebra mussel) studies increased dramatically during the 1990s or later as the species executed high profile and high impact invasions in new localities. Interestingly, the relative growth rate of publications on biological invasions is nearly identical to that for climate change, although the latter is a much larger field with many more studies published overall.

5.4 CONCLUSIONS

Authors have discussed how Charles Elton's views on invasions strongly reflected his particular experiences and interests (Davis et al. 2001; Richardson & Pyšek 2008). Similarly, publication patterns for different non-indigenous species reflect differences in their importance to, interest in or utility of these species to humans. Changes in human interest alter the frequency and locations at which species are intentionally moved globally (Wilson et al. 2009), just as changes in the operation or pathways of principal vectors affect the global movement and unintentional introduction of non-indigenous species (Carlton 1985). Despite an enormous diversity of species that have been introduced and established in ecosystems throughout the world, and a burgeoning number of case studies that have accrued since Elton (1958), much of invasion biology has developed from studies of a relatively small group of taxa. It remains to be determined how this bias may have influenced key concepts in the field. The surge in interest in invasion biology provides an opportunity to explore concepts using a wider array of taxa and habitats studied.

ACKNOWLEDGMENTS

We are grateful for the invitation from Dave Richardson to participate in the Charles Elton Symposium and for helpful comments on the paper from Dave Richardson and two reviewers. We acknowledge financial support from NSERC discovery grants to H.J.M. and A.R., and from the Canadian Aquatic Invasive Species Network (CAISN).

REFERENCES

- Aronson, R.B., Thatje, S., Clarke, A., et al. (2007) Climate change and invasibility of the Antarctic benthos. *Annual Review of Ecology, Evolution and Systematics*, **38**, 129–154.
- Bij de Vaate, A., Jażdźewski, K., Ketelaars, H.A.M., Gollasch, S. & Van der Velde, G. (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1159–1174.
- Carlton, J.T. (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology*, **23**, 313–371.
- Carlton, J.T. (1999) Molluscan invasions in marine and estuarine communities. *Malacologia*, **41**, 439–454.
- Carlton, J.T. (2008) The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. *Journal of Great Lakes Research*, **34**, 770–773.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish* and Fisheries, **10**, 235–251.
- Cristescu, M.E., Witt, J., Hebert, P.D.N., Grigorvich, I.A. & MacIsaac, H.J. (2001) An invasion history for *Cercopagis* pengoi based on mitochondrial gene sequences. 2001. *Limnology and Oceanography*, **46**, 224–229.
- Darling, J.A., Bagley, M.J., Roman, J., Tepolt, C.K. & Geller, J. (2008) Genetic patterns across multiple introductions of

the globally invasive crab genus *Carcinus*. *Molecular Ecology*, **17**, 4992–5007.

- Davis, M.A., Thompson, K. & Grime, P. (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions*, 7, 97–102.
- Drake, J.M. & Bossenbroek, J.M. (2004) The potential distribution of zebra mussels in the United States. *Bioscience*, **54**, 931–941.
- Elton, C.S. (1958) The Ecology of Invasions by Animals and Plants. Methuen, London.
- Goudswaard, K.P.C., Witte, F. & Katunzi, E.F.B. (2008) The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. *Environmental Biology of Fishes*, **81**, 127–139.
- Haack, R.A. (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research*, **36**, 269–288.
- Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal* of Applied Ecology, **46**, 10–18.
- Lancioni, T. & Gaino, E. (2006) The invasive zebra mussel Dreissena polymorpha in Lake Trasimeno (Central Italy): Distribution and reproduction. Italian Journal of Zoology, 73, 335–346.
- Levine, J.M. & D'Antonio, C.M. (2003) Forecasting biological invasions with increasing international trade. *Conservation Biology*, **17**, 322–326.
- Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2007) Invasion Ecology. Blackwell, Oxford.
- Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2004) 100 of the world's worst invasive alien species a selection from the global invasive species database. 6–7. Invasive Species Specialist Group and Group of the Species Survival Commission, Auckland, New Zealand.
- Matsuishi, T., Muhoozi, L., Mkumbo, O., et al. (2006) Are the exploitation pressures on the Nile perch fisheries resources of Lake Victoria a cause for concern? *Fisheries Management* and Ecology, **13**, 53–71.
- May, G.E., Gelembiuk, G.W., Panov, V.E., Orlova, M.I. & Lee, C.E. (2006) Molecular ecology of zebra mussel invasions. *Molecular Ecology*, 15,1021–1031.
- O'Dowd, D.J., Green, P.T. & Lake, P.S. (2003) Invasional 'meltdown' on an oceanic island. *Ecology Letters*, **6**, 812–817.
- Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alieninvasive species in the United States. *Ecological Economics*, 52, 273–288.
- Pyšek, P., Richardson, D.M. & Jarošík, V. (2006) Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. *Preslia*, **78**, 437–468.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z. & Weber, E. (2008) Geogrpahical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, 23, 237–244.

- Rajagopal, S., Pollux, B.J.A., Peters, J.L., et al. (2009) Origin of Spanish invasion by the zebra mussel, *Dreissena polymorpha* (Pallas, 1771) revealed by amplified fragment length polymorphism (AFLP) fingerprinting. *Biological Invasions*, 11, 2147–2159.
- Reaser, J.K., Meyerson, L.A., Cronk, Q., et al. (2007) Economical and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, 34, 98–111.
- Reid, P.C., Johns, D.G., Edwards, M., Starr, M., Poulin, M. & Snoejs, P. (2007) A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800000 years. *Global Change Biology*, **13** 1910–1921.
- Ricciardi, A. (2006) Patterns of invasion of the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, **12**, 425–433.
- Ricciardi, A. & MacIsaac, H.J. (2008) The book that began invasion ecology. *Nature*, 452, 34.
- Richardson, D.M. & Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions*, 14, 161–168.
- Ruiz, G.M., Rawlings, T.K., Dobbs, F.C., et al. (2000) Worldwide transfer of microorganisms by ships. *Nature*, 408, 49–50.
- Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2007) The (bio)diversity of science reflects the interests of society. *Frontiers in Ecology and the Environment*, 5, 409–414.
- Wilson, J.R.U., Proches, S., Braschler, B., Dixon, E.S. & Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology* & Evolution, 24, 136–144.
- Wonham, M.J. & Pachepsky, E. (2006) A null model of temporal trends in biological invasion records. *Ecology Letters*, 9, 663–672.

APPENDIX 5.1

Fields from the ISI searches which were retained in our survey included the following: ecology, evolutionary biology, biology, oceanography, limnology, mycology, multidisciplinary sciences, genetics and heredity, biodiversity conservation, entomology, environmental sciences, marine and freshwater biology, ornithology, plant sciences, agriculture: multidisciplinary, agronomy, forestry, horticulture, geography, physical water resources, agriculture, dairy and animal science, microbiology, toxicology, remote sensing, and virology. Forty-six additional fields tracked by the ISI Web of Science were excluded.