



## Charles S. Elton and the dissociation of invasion ecology from the rest of ecology

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**Abstract.** Despite several decades of research, the field of invasion ecology has not been very successful in developing reliable generalizations regarding the mechanisms and predictability of invasions. In this essay, we argue that one impediment in the field's development has been that the field of invasion ecology has largely dissociated itself from other subdisciplines of ecology, particularly succession ecology. Taking an historical approach, we suggest that this dissociation began with Charles S. Elton, the generally acknowledged father of invasion biology. We argue further that, despite periodic calls to end what some have regarded as a spurious distinction between native colonizers and introduced invaders,

invasion ecology has continued to pursue its own generalizations with limited success. We suggest this dissociation may be exacerbated further by incentives produced by the realities of publishing and securing funding for research and also by the use of electronic search engines to identify related articles. We offer several examples of how invasion ecology has benefited from research on succession and regeneration conducted on native species and conclude that the field of invasion ecology would do well to do more of this type of communication and collaboration among subdisciplines.

**Key words.** Biological invasions, invasion ecology, succession, Charles Elton.

### INTRODUCTION

Species invasions are widely recognized as a serious threat to environments and economies throughout the world (Wilcove *et al.*, 1998; Dukes & Mooney, 1999; Pimental *et al.*, 2000). Unfortunately, ecologists have not been able to provide much assistance to land managers because the field of invasion ecology has progressed so slowly. A recent assessment of the field has concluded that it is still largely anecdotal, with few reliable generalizations (Williamson, 1999). We believe that the field's development has been hampered for decades due to an unfortunate dissociation from other fields of ecology, particularly succession ecology.

The dissociation of invasion ecology from succession ecology is apparent from any casual

examination of the bibliographies of papers from the two fields. Each seldom cites the other. For example, three of the most recent and thorough assessments of invasion ecology are by Lonsdale (1999), Williamson (1999), and Dukes & Mooney (1999). Together the three articles contained 182 citations. Of these citations, 106 included the words 'alien', 'nonindigenous' and/or some form of the word 'invasive or invader'. Not one citation includes the words 'succession', 'recovery', or 'secondary'. A very different pattern is revealed by a review of the bibliographies of recent succession articles. For example, three recent articles on subalpine forest succession (Donnegan & Rebertus, 1999), tropical succession (Hughes *et al.*, 1999) and succession following hurricanes, volcanic eruptions and massive forest fires (Turner *et al.*, 1997) contain 202 references combined. In this

case, only two citations included the words 'alien' 'nonindigenous', 'exotic' or some form of the word 'invasive' or 'invader', while 52 included the word 'succession', 'recovery' or 'secondary'. Perusals of other recent succession and invasion articles revealed the same stark lack of overlap in literature being cited.

During the past half-century, the increase in our understanding of successional processes, and of the key role of regeneration in plant communities, is one of ecology's great successes (Glenn-Lewin *et al.*, 1992). Hundreds, if not thousands, of studies have been conducted, with the results reported in thousands of papers and presentations. There currently exists an enormously rich literature of succession ecology that is being virtually ignored by many researchers studying invasions. Much is known about the dynamics of recolonization of disturbed sites, habitat conditions that facilitate recolonization, subsequent facilitation of establishment and attributes of successional colonizers. From an ecological perspective, an 'exotic invader' and a local species that has come into a habitat following a disturbance are both *colonizers*, meaning that they have dispersed to and become established in a new environment (Levine & D'Antonio, 1999; Davis & Thompson, 2000; Richardson *et al.*, 2000b). All of this information and theory from successional ecology could be used to inform our understanding of the invasion process. When did this unfortunate dissociation occur?

## THE INFLUENCE OF CHARLES S. ELTON

The unofficial father of invasion ecology is Charles Elton, whose seminal 1958 book, *The Ecology of Invasions by Animals and Plants*, has been cited by virtually every major invasion paper since its publication. Unquestionably, his book stimulated an enormous amount of research in the area of invasion ecology (Simberloff, 2000). However, at the same time, Elton may also have unintentionally handicapped the field's subsequent development. Elton based his 1958 book on a series of radio broadcasts he presented called 'Balance and Barrier'. In his book, Elton made it clear that there was a distinct group of species that could disrupt ecological balance if barriers to their movements were removed. On page 4 of chapter one,

Elton wrote, there are 'two rather different kinds of outbreaks in populations: those that occur because a foreign species successfully invades another country, and those that happen in native or long-established populations. This book is chiefly about the first kind, the invaders'. Thus, the dissociation between succession and invasion ecology began at the very beginning with Elton himself.

It is interesting to reflect on why in 1958 Elton chose to single out invasions as a separate and unique phenomenon, in particular separate from successional processes. His earlier writings do not reflect this distinction. In his 1927 book, *Animal Ecology*, Elton actively promotes the idea of succession. Elton's notes indicated he was strongly influenced by the work of V. E. Shelford, who had applied the notion of succession to animals (Southwood & Clarke, 1999). Chapter 3 of Elton's (1927) book was titled 'Ecological Succession'. In this chapter, Elton describes the movements of plants and animals that occur during the succession process and, as pointed out by Southwood & Clarke (1999), Elton was active in developing the notion of succession. In the same book, Elton also included a chapter titled 'Dispersal'. Here he speaks of the 'spreading of species' and states that dispersal 'takes place through migration or spreading of the environment, e.g. by ecological succession'. He also refers to species extending their ranges and distributions. Elton did use the word 'invasion' in his book, but not in a way to distinguish one sort of dispersal or spreading from another (Richardson *et al.*, 2000b). Interestingly, the word 'invasion' did not appear in the index of the book, also perhaps indicating that he was according the word no particular importance. For discussions of the various ways in which modern ecologists use the term, see Davis & Thompson (2000) and Richardson *et al.* (2000b).

Elton may be most famous for his work on population dynamics of animal populations, particularly the population dynamics of northern native rodents (1942). Elton's primary focus in his 1942 book, *Voles, Mice and Lemmings: Problems in Population Dynamics*, was on population fluctuations and periodic mass movements of rodents into new areas. He did periodically use the word 'invasion' in this book, but again he did not give the word a unique meaning, and the

word 'invasion' is not included in the index of this book either. Thus, although steeped in the notions of changing habitats and dispersing organisms, 16 years later, in 1958, Elton chose not to incorporate his views on invasions into the existing succession paradigm that he had helped develop. Instead, he chose to starkly characterize invasions as something unique. Had something happened during the intermittent period that might explain this change in perspective?

A clue may lie with his experiences during World War II. Most of Elton's work on rodents was carried out in Great Britain between 1931 and 1939. When Britain became involved in the war Elton, like other university scientists, applied his knowledge and expertise to the war effort. In his own words, Elton (1942) reported, 'The outbreak of war in 1939 interrupted the progress of this research on voles in Britain, although the organization and ideas have been turned to the immediate needs of protecting food from rabbits, rats, and house mice as part of national defence.' In particular, Elton was asked to try to find ways to control the brown rat, the black rat, the house mouse and the European rabbit (Southwood & Clarke, 1999). The black rat was introduced into England around the 11th century, the European rabbit in the late 12th century, the brown rat in the 18th century and the house mouse in pre-Roman times. Thus, all four pest species were introduced species. This group of animals was very different from those he had been working on just a few years before in the Arctic. These were not native rodents that had been living in their environments for thousands of years. These were newcomers and huge pests causing great damage and even threatening the country's war effort. Elton took his military directive seriously and worked vigorously at developing ways to reduce the populations of these pests and their effects on the country's food supply, which was determined by Elton and his staff to be far larger than originally believed (Southwood & Clarke, 1999).

There is another reason why the war may have transformed Elton's perspective on invasions. Throughout the war years, British people were much more concerned about a very different kind of invasion, one far worse than a rodent infestation. They feared invasion by Germany. For Elton, invasion was at the centre not only of his work but also of his country's psyche. Thus, it is

perhaps not surprising that Elton began his 1958 book using war metaphors. In the book's very first paragraph he wrote: 'It is not just nuclear bombs and war that threatens us. There are other sorts of explosions, and this book is about ecological explosions.' His book focused almost entirely on the notorious invaders, such as the chestnut blight in America, the North American muskrat in Eurasia, sea lampreys in the Great Lakes and even plagues, including the influenza epidemic and potato blight.

We cannot know for sure whether or not his wartime experiences influenced Elton's views of invasion; however, he did continue this new perspective in his later writings. In his 1966 book, *The Pattern of Animal Communities*, he describes three types of dispersal: 'normal movements of species that live in the place or at least visit it regularly'; 'random mass bombardments by native species from outside the home area'; and 'genuine invaders carried by man from abroad'. His 1927 book contained a chapter entitled 'Dispersal', while a similar chapter in his 1966 book was entitled 'Dispersal and Invaders'. Not surprisingly, the word 'invasion' appears in the index of the 1966 book. Thus, 8 years following the publication of *The Ecology of Invasions by Animals and Plants*, Elton's view had not changed. Despite his earlier writings, he now appeared to view invaders as a distinct group of organisms and invasion as a process distinct from the colonizations that are an integral part of many successions.

## THE PERPETUATION OF THE DISSOCIATION

Even though Elton may have initiated the dissociation of invasion ecology from succession ecology, how has this dissociation managed to continue for more than 40 years? In fact, despite Elton's clear dichotomous declaration, several investigators over the years have viewed the distinction as spurious and called for an end to it (Johnstone, 1986; Huston, 1994; Thompson *et al.*, 1995). Unfortunately, these calls have generally been ignored, and the field of invasion ecology has largely continued to search for its own generalizations, with limited success.

We think most ecologists during the past few decades, like Elton, and like the rest of the public, have focused on the headline invaders, a small

group of plants and animals that are not representative of the very large group of species that are currently colonizing new areas of the globe. For example, the official catalogue of alien plants in Great Britain lists 3586 species (excluding grasses), of which 885 are officially classified as established, but only a few per cent of these are creating any significant ecological or social problems. We believe this preoccupation with a few conspicuous invaders has contributed to the belief that invasion is a unique phenomenon, and hence one requiring a special explanation. In turn, this belief has perpetuated the dissociation between invasion ecology and the rest of ecology. This is despite a few attempts to bridge the gap, including the British Ecological Society Symposium on *Colonization, succession and stability* (Gray *et al.*, 1987) and the paper on 'How do species dominating in succession differ from others?' by Prach & Pyšek (1999). Rejmánek (1989), in the influential volume on biological invasions edited by Drake *et al.* (1989), specifically linked invasion and succession. That his paper did not have more impact is further evidence of the persistent isolation of invasion ecology.

Even given the historical dissociation we have just described, the isolation of invasion ecology from other subdisciplines seems extreme to us. We think two other factors may have contributed and may still be contributing to this isolation. First, we believe that funding and publication pressures prompt ecologists to promote new and exciting research themes. When a new research theme can be projected as distinctive, important and under-researched, it is often more likely to be funded or published. Ecology may now be paying a price for this proliferation of speciality areas. Instead of collaborating by exploiting common interests and common underlying ecological mechanisms, subdisciplines seem to be severing ties with one another as their specializations begin to create separate identities, evidenced by separate meetings, new specialized journals and lack of reciprocal citations.

Secondly, we wonder whether the increased use of search engines and abstracting journals to identify related articles might be exacerbating the dissociation we have described. Using key words and words in titles, such searches, while convenient, may expose authors to a narrow range of sources if speciality areas are not citing one

another. If not used with discretion, literature searches performed primarily with search engines may actually reduce connections in ecological thought, resulting in more narrow and specialized papers and less synthesis. In addition, search engines may promote citing of papers published in a few prestigious journals that publish much of the current mainline research in a field. Thus, new and/or unorthodox insights or perspectives that might of potential value but are published in more specialized or regional journals may be overlooked. In any case, the use of search engines clearly emphasizes the care that should be taken when identifying 'key words' for published articles.

## SUMMARY AND CONCLUSION

In summary, we hope that this historical overview will prompt the field of invasion ecology to re-examine its roots and connections to other research areas. Although we have focused on the dissociation between invasion ecology and succession ecology, we think that invasion ecology has ignored other subdisciplines as well. The study of gap dynamics (Pickett & White, 1985), metapopulation dynamics (Hanski, 1999), weed science (Cousens & Mortimer, 1995) and restoration ecology (Whisenant, 1999) all involve colonization of habitats and could provide helpful perspectives for invasion ecologists. This is not to say that all the problems of invasion ecology would be solved if invasion biologists paid more attention to the literature on succession or any other branch of ecology. However, different ecological subdisciplines are often asking the same questions and coming to similar conclusions. For example, recent separate reviews of restoration ecology, plant succession and invasions all concluded that mutualisms, such as those involving animal dispersers and pollinators and mycorrhizal fungi, can play an important role in the establishment of (new) species (Prach *et al.*, 1997; Handel, 1997; Richardson *et al.*, 2000a). We believe that unnecessary isolation among these subdisciplines may be inhibiting opportunities for synergy.

The potential value that can be gained by 'borrowing' insights from successional and regeneration dynamics of native species is exhibited by several studies of the invasion dynamics of *Pinus* species in the southern hemisphere (Richardson & Bond, 1991; Richardson *et al.*, 1994; Higgins &

Richardson, 1998). In these studies, information gathered from previous investigations of the spread and regeneration of *Pinus* species within their natural ranges was used to help develop models for describing and predicting the invasion dynamics of pines in a range of southern hemisphere habitats. Another example is the fluctuating resources hypothesis of invasibility (Davis *et al.*, 2000) that was developed from findings and insights produced by several studies of succession (Grime, 1988; Davis *et al.*, 1998, 1999). We believe that the field of invasion ecology will benefit from more efforts of these sorts and that existing insights and knowledge from succession ecology and other subdisciplines can be used to advance the study of invasions.

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### REFERENCES

- Cousens, R. & Mortimer, M. (1995) *Dynamics of weed populations*. Cambridge University Press, Cambridge.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**, 528–534.
- Davis, M.A. & Thompson, K. (2000) Eight ways to be a colonizers; two ways to be an invader. *Bulletin of the Ecological Society of America* **81**, 226–230.
- Davis, M.A., Wrage, K.J. & Reich, P.B. (1998) Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* **86**, 652–661.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T. & Muermann, C. (1999) Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water–light–nitrogen gradient. *Plant Ecology* **145**, 341–350.
- Donnegan, J.A. & Rebertus, A.J. (1999) Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* **80**, 1370–1384.
- Drake, J., Mooney, H.A., Di Castri, F., Groves, R., Kruger, F.J., Rejmánek, M. & Williamson, M., eds (1989) *Biological invasions: a global perspective*. Wiley, Chichester.
- Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* **14**, 135–139.
- Elton, C.S. (1927) *Animal ecology*. Sidgwick & Jackson, London.
- Elton, C.S. (1942) *Voles, mice and lemmings: problems in population dynamics*. Clarendon Press, Oxford.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Elton, C.S. (1966) *The pattern of animal communities*. Methuen, London.
- Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T., eds (1992) *Plant succession: theory and predictions*. Chapman & Hall, London.
- Gray, A.J., Crawley, M.J. & Edwards, P.J., eds (1987) *Colonization, succession, and stability*. Blackwell Scientific, London.
- Grime, J.P. (1988) The C–S–R model of primary plant strategies: origins, implications, and tests. *Plant evolutionary biology* (ed. by L.D. Gottlieb and S.K. Jain), pp. 371–393. Chapman & Hall, London.
- Handel, S.N. (1997) The role of plant–animal mutualisms in the design and restoration of natural communities. *restoration ecology and sustainable development* (ed. by K.M. Urbanska, N.R. Webb and P.J. Edwards), pp. 111–132. Cambridge University Press, Cambridge.
- Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.
- Higgins, S.I. & Richardson, D.M. (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. *Plant Ecology* **135**, 79–93.
- Hughes, R.F., Kauffman, J.B. & Jaramillo, V.J. (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* **80**, 1892–1907.
- Huston, M.A. (1994) *Biological diversity*. Cambridge University Press, Cambridge.
- Johnstone, I.M. (1986) Plant invasion windows: a time-based classification of invasion potential. *Biological Review* **61**, 369–394.
- Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536.
- Pickett, S.T.A. & White, P.S., eds (1985) *The ecology of natural disturbances and patch dynamics*. Academic Press, New York.
- Pimental, D., Lach, L., Zuniga, R. & Morrison, D. (2000) Environmental and economic costs of non-indigenous species in the United States. *Bioscience* **50**, 53–65.
- Prach, K. & Pyšek, P. (1999) How do species dominating in succession differ from others? *Journal of Vegetation Science* **10**, 383–392.

- Prach, K., Pyšek, P. & Šmilauer, P. (1997) Changes in species traits during succession: a search for pattern. *Oikos* **79**, 201–205.
- Rejmánek, M. (1989) Invasibility of plant communities. *Biological invasions: a global perspective* (ed. by J. Drake, H.A. Mooney, F. Di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 369–388. Wiley, Chichester.
- Richardson, D.M., Allsopp, N., D'Antonio, C., Milton, S.J. & Rejmánek, M. (2000a) Plant invasions—the role of mutualisms. *Biological Reviews* **75**, 65–93.
- Richardson, D.M. & Bond, W.J. (1991) Determinants of plant distribution: evidence from pine invasions. *American Naturalist* **137**, 639–668.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000b) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**, 93–107.
- Richardson, D.M., Williams, P.A. & Hobbs, R.J. (1994) Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography* **21**, 511–527.
- Simberloff, D. (2000) Foreword *The ecology of invasions by animals and plants* (by C.S. Elton) pp. vii–xiv. University of Chicago Press, Chicago.
- Southwood, T.R.E. & Clarke, J.R. (1999) Charles Sutherland Elton. *Biographical memoirs of Fellows of the Royal Society of London* **45**, 129–146.
- Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: more of the same? *Ecography* **18**, 390–402.
- Turner, M.G., Dale, V.H. & Everham, E.H. III (1997) Fires, hurricanes, and volcanoes: comparing large disturbances. *Bioscience* **47**, 758–768.
- Whisenant, S.G. (1999) *Repairing damaged wildlands: a process-oriented landscape-scale approach. Biological conservation, restoration, and sustainability* 1. Cambridge University Press, New York.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *Bioscience* **48**, 607–615.
- Williamson, M. (1999) Invasions. *Ecography* **22**, 5–12.