Foreword to Chapter Six

Daniel Simberloff and Anthony Ricciardi

In previous chapters Elton focused on invasions with striking impacts; here he explored reasons why such invaders succeeded and others either failed to survive or remained restricted and innocuous. By "balance between populations," Elton did not refer to the ancient and persistent idea of a "balance of nature,"[XXV] which he had previously forcefully rejected: "The 'balance of nature' does not exist…. The numbers of wild animals are constantly varying … and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable."[VII] In this chapter he argued that the balance between species is constantly changing in every country.

His main conclusion was telegraphed by the title: populations interact with one another, and failed or restricted invasions were resisted by native species or by humans, while the successful ones somehow escaped the balance experienced in their native range. Fundamental knowledge about the forces establishing this balance is, in Elton's view, a

D. Simberloff (✉)
Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN, USA
e-mail: dsimberloff@utk.edu

A. Ricciardi
Redpath Museum and McGill School of Environment,
McGill University, Montreal, QC, Canada
e-mail: tony.ricciardi@mcgill.ca

C. S. Elton, *The Ecology of Invasions by Animals and Plants*,
https://doi.org/10.1007/978-3-030-34721-5_11

"life-and-death need." He termed the negative effects of native species on invaders "ecological resistance"; it is now called "biotic resistance." As an example of the role of absence of enemies in the new range (further elaborated in Chap. 7), Elton cited the contrasting fate of introduced *Eucalyptus* in California, New Zealand, and South Africa. When he wrote *EIAP*, California trees, introduced by seed, lacked both introduced and native phytophagous insects, while New Zealand and South African *Eucalyptus* stands were plagued by Australian insect species introduced with the initial young trees. However, beginning in 1983, many Australian *Eucalyptus* pests have arrived in California, perhaps through covert deliberate introduction by opponents of nonnative trees.[XXI]

Elton perceptively recognized the value of research on why certain invasions fail, an understudied focus until recently.[XXIX] He detailed the long presence of *Lamium album* (white dead-nettle), "never … admitted into the natural vegetation of Britain" despite presence for hundreds of years. Rather, it is abundant on roadsides and waste areas. Elton did not offer an explanation but said the reasons for the failure, and whether *L. album* would replace or just add to natives if it did invade, "perhaps is the single most important problem lying underneath all the facts of the present book" (p. 161). It will be interesting to see if the recent two-month advance in flowering time of *L. album* in Britain, the greatest among 385 species,[IX] leads to invasion. Earlier flowering times and modifications in other ecological processes in response to global warming have become prominent research topics.[XX]

Elton detailed another ultimately failed invasion, the famed collapse of previously enormously abundant Canadian pondweed (*Elodea canadensis*) in Great Britain. He found no relation to human actions and saw it as mysterious, which it remains over a century later.[XXVI] In a note tucked into the proof copy, Elton cited Stout[XXVII] to the effect that, in New Zealand, *E. canadensis* is "settling down, tho' dom. in places." However, *E. canadensis* remains highly invasive in New Zealand, displacing native vegetation[XII] despite very low genetic diversity.[XV] Spontaneous collapses are uncommon but not unheard of.[XXVI] The recent collapse in the Mediterranean of the "killer alga" *Caulerpa taxifolia*[I] is eerily reminiscent of the *E. canadensis* case, down to the similar tentative hypotheses.

Where human actions were not involved, Elton attributed most invasion failures to biotic resistance, which he saw as usually highly complex. Citing the 12 years of research by his Bureau of Animal Population (BAP) in Wytham Woods near Oxford, he noted 2,500 animal species so far tallied, in a variety of connected habitats with many interactions, such as competition, predation, and parasitism, combining

to resist any invader. The complexity of such a scenario hindered attempts to understand particular failures. Elton believed that the fact that most introduced plant species in Britain were found in disturbed areas with fewer species results from the intense ecological resistance posed by complex communities such as that of Wytham Woods; he returned to this theme in Chap. 8. Many studies of the trajectories of invasions have documented biotic resistance, but many other forces play roles, often decisive ones.[XVII] The Wytham Woods research was the basis of the large treatise Elton considered his masterwork, *The Pattern of Animal Communities*,[VIII] which described the division of species into habitats and interactions among habitats and species. Ironically, this work is rarely cited today, while his little popular book on invasions has become an ecological classic.

Although emphasizing biotic resistance, Elton of course realized that some invasions failed or were limited by climate. Perhaps he intended his second edition to be explicit on this point. Among inserted notes in this chapter of the proof copy is a copy of a 1969 letter to the *Guardian*[VI] describing the invasion of southern England by the South American aquatic plant *Azolla filiculoides*, asserting that its rapid spread was stemmed by hard winters. The species is still invasive in parts of Great Britain, still limited by cold winters, but there is some evidence of evolution since its arrival adapting it to the British climate;[XIII] and, of course, the climate is warming.

For a few failed invasions, Elton saw deliberate human efforts as causal, such as the exclusion of the Colorado potato beetle from Great Britain, which continues to this day despite occasional incursions.[III] Among large-scale successful eradications, he cited an early eradication of the Mediterranean fruit fly in Florida, eradication of *Anopheles gambiae*, a malaria vector, in Brazil, and eradication of several foot-and-mouth disease invasions of the United States. Elton detailed the eradication of the muskrat in Britain, in which his own BAP was heavily involved.[XXIV] He doubtless was also thrilled with the later larger scale eradication of the nutria,[X] which the Bureau had also studied. Elton depicted the nutria in Plates 12 and 13, and a marginal note in Chap. 1 of the proof copy cites a map of its distribution in Britain in 1966, but we found no mention of the successful eight-year eradication campaign ending in 1988 in his notes or the archives. Elton would also have rejoiced in the rapidly growing number of successful eradications of island invaders.[XIV]

Elton was particularly concerned with whether invasions diminish or eliminate native species populations, as noted in the *Lamium* example above. He recalled from Chap. 5 the decline of a British oyster drill in the

face of invasion by an American oyster drill and called attention to the impact of the starling invasion of North America on native bluebird and northern flicker populations in towns. He particularly noted another example studied by the BAP—the decline in Britain of the native red squirrel in the face of invasion by the North American grey squirrel. Elton cited this replacement as an example of "our ignorance of the nature of competition." In this case, the basis of resource competition is now well understood, and it is known, as it was not when Elton wrote, that a key impact of the grey squirrel on the red squirrel is introduction and transmission of lethal squirrelpox virus.[XXIII] Further, the grey squirrel was released from captivity in Italy in 1948 and began spreading rapidly in 1970.[II] An eradication campaign there was halted by a lawsuit based on animal rights,[II] and the grey squirrel is now dispersing northward and eastward, nearing France.[XXIII]

Elton ended this chapter with a list of four introduced amphipods that had spread in Great Britain but seemed not to affect native species, plus two native amphipods that appeared to be mutually exclusive. Of the four invaders, *Eucrangonyx gracilis*, *Gammarus fasciatus*, and *Orchestia bottae* remain present but are not recorded as affecting natives. *Corophium curvispinum*, now highly invasive in the Rhine, has spread further in Britain and is an important food for some native fish.[XI] A potentially devastating amphipod invasion into Britain occurred in 2010, that of the "killer shrimp" *Dikerogammarus villosus*.[XIX] This Ponto-Caspian species spread widely in much of central and western Europe after the opening of the Danube-Main-Rhine canal in 1992 and quickly had massive impacts on native species in the Rhine.[XXVIII] Several Ponto-Caspian invertebrates have invaded widely since Elton wrote, with substantial impacts on native species; for instance, the amphipod *Echinogammarus ischnus* has replaced *Gammarus fasciatus* in parts of the Great Lakes.[XXII] As for the two native British amphipods Elton suggested were mutually exclusive, *Gammarus duebeni* (*G. d. celticus*) and *G. pulex*, introduction of the latter has subsequently often led to replacement of the former, and the mechanism has been identified as intraguild predation rather than competition.[V] A more recent analysis using long-term multi-site data from the Isle of Man (combining data from studies cited by Elton with modern field surveys) suggested that *G. d. celticus* resists incursions by introduced *G. pulex* at sites with good water quality.[XVIII]

Elton was an engaging writer with a wry, understated sense of humor. In this chapter, his stories of how he inadvertently carried chafer beetles to Great Britain in acorns he brought back from visiting Aldo Leopold in Wisconsin, and of his friend bringing in beetles in buttons on an

Egyptian shirt, were elegant introductions to the topic of preventing invasions. He indicated progress in this effort by asserting that "no one is likely to get into New Zealand again accompanied by a live red deer" (p. 155). This chapter is also laden with metaphors of war ("battlefields," "repel invaders," destroying "bridgeheads," "spearheads," "bombarding" species, "commando forces") and began with the explicit analogy. Elton has been criticized for using martial metaphors on the grounds that they lead to xenophobia and contribute to counterproductive militaristic patterns of thought.[XVI] No evidence is forthcoming for either of these effects, and, in any event, such language is so embedded in popular culture (e.g., the war on cancer, the war on drugs) that it will not likely be banished from writing about biological invasions. Davis et al.[IV] suggest that Elton's martial attitude toward invasions was colored by his experiences during World War II, when the BAP devoted its research to eradicating introduced rodents from Britain in support of the war effort. However, as we mentioned in our Introduction, Elton's interest in invasions and use of martial metaphors was present well before the war.[XXIV]

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