

# Foreword to Chapter Three



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In Chap. 3, Elton invoked the notion of a homogenized world owing to invasions: “If we look far enough ahead, the eventual state of the biological world will become not more complex but simpler—and poorer.” He illustrated the concept with the elegant example of six great liquid-filled tanks (ersatz continents), each possessing unique chemical solutions, connected by narrow tubing (human transportation systems) blocked by taps (geographic barriers). The taps, he noted, are being opened with greater frequency and the result has been a slow but ever-increasing homogenizing mixture. Today, biotic homogenization is well recognized as another layer of anthropogenic global change.<sup>[XXVII]</sup>

Elton casually estimated the number of species that had spread beyond their natural ranges as being in the tens of thousands, and of these, he wrote, thousands had noticeably affected human society by causing loss of life or socioeconomic damage. Readers may find this ratio reminiscent of the “Tens Rule,”<sup>[XLIII]</sup> the hypothesized statistical tendency of the proportion of successfully introduced species that become pests to be approximately 1 in 10. Researchers still have only a vague understanding of the numbers of non-native species that have become established worldwide for many

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major taxonomic groups, but current records for macroscopic species are indeed in the tens of thousands.<sup>[XXXVII]</sup> Some of these invasions have had very conspicuous effects, whereas many others appear innocuous; however, the individual impacts of the vast majority of these invasions have not been studied, so it is not known with reasonable certainty whether their effects on ecosystems or society are insignificant.<sup>[XXXIX]</sup> The risk of unintended or unforeseen consequences of invasions is better appreciated today, after research has revealed a very broad scope of direct and indirect effects that are generally difficult to predict or detect.<sup>[XXXV,XXXIX]</sup>

Using the United States as a case study of continental invasions, Elton listed examples of the introductions of several insects originating from various regions of the world. One of these was the Japanese beetle *Popillia japonica* introduced to New Jersey with plant nursery stock before 1916. Elton described the beetle's spread over a 25-year period as a series of concentric increases in area that exemplify neighborhood diffusion, which has become recognized as a distinct pattern of spread for certain groups of invading species.<sup>[XX]</sup> Elton noted that the beetle was regarded as only a minor pest in Japan, in contrast to its rapid population growth and infestations in the USA. Today, it is considered as the most widespread and destructive insect pest of turf grass and nursery crops (and, to a lesser degree, fruit crops and ornamental plants) in North America. By the end of the 1990s, the beetle was established in all states east of the Mississippi River (except Florida) and in most provinces in eastern Canada.<sup>[VI,XXXIII]</sup> It also became established in a few western American states, although some recurring introductions in California were successfully eradicated. In the early 1970s, it invaded Terceira Island of the Azores after escaping from a US air base.<sup>[XXXIII]</sup> In 2014, it was discovered for the first time in mainland Europe (Italy).<sup>[XIV]</sup> Further, rapid global expansion under climate change is expected.<sup>[XXIII]</sup>

As another example, the spread of the European beech scale insect *Cryptococcus fagi* in Atlantic Canada was depicted (Fig. 27). In the proof copy of *EIAP*, above Fig. 27 there is a note in pencil referring to a paper by Pimentel<sup>[XXXI]</sup> that reviewed the ecology of insect invaders of the Canadian maritime provinces. This paper would have been an appropriate reference in a subsequent edition, as it provided several interesting observations and insights, some inspired by *EIAP*, including the fact that the region contains international ports surrounded by human-modified environments and simplified plant and animal communities unlikely to resist invasions. Moreover, Pimentel opined, à la Elton, that the lack of evolved equilibrium between the invader and its recipient community was a prime reason for outbreaks of introduced insects.

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Elton also described North America as an important *donor* region for herbivorous insect invasions abroad, citing examples of the American vine aphid *Phylloxera vitifolii*, the Colorado potato beetle *Leptinotarsa decemlineata*, and the fall webworm *Hyphantria cunea*. Painting a picture of continents under siege, Elton listed a plethora of other plant pests with diverse invasion histories in North America and other areas of the world. Presciently, he predicted that some introductions that were relatively recent at the time would become more important in the future. One of these was the golden nematode *Globodera (Heterodera) rostochiensis*, native to South America<sup>[XXXII]</sup> and discovered in the USA on Long Island, New York, in 1941. It may have been transported years earlier in military equipment returning from Europe after the First World War;<sup>[XV]</sup> the species was known to occur in Europe since at least the early 20th century, having probably arrived with potatoes from Peru.<sup>[XXXII]</sup> It had been found in Africa and the Middle East by the time Elton published his book. Since then, it has been recorded in India in 1961, Canada in 1962 (where it occurs in Newfoundland, Quebec, Alberta and British Columbia<sup>[VIII]</sup>), India in 1961, Mexico and Japan in the early 1970s, Australia in the 1980s, Pakistan and the Philippines in the 1980s, and Indonesia in 2003.<sup>[IX]</sup> A similar congeneric species, the pale cyst nematode, *G. pallida*, was recognized as distinct from *G. rostochiensis* since the 1970s<sup>[XLI]</sup> and appears to be a more aggressive global pest of potato crops.<sup>[XV]</sup> A species that certainly fits the pattern of extraordinarily aggressive behaviour and infestation outside its native range is the Argentine ant *Linepithema (formerly Iridomyrmex) humile*. Elton described its spread in the United States, South Africa, and Australia and noted its tendency to eliminate native ants. It subsequently invaded Europe, the UK, New Zealand, Japan, and various islands.<sup>[XLI]</sup> Several other ant species have likewise invaded continents and islands worldwide<sup>[I,III,XVI,XIX]</sup>, and these global expansions surely would have captured Elton's attention.

Elton attributed the pattern of elevated infestations and aggressive spread of insects in invaded regions compared to their native ranges to the absence of effective natural enemies. He first introduced this concept 30 years earlier in *Animal Ecology*,<sup>[XII]</sup> in which he attributed the gypsy moth increase and spread in North America to the absence of natural parasites that keep its numbers down in Europe; now termed the Enemy Release Hypothesis, this is the basis of classical biological control. Elton highlighted the Australian cottony cushion scale insect *Icerya purchasi* as a major threat to citrus crops that was subsequently controlled by a natural enemy (the vedalia beetle *Rodolia cardinalis*) introduced

intentionally from the native region of the scale insect in what became a classic case of biological control. The same control agent was introduced in several other countries with similar results, eliciting exaggerated optimism about the use of biocontrol agents.

Years before the publication of *EIAP*, pathogens were known to be damaging invaders of continents, as exemplified by Dutch elm disease, which is caused by a fungus dispersed by beetles; the disease is now known to involve two species of *Ophiostoma* believed to originate from Asia. As described by Elton, the first pandemic was caused by *O. ulmi* in Europe and North America from the 1920s to the 1940s but declined thereafter in Europe, possibly because of deleterious viruses within *O. ulmi* populations.<sup>[V]</sup> The second pandemic began in the 1960s and was caused by the previously undescribed species *O. novo-ulmi*, which has proven to be even more destructive.<sup>[VI]</sup> Multiple introductions of the fungus were driven by sequential importations of elm timber across the northern hemisphere; an importation of diseased timber from Canada in the 1960s introduced *O. novo-ulmi* to the UK,<sup>[VI]</sup> from which it subsequently spread throughout western Europe.

In contrast to invasive invertebrate pests, virtually all of which were introduced inadvertently, most mammals apart from rodents were transported to other continents intentionally.<sup>[XXIX]</sup> The same can be said for most birds<sup>[XXVIII]</sup> and fishes,<sup>[XXVI]</sup> as well as many amphibians and reptiles,<sup>[XXIV]</sup> as there now exist very detailed databases and published compilations documenting the global histories of these introductions. Elton alluded to widespread transplantations of fish for sport, food, and mosquito control. He also recognized the growing importance of tropical fish species in trade, whose modern-day numbers exceed Elton's estimate of "hundreds of kinds" by an order of magnitude.<sup>[IV,XXX,XXXIV]</sup> There are over 1100 species of fishes in the pet trade in southwestern Europe.<sup>[XXX]</sup> More than one billion live fishes belonging to over 200 species were imported into the US in the early 2000s primarily for the pet industry and aquaculture.<sup>[XL]</sup> In particular, Elton cited anecdotal reports of tropical aquarium fishes escaping and breeding in the Florida Everglades. A penciled note in the proof copy referring to a 1971 magazine article<sup>[X]</sup> indicated Elton's intention to add the example of "walking catfish" (*Clarias batrachus*), which invaded Florida in the late 1960s. Another intended addition is indicated by a reference card that cited a 1971 article<sup>[XXI]</sup> describing the pike killifish (*Belonesox belizanus*) as another tropical species that became established in southern Florida through the aquarium trade in the late 1950s or early 1960s. The diversification of the pet trade and its consequences have become quite apparent over the past half century. Aquarium releases have led to

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widespread invasions by freshwater and marine fishes,<sup>[XXXVIII]</sup> including Indo-Pacific lionfish *Pterois* spp.—perhaps the most damaging marine fish invasion recorded to date.<sup>[XVIII]</sup> The pet trade is also ultimately responsible for the ongoing invasion of reptiles worldwide, including the Burmese python, which has proven to be a significant threat to biodiversity in Florida.<sup>[XI]</sup> Severe threats to biodiversity are also associated with animal pathogens moved through pet trade.<sup>[XLIV]</sup>

Elton viewed islands and insular habitats in general as being highly susceptible to invasion. In a letter to a colleague regarding Philippine geckos invading Mexico, Elton admitted “I am always interested in successful invasion from an island to the mainland.”<sup>[XIII]</sup> This interest seems to be reflected in his highlighted examples of Australian insects invading other countries. Elton might have been similarly fascinated by the scores of freshwater and brackish water species from the river deltas and estuaries of the Black, Caspian and Azov basins that have rapidly colonized inland waters of Europe and the North American Great Lakes in recent decades.<sup>[III,XXXVI]</sup>

Finally, the reader will note that in this chapter Elton offered a key generalization: “...invasions most often come to cultivated land, or to land much modified by human practice.” He elaborated on this theme further in Chap. 8, where he warned that ecosystems are more vulnerable to a destructive invasion after they have been simplified, such as through land conversion. This proposition laid the foundation for two longstanding hypotheses in ecology that relate invasion risk to diversity<sup>[XXII]</sup> and disturbance,<sup>[XVII,XXV]</sup> respectively (see foreword to Chap. 8).

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