Foreword to Chapter Eight

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Chapter 8 departs from the theme of invasions; it is about conservation—what Elton meant by it and how to achieve it. Although Elton is well known for his pioneering writings on invasions and on animal ecology, his contributions to conservation, though vast, are not widely recognized.[XLII] In fact, he greatly influenced the development and implementation of a British national policy on conservation and wrote more generally about the need for and means of achieving conservation. His involvement in conservation developed apace with his ecological research, including on invasions. Several of the observations he described in earlier chapters are found here as he defined the problem and a possible response.

He began with three questions that we would now recognize as underpinning environmental ethics, although he was writing fifteen years before what might be seen as the explicit founding of the field.[XXXIX] (1) Do non-human animals "have a right to exist and be left alone, or at any rate … not be persecuted or made extinct as a species?" (p. 201). (2) We appreciate nature because it is interesting, beautiful, exciting, and provides recreation, but is this instrumental value of nature for humans an adequate basis for conservation? (3) We use nature for material goods, from farms, forests, and fisheries, but is not this use as the basis of the

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conservation problem, "the worm in the heart of the rose" (p. 202)? Here he explicitly attributed the problem to rapid human population growth, "introducing too many of ourselves into the wrong places" (p. 202) and bringing along invasive plants and animals.

Environmental ethics is now a major field, with a respected journal (*Environmental Ethics*) that began in 1979 and many textbooks and monographs.[XXXVIII] A major persistent theme is Elton's first question: do individual animals (and plants) have intrinsic worth, do rights (including to exist and not be persecuted) flow from this worth, and do such rights extend to collective entities such as populations or species?[XXXVI] Ecologists will recognize the instrumental values to humans in Elton's second question as the "cultural services" and those in his third question as the "provisioning services" (and perhaps also the "regulating" and "supporting services") of the Millennium Ecosystem Assessment,[XXIX] which has achieved great prominence and elicited much controversy in the conservation and environmental communities by casting all of nature as a bundle of "ecosystem services" for humans.[XL]

Elton's response to these questions was to suggest a coexistence between humans and nature, and the principles of this coexistence are what he defined as *conservation*: "This means looking for some wise principle of coexistence between man and nature, even if it has to be a modified kind of man and a modified kind of nature. This is what I understand by *Conservation*" (p. 211). At this point, Elton introduced a hypothesis that became a dominant principle in conservation and spurred much ecological research, the idea that high species diversity (which we now term "species richness" or "biodiversity") or complexity stabilizes ecosystems. In fact, until the explosion of interest in biological invasions in the 1980s, Elton was probably best known among ecologists for this hypothesis and for the conception of nature as organized into food chains. Elton later elaborated on this hypothesis, and on the role of complexity in resisting invasions, in a 1967 lecture at the University of Glasgow, focusing specifically on the extent to which rare species in a community contribute to stability: "Complex communities are less vulnerable to disturbance especially from new invaders. The complexity includes not only diversity of species and their food inter-relations, but effects on habitat, and also interspersion of habitat components and their differing communities."[XIV] In his book, he adduced six reasons for his hypothesis, only one of which relates directly and one indirectly to biological invasions.

First, although Elton was no enthusiast of mathematical models, he noted that simple models of one predator species and one prey species,

even without externally imposed "shocks," show drastic fluctuations of population sizes. He cited no specific literature but was surely referring to the Lotka-Volterra equations of the 1920s. Correspondence with Vito Volterra regarding Elton's conclusion that external factors are not in themselves necessary to cause fluctuations in the populations of wild animals led Volterra to reply, "I am very glad to hear that your ideas agree perfectly with those I have expressed in a mathematical form."[XXII] This line of reasoning was widely cited and pursued, but in 1973 Robert May showed that, in fact, complexity of food web models actually, on average, decreased stability.[XXVII] This type of research on mathematical models of trophic webs has proliferated greatly, particularly employing simulations,[I,XLV] and has more recently been supplemented by network analyses incorporating non-trophic interactions.[XXIII]

Second, Elton cited classic laboratory experiments on single prey-single predator systems, particularly those of Georgy Gause,[XVIII] showing how difficult it is to keep one or both species from going extinct. Simple microcosms such as these continue to be employed in various community-level studies,[XXXII] but their relevance is debated.[II,VI] Third, he pointed to Chap. 4, with all the examples of island ecosystems devastated by biological invasions, which he contrasted with the relative dearth of such devastation on continents, with their greater numbers of species.

Fourth, Elton suggested that both invasions and outbreaks (of both native and nonnative species) occur most frequently on cultivated land, and cultivation entails three kinds of simplification, all tending to reduce species richness. Much cultivation is of nonnative species introduced without natural enemies from their native range, many of these are deliberately grown in monocultures, and often other species associated with the cultivated species, perceived as harmful, are deliberately killed, along with incidental death of many other species. Elton noted several exceptions—nonnatives invading more or less pristine habitat—including the grey squirrel and European sycamore in his Wytham Woods field site, but he emphasized that Wytham Woods, with its species-rich native community (see Foreword to Chap. 6), had but three or four prominent invaders. The relationship of native species richness to invasibility has been an abiding research topic, particularly since Stohlgren and colleagues[XLVIII] pointed to several examples countering Elton's suggestion that native biodiversity poses a sort of biotic resistance (cf. Foreword to Chap. 6). In fact, various processes can generate either positive or negative relationships between native species richness and invasibility, and the relationship, if present at all, varies from site to site, and taxon to

taxon, and the scale at which one seeks the phenomenon.[XVII] As for the role of disturbances, including cultivation, in favoring invasions, in many circumstances this has been shown to be the case.[XXIV] For many plant invasions, this occurs because the disturbance liberates resources (e.g., light or nutrients) that invaders quickly exploit.[XI] However, invasions often occur in undisturbed habitats.[XXVI]

Fifth, Elton pointed to an apparent relative lack of outbreaks in species-rich tropical forests. He was tentative on this point and felt that complexity of these communities was only part of the reason. Curiously, in a book about invasions, Elton did not specifically suggest that tropical forests resist invasions by nonnative species, although this pattern has frequently been claimed,[XVI,XXI] often citing Elton. Elton himself later foreswore his original claim of lack of outbreaks in tropical forests,[XII] ascribing his changed view to the accumulation of more data and suggesting that a previous scarcity of such outbreaks was due only to the vast expanse of undisturbed tropical forest, now giving way to destruction and fragmentation. As for invasions, several authors have noted relatively few invasions of tropical forests to date,[XVI,XXXV,XXXVII,L,LI] though they generally reject the notion that greater native diversity producing greater resistance causes this paucity. Rather, they focus on such features as low propagule pressure and especially the great amount of remaining undisturbed tropical forest, and all point to the danger that rapidly increasing tropical deforestation and fragmentation will greatly increase invasions. Elton himself, in his last publication and one published just before it, based on literature and his field research in two Neotropical forests, warned that deforestation would cause increasing instability and a wave of extinction in tropical forests.[XII,XIII] In fact, he anticipated by a year a call by several ecologists, ostensibly based on the equilibrium theory of island biogeography, to the effect that huge, undisturbed nature reserves are required to stem extinction and that small nature reserves will not suffice.[XLI]

Elton's sixth support for his hypothesis that biodiversity and complexity confer stability consists of observations on Canadian orchards in which use of DDT and a fungicide targeting particular pests induced great increases in other pests, attributable to incidental destruction of natural enemies of the latter, "upsetting the relationships between pests and their natural enemies and parasites" (p. 151). He contrasted these orchards with unsprayed Canadian and British ones with low pest numbers and many natural enemy species. Here, of course, he anticipated a major message of Rachel Carson's *Silent Spring* (1962),[VIII] which featured the inimical effects of using pesticides on two invaders in North

America (gypsy moth and fire ant) and which transformed environmentalism. Carson cited Elton's *EIAP* at several points and invited him to write an introduction to the British edition of *Silent Spring*, which he declined.[IX] Carson was heavily influenced by Elton's book and Chap. 8 in particular, as witness her remarkable 1958 letter to Edward O. Wilson:

> *I am already indebted to you for many things, but perhaps most of all for your reference to Elton's 'Ecology of Invasions.' I had not heard of it until you mentioned it, although I know his earlier work on populations. I found this enormously stimulating. It cuts through all the foggy discussion of insect pests and their control like a keen north wind.*[VII]

Elton warned early about the biodiversity consequences of pesticide spraying and played a lead role in 1951–1952 in spurring the Nature Conservancy of Britain to object, with some success, to spraying roadside verges.[XXXIII] He certainly intended to expand on this issue in the second edition, as he had tucked notes on later cases of insect outbreaks caused by pesticide use[X,XV,XXV] into the proof copy, as well as an article on problems caused by insecticide resistance.[III]

Elton did not believe that that all spraying could or even should be stopped, in orchards and elsewhere. Rather, he advocated a version of what is now called "integrated pest management",[XXXIV] entailing reduced and very judicious pesticide use, managing habitat to favor natural enemies of pests, and biological control—the deliberate introduction of natural enemies from the native pest range. Elton was particularly enthusiastic about the latter approach, despite recognizing the danger of non-target impacts (see Foreword to Chap. 4). He exemplified the prospects of this method with two examples from control of non-native scale insect pests of California citrus. The success of a chalcid wasp controlling red scale that he heralded was later improved still further by introduction of congeneric wasps better suited to certain California climates.[XXXI] The other example, deliberately propagating a weed in order to allow black scale to persist so that its parasitoid population does not dwindle during periods when the citrus host of the scale is not abundant,[XLIV] was a "thinking outside the box" approach that has faded from memory. The problems of synchronizing pests and biological control agents and need for alternative hosts have been persistent ones.[XLVII] For instance, introduction of the beetle *Diorhabda carinulata* to control tamarisk in the American Southwest was not sufficient in the southern part of the range because the beetle entered

diapause too early, but two congeners were introduced from more southern regions that remain active later in the season.[XX]

Elton's book is widely cited[XIX,XXX] as an inspiration for the persistent popular idea in conservation that species diversity or complexity fosters ecosystem stability.[XXVIII] Elton likely was originally intrigued by this idea through his interactions with his friend Aldo Leopold, who proposed the concept in various writings from the 1940s.[XLIII] To a large extent, this paradigm of diversity begetting stability has been superseded, at least in academic conservation literature, but it greatly influenced the development of the current hypothesis that species diversity is a key determinant of ecosystem function, which has inspired abundant empirical research and debate.[XLVI,XLIX] Much current literature on this issue and related ecological matters involves shifting the currency of species diversity or richness to number of functional types or groups.[IV,V]

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