

Part 1

Historical Perspectives

A WORLD OF THOUGHT:
'*THE ECOLOGY OF
INVASIONS BY ANIMALS
AND PLANTS*' AND
CHARLES ELTON'S
LIFE'S WORK

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1.1 INTRODUCTION

In this chapter, I present a personal view of the Elton canon: the body of work created by Charles Elton during his whole working life. *The Ecology of Invasions by Animals and Plants* (hereafter abridged as '*Ecology of Invasions*' or '*EIAP*') was produced something like two-thirds of the way through this long period of productivity. I suggest its origins and impacts are best appreciated when viewed as part of Elton's overall intellectual contribution. That *EIAP* may be regarded as foundational to a whole subsequent field of study is indisputable (Richardson & Pyšek, 2007, 2008; but see Simberloff, this volume, for a different view) and yet, I shall show that this is only one of several highly productive and important areas of work that originated within the body of work for which Elton was responsible during his long life.

1.2 THE ECOLOGIST AND THE MAN

Charles Sutherland Elton (1900–1991) did not invent the discipline of animal ecology: that evolved from the many musings of earlier naturalists, beginning to precipitate into modern scientific form courtesy of Charles Darwin, Alfred Russel Wallace and Victor Shelford, among others. Indeed many of the concepts usually associated with Elton's ideas had existed in more or less nascent form in earlier years. The idea of a food chain (although not the phrase) had been described well over 100 years earlier (Bradley 1718; Egerton 2007). The general notion of a pyramid of numbers or at least the underlying 'rule of ten' had been stated clearly and generally by Karl Semper in 1881. The broadening of these simplifications of trophic interactions into food webs began with a series of specific diagrams as early as 1912 (Pierce et al. 1912) and these early efforts are described in detail by Egerton (2007). Even the term 'niche', so often now eponymic with Elton, had been used by Grinnell as early as 1904 and developed significantly in his famous article on the California thrasher (Grinnell 1917). It was Charles Elton, though, who gathered up, clarified and connected these ideas into a cogent whole in his 1927 book *Animal Ecology* and, to my way of thinking, so set an agenda for the entire emerging field of animal ecology. It also established ecological ground rules that subsequently underpinned the emergence of formal conservation agencies in both the UK and USA.

This short text remains vital reading for all ecologists and is a model of clear thinking, pithy writing and penetrating insight. As well as incorporating the concepts already mentioned he also built substantially on Shelford's ideas on succession within natural communities. The insights presented so well in *Animal Ecology* had derived from Elton's years as a general naturalist during his youth and early adulthood in England. In addition, he had spent three very formative seasons before and after graduating from Oxford on expedition in Spitzbergen and Norwegian Lapland observing the ecological communities and animal populations in that almost canonical landscape where, perhaps, the grand patterns can be perceived more clearly because the component parts, so confusing and diverting in less extreme environments, are relatively few in number.

Elton's career has been described at length by his thorough and sympathetic obituarists (Macfadyen 1992; Southwood & Clarke 1999). I repeat here only the observations that Elton's scientific contributions during a long scientific career were marked by a series of contrasting but perhaps surprisingly coherent set of major books, each in itself a landmark for the developing subject. *Animal Ecology* (1927) was succeeded by *Voles, Mice and Lemmings* (1942), *The Ecology of Invasions by Animals and Plants* (1958) and, finally, *The Pattern of Animal Communities* (1966). These undoubtedly seminal contributions should, in my view, be joined by his swansong paper on tropical rainforest biodiversity published in the *Journal of Animal Ecology* in 1967. I shall return to this last major publication towards the end of this account.

From 1932 until his retirement in 1967, Elton worked with a small group of other ecologists and graduate students in the Bureau of Animal Population (the BAP), within but not physically part of the Department of Zoology of the University of Oxford (Crowcroft 1991). It was my privilege to join that group as a doctoral student in October 1966: one of two 'final' students of the BAP. I was supervised, formally, by H.N. Southern but my entry to the Bureau and progress within it were closely directed by Elton himself. Elton's influence within the Bureau was all pervasive. A quiet, even unprepossessing, man, Elton nevertheless imposed his style and philosophy on the life of the Bureau and those of us who were part of the enterprise were willing participants in what we took to be a noble endeavour. I for one have not deviated from that view in the ensuing 40 years.

Life in the Bureau revolved around afternoon tea. Coffee was indeed taken in the mornings but was a low-key affair, usually huddled within the small kitchen. Coffee was an event of small meetings: for us students it was full of surprises. 'Roger, I wonder if I could introduce you to our visitor ... this is Julian Huxley' was just one of several unexpected encounters, later to be treasured as an era in biology gradually passed away. But afternoon tea was of greater splendour altogether. The library of the BAP, normally open to questing undergraduates, would be closed. Elton would preside at the head of the long scrubbed table and the rest of us – staff, students, technicians, distinguished visitors and assistants – would range down either side. If there was some event to be marked, the 'boss' (Elton) would shyly slide a large bag of cream buns onto the table alongside the giant teapot. It was at one such event that I arrived early and discovered that, briefly at least, Elton and I were the only ones at table. 'Tell me', he said, 'what do you do for exercise?' I diffidently said that I played a little squash but his retort took me not a little by surprise. 'I used to box, you know. I knocked a man out once'. All this presented in a quiet, near whisper and emanating from this small balding man renowned, among we post-graduates, for routinely wearing at least one of his several, concurrent, sleeveless pullovers, inside out.

Perhaps this anecdote, though, captures Elton's intellectual impact as well as the man himself. Intellectually speaking he produced knockout blows from what some thought of as an unlikely source. Indeed his impact is, in my view, still not fully appreciated. Much later, while I was a Bullard Fellow at Harvard in 1998, Ernst Mayr, after grilling me about *my* intellectual antecedents actually said, 'Ah yes, Elton ... we expected so much more of him!' It was not exactly clear in this conversation exactly who 'we' were but I can only say that most of the current trends in animal ecology now owe much to Elton: so pervasive are these debts that most do not question their actual foundations.

1.3 ECOLOGY OF INVASIONS IN CONTEXT

Ecology of Invasions, as much of this book testifies, is a work of lasting impact (see also Richardson & Pyšek 2008). I have heard it said that the book was 'ahead of its time', but this is misleading. It was, in fact, very

much of its time, harking back to the very beginnings of what was then seen as the modern renaissance in biology, reviewing and critiquing the current state of play and then setting a research agenda which is, only now, receiving the attention it demands. Elton presents his thoughts in *EIAP* very much as part of the ecological sub-science of biogeography. It is significant that Elton begins his thesis in *EIAP* with a reprise of Wallace's views of biogeography. Bear in mind that, in 1954, the prevailing paradigm in biogeography was an entirely dispersalist one. Wegener's (1915) ideas of continental drift were still considered by most as part of the lunatic fringe (indeed, so I was taught during my undergraduate years at Imperial College as late as 1965, admittedly by a very conservative and elderly teacher). It was not until 1959 that Heezen, Tharp and Ewing first published their findings confirming the existence of the mid-Atlantic ridge which finally began the process which eventually led to mainstream acceptance of the ideas of a dynamic Earth with vicariant continents (see Miller 1983, for a full, popular account of this process). Of course, this is not to say that Elton was unaware of Wegener's 'crazy' idea. According to Macfadyen (1992) he was actually a keen proponent and advocate for the ideas of vicariance.

However, in 1954, Elton stated that the set of continents was to be regarded as always having been an archipelago. Accordingly his preoccupation with natural and anthropogenic animal movement was to be seen as the very core of biogeography: spatial patterns were to be understood only by examination of past and present movements of organisms (or their ancestors) across the face of the Earth. Davis et al. (2001) draw a long bow (in my view) when claiming that the 1958 book was an entirely new direction in Elton's work. Notwithstanding the fact that Elton's choice for a prize before his (unsuccessful) school graduation, was a set of the works of A.R. Wallace (Southwood & Clarke 1999), his earlier works are redolent with ideas of animal movement across landscapes, and the process of what we would now call community assembly. Indeed, as pointed out by Sir Alister Hardy (1968), Elton compared the processes of dispersal among locations (Elton 1930) with the Mendelian rearrangements of genes that take place within organisms. This was part of a set of ideas in which Elton suggested that animals selecting habitats through re-location should be regarded as a complement to the environmental selection of individuals that

is at the heart of ideas of natural selection. Certainly in *EIAP* he emphasizes the subset of species that have been particularly effective at invading new territory, especially if given a helping hand by humans. However, I suggest this is simply the spin he chose to put on this particular phase of his ongoing synthetic work rather than a new direction of thought.

Preparation for this chapter has brought me into contact with the (to me) more or less arcane activities of historians of science. Two doctoral dissertations have concerned themselves largely with the prelude to, genesis of and consequences arising from *EIAP* and Elton's associated work (Cox 1979; Chew 2006). I have had access only to Chew's work. There has been a, perhaps inevitable, hagiographic tone to most of the recent writings about Elton. Chew, though, presents his analyses as a sort of 'anti-hagiography' (to coin a word) belittling Elton's achievements, originality, even the world-view of those who have created the field of invasion biology subsequent to *EIAP*. Of course Chew is entitled to his opinion and his accounts of the surviving private and professional correspondence of Elton, particularly with the American proto-conservationist Aldo Leopold, are both insightful and useful – even to a hagiographer!

It true to say that Elton was a man of his time and, in the English sense, of his class. He emerged from an intellectual middle-class background, grew up and lived in a time of global conflicts, and was deeply moved and changed by early personal tragedies. That all of this could be true without affecting his work is not to be imagined. Yet to suggest that a preoccupation with biotic invasions and clear contradistinctions between 'native' and 'exotic' biotas reflected both an inbuilt militarism and, even, an incipient xenophobia is, to my mind, overegging the pudding. Chew describes *EIAP* as 'Elton's idiosyncratic jeremiad' and an 'alarmist book'.

One other 'yes, but ...' comment comes to my mind from Chew's writing. He suggests that Elton 'seldom played the public intellectual'. I suggest that this is not the case but that the public nature of Elton's contribution – in popular writing, broadcasting and committee work – was of a different kind from that we associate with 'public intellectuals' currently. The social structure of intellectual life in early to mid-century Britain was both well established and formal. There remained a tendency still to speak of 'the Universities' – meaning Oxford and Cambridge (only) – and those who occupied senior positions within them commanded both public respect yet, themselves, followed an unwritten

code of behaviour both within and beyond academe. Elton's position as a reader within the Oxford system was senior indeed – probably most closely to be compared to a research chair currently. Accordingly, his 'public' impact was subtle and political rather than highly visible and vocal. I return to this point when discussing his role in the establishment of the Nature Conservancy within the UK.

Ecology of Invasions was the first of Elton's major works that concerns itself entirely with an ecological process rather than classifying, describing and hypothesizing about the patterns he observed on the landscape. Perhaps the other outstanding and out-of-time innovation in the book is its conclusions about conservation. Conservation as an activity devoted to the preservation of natural landscapes (in contrast to the maintenance of populations of game animals for hunting) was not a mainstream activity in the early 1950s. Although advocated by Wallace as early as 1910, the British Nature Conservancy had been established only nine years before the publication of *EIAP*. In no small part the establishment of this body, now known as English Nature, resulted from the report of a committee of which Elton was a key member (Macfadyen 1992). So, to find the final two chapters of the book devoted to conservation in a very modern way was a major innovation for its time (Richardson & Pyšek 2007). I happened on the following on page 145 of the book: '... only this [conservation] is concerned with reducing direct power over nature, not increasing it; of letting nature do some of the jobs that engineers and chemists and applied biologists are frantically attempting now.' I think we would currently rephrase that as conserving to maximize ecosystem services!

Elton had engaged in an extended (if sometimes one-sided) correspondence with the American conservation advocate, Aldo Leopold, after their first meeting at the Matamuk Conference on Biological Cycles in 1931 (see also Hobbs & Richardson, this volume). Chew (2006) presents an extended account of their correspondence and the interplay of ideas which, in both instances, contributed substantially to the subsequent development of formal conservation efforts in both their nations. In Britain this took the form of a powerful and pervasive government bureaucracy with relatively little private investment and involvement. In the USA a much more 'mixed' model was adopted. As early as 1942 Elton had set out principles for the establishment of government-run nature reserves in a memo-

randum to A.G. Tansley who was running a committee of the British Ecological Society examining such matters. This memorandum, analysed at length by Chew (2006), ranged over many issues including that of invasive species. It also raised the ideas of what we would now call biophilia (*sensu* Wilson 1984) as well as the more mundane aspects of reserve design. Much of this manifesto was included in the final report of the British Ecological Society Committee (Chew 2006). Elton subsequently became a member of the Science Policy Committee of the nascent Nature Conservancy and remained a member until 1956 (Macfadyen 1992). During this period the highly influential Nature Conservancy Act (1949) was formulated and voted into law. According to Eric Duffey (quoted by Macfadyen 1992) it was through Elton's influence that a research branch was added to the provisions of the Act. He promoted ecological survey (with associated taxonomic services) and detailed ecological work on species (both native and exotic) of applied significance. The system of field stations established as part of the Nature Conservancy (later transmuted into the Natural Environment Research Council) was the result and an ongoing stream of influential ecological reports and actions followed.

Elton was concerned about the conservation of communities and, indeed, *EIAP* is primarily about community ecology: the breakdown of Wallace's realms, the impact of invasives upon native assemblages of animal species, and the way in which exotics insert themselves into existing food-chains within their recipient communities. This overarching concern with communities brings me to the final set of comments I make in this attempt to put Elton into the context of the history of ecology.

1.4 THE CONCERN WITH COMMUNITIES

Like Wallace, Elton was as much concerned with the community ecology of animals as he was with understanding individual populations. Of course, most of the practical work undertaken at the BAP was about populations of mammals and birds, and most of the examples that are described so clearly in *EIAP* are of single, often exotic, pest species for which adequate data had been collected primarily by those concerned with impacts or potential impacts on economic productivity. This did not, however, undermine Elton's persist-

ent preoccupation with ecological communities. Indeed yet another percipient aspect of *EIAP* was its presentation (among the first) of the ongoing conundrum of the relationships between complexity and stability. To say that Elton's comments in *EIAP* (together with those of MacArthur (1955)) set running a robust and muscular 'hare' would be an understatement (although the invasive species metaphor amuses me). Recent overviews of this ongoing debate include that of Lehman and Tilman (2000).

This concern with animals within communities was a unifying theme of Elton's entire body of work, diverted only during World War II into pest biology of rats and mice (Chitty & Southern 1947). Since the 1930s there had been, more or less, a split in ecology along taxonomic and thematic lines. Population ecology was regarded as the very stuff of animal ecology (at least until John Harper's seminal book in 1977) whereas community ecology was principally about associations of plants. I hasten to add ecology did not start out that way but that is how things developed. The demands and funding for pest control, fisheries management and game conservation (for hunting) drove the single-species approach so evident in animal studies. In this binary world of the 1940s, 1950s and 1960s, Elton's approach ran counter to the mainstream.

Animal ecology as it blossomed in the first half of the 20th century was part of the diversification of biology that stemmed from the earlier general acceptance of Darwinian ideas of evolution, especially once these were incorporated with Mendelism as part of the 'new synthesis'. It had been early appreciated that comparative anatomy could only go so far in elucidation of the mechanisms of evolution. Living organisms interacting with their environments held the key to further progress. Along with the ecology of animals (and plants) the disciplines of animal behaviour (ethology) and ecological and population genetics emerged. These were the fields that looked explicitly at whole organisms and complimented the advances in physiological, cellular and biochemical biology that took place concurrently. Not until the much more recent emergence of molecular phylogenetics would we have more effective tools for examining the mechanisms and outcomes of evolution.

Within ecology there was a tendency to regard population ecology and, later, behavioural ecology, as the 'real' fields of study within the evolutionary paradigm. After all, selection works by modifying the genetic heritages of individuals, and we measure this

by examining changes in gene frequencies at the level of the population. So how does community ecology – the ‘tangled bank’ of Darwin’s remarks in *Origin of Species* – justify itself under the bright lights of evolutionary thought? The answer, of course, is that individuals and populations do not live in isolation. They evolved and continue to exist (and evolve) in more or less complex webs of interactions in a landscape of locations which present a mosaic of physico-chemical profiles among which organisms move to greater or lesser extents. In a way, community ecology is the top-down approach to understanding evolution in action incorporating as it does both organism and environment as a dynamic whole. The ecology of individuals and populations represents a bottom-up approach in which we study the component parts of communities in a reductionist fashion. These two approaches each feed from the other – and no one was more aware of this than Elton. His capabilities and propensities as a naturalist – like my own – kept his enthusiasm at the level of syntheses. His 1930 vision of animal populations and, by inference, the communities of which they were part, responding to unfavourable conditions by moving across a landscape of diverse selective environments, was perhaps the clearest statement of his awareness of this community/evolution nexus.

The publication of *EIAP* really marked a transition in Elton’s career. The University of Oxford had acquired the Wytham Woods estate in 1942 and, from 1945 onwards, Elton had organized the work of the Bureau and its students around a wide-ranging ecological survey of the many habitat types occurring within the estate (Grayson & Jones 1955; Elton 1966). This survey was structured around a database system in which species-specific ecological information was cross-referenced with information on the different habitat components. Nested within this quintessential community-approach were many more or less independent studies of the population dynamics of selected (principally vertebrate) species.

This ground-breaking ecological survey began to come to an end (although much ecological research continued, and continues, on the Wytham Estate) with the publication of Elton’s 1966 book *The Pattern of Animal Communities*, and with the forced disbanding of the BAP upon Elton’s retirement in 1967 (Crowcroft 1991). This book was Elton’s *magnum opus*, yet it never received the prominence of some of his earlier works. From my perspective there are two reasons for this. First, the merely technical. Elton and his co-workers on

the Wytham survey were attempting to construct and interrogate a database that was complex and multidimensional. Modern electronic databases handle such structures with ease: they were not available in the 1950s and 1960s. Elton erected procedures based on record cards and kalamazoo slips, which were cumbersome to use and somewhat opaque to the casual user. Further, and of greater intellectual moment, was the fact that the survey was based upon an insightful but essentially static classification of habitats (Elton & Miller 1954). For me, it was not until Southwood (1977) published his marvellous ‘habitat temple’, as part of his presidential address to the British Ecological Society in 1976, that the synthesis between life-history strategies, ecological processes, habitat type and community structure became clear.

Southwood, too, was part of the natural historical school of ecology of which Elton was, perhaps, the pre-eminent member and which had dominated the science in Britain since its inception. Southwood, though, was of a later generation with more quantitative skills than Elton. (Much as Elton respected mathematical approaches he was never, by his own admission, a skilled numerical analyst.) It was no surprise, though, when Southwood inherited the mantle of the premier ecological synthesist on the UK scene after Elton’s retirement and, in 1991, his death.

Upon retirement, Elton continued the day-to-day maintenance of the Wytham Survey and its vast body of records, collections, literature and supporting information. Neither he nor anyone else published extensively on the survey as a whole after that time. He had, though, one more ace up his sleeve. In 1973 he published ‘The structure of invertebrate populations inside Neotropical rain forest’ in the *Journal of Animal Ecology*. At the time I remember distinct if mild controversy over whether the approach taken was appropriate or the insights justified: there was an unspoken notion that it was the author’s name that got this manuscript through the journal’s processes rather than its content. I would say, in fact, that the paper’s ‘problem’ was that it was more than a decade ahead of its time. It is only in the light of the burst of ecological activity and commentary that followed Erwin’s paper on tropical forest diversity published in 1982 (see, for example, Erwin & Scott 1980; Erwin 1982; May 1986; Stork 1988) that Elton’s true prescience becomes apparent.

Elton’s 1973 paper is written in narrative style reminiscent more of the approach adopted in his books than the dry and dull text typical of most scientific papers of

the era. Nevertheless it is full of insights that subsequently have been addressed by whole schools of research (most apparently unaware of the Elton paper). In the 1973 paper he pioneered the use of a 'morpho-species' approach to deal with a highly diverse, taxonomically challenging tropical fauna. In addition he promoted the idea of multi-method surveys of tropical diversity for circumventing the biases inherent in any one method. He noted the great dominance of tropical invertebrate faunas by singletons. Elton measured and commented on the apparent imbalance between predatory and non-predatory species in his invertebrate samples and compared available explanations for this. He contrasted top-down explanations (where the plethora of predators was responsible for the dearth of non-predators) with bottom-up explanations (where the low levels of non-herbivores reflected an evolutionary product driven by the scarcity of available resources beneath the forest understorey). He recognized the value of size/abundance analyses as a way of examining species packing. Finally he noted that the abundance of invertebrates in what he called the field layer (up to 2 m from the ground) was low and he speculated on the relative importance and richness of the canopy (which he had no means of accessing). In an Appendix he added comments on the roles of ecological engineering species such as army ants. All of these insights foresaw an agenda for tropical biodiversity studies that has been realized over the past 30 years (for a summary of this development see the papers in Basset et al. (2003)).

Of course, I am not suggesting that those engaged in tropical biodiversity research over that period pursued the topics they did because of Elton's paper: some did, others did not. I simply make the point that the 1973 paper, like virtually all of the Elton canon, was extraordinarily original, perceptive and trend-setting. *Ecology of Invasions* was and remains an extraordinary, important work. It stands out among Elton's post-war products as having been noticed and appreciated yet it is perhaps no more perceptive and insightful than most of his other works.

Perhaps the social moral from this reflection on the life and work of Charles Elton is that there is huge intellectual and, in consequence, practical gain to be had from allowing brilliant scientists to follow the maze of their own imaginings. The only necessity is that from time to time they produce lucid, accessible accounts of their thoughts. As Elton wrote to Leopold in 1945:

'Don't you think we must all resist the deluge of ad hoc work and just sit and think?'

Elton did this to perfection. Yet the tediousness of centralist bureaucracies eventually caught up with him, undervaluing, even degrading, his life's work. This bureaucratic disease has become an epidemic since the 1970s. It is unlikely we shall see Elton's like again, and that will to our great disadvantage.

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