

Functionalism without Selectionism: Charles Elton's "Functional" Niche and the Concept of Ecological Function

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Abstract

This article offers an analysis of ecologist Charles Elton's "functional" concept of the niche and of the notion of *function* implicitly associated with it. It does so in part by situating Elton's niche concept within the broader context of the "functionalist-interactionist" approach to ecology he introduced, and in relation to his views on the relationship between ecology and evolution. This involves criticizing the common claim that Elton's idea of species as fulfilling functional roles within ecological communities committed him to an idea of communities as units of selection (e.g., Kimler 1986). While such a claim implicitly attributes to Elton an understanding of function along the lines of the *selected-effects* theory of function advocated by many biologists and philosophers of biology, Elton's use of the niche concept, I maintain, involves an understanding of function more along the lines of alternative nonselectionist theories such as the *causal-role*, *goal-contribution*, and *organizational* theories. I also briefly discuss how ecologists after Elton also tend to have typically adopted a nonselectionist understanding of the function concept, similar to his.

Keywords

Community ecology; Ecological function; Ecological niche; Charles Elton; Multilevel selection; Selected-effects theory

Introduction

Animal-community ecologist Charles Elton (1900–1991) is renowned, among other things, for his popularization of concepts now central to ecological science, such as *food chain*, *food cycle* (essentially what we now call a *food web*), the *pyramid of numbers*, and the *ecological niche*. It is commonly thought that Elton's understanding of the ecological niche diverged from the ways in which his predecessor Joseph Grinnell (1877–1939) and later ecologists, from Evelyn Hutchinson (1903–1991) onwards, understood this concept. Specifically, Elton seems to have understood the niche as the *function* or *functional role* fulfilled by a species within its ecological community (see, e.g., Cox 1979, p. 99; Hagen 1992, pp. 52–53; Jax 2010, p. 79). As we shall see, his understanding of niche is reflected, in part, in the analogy he drew between species' niches and "trades or

professions of jobs in a human community.” This functional understanding of the niche contrasted with Grinnell and many later ecologists’ use of the concept to refer primarily to a species’ *ecological requirements*—that is, to the biotic and abiotic conditions that enable it to thrive in a given ecological context (see Alley 1985, pp. 414–415; Leibold 1995, pp. 1372–1373).¹

Despite the tendency to attribute to Elton a *functional* understanding of niches (i.e., an understanding of niches as ecological *functions* or *functional roles*), the notion of ecological function underlying Elton’s niche concept has never been closely analyzed by historians and philosophers of science. A clear understanding of Elton’s niche concept and of its place in the history of ecology, however, would seem to require such an analysis. Biologists are known to have used the function concept in a plurality of ways (see Wouters 2003), such that, in itself, saying that Elton understood niches as *ecological functions* or *ecological functional roles* gives us at best only a vague idea of what he might have had in mind. Moreover, an analysis of the notion of ecological function implicit in Elton’s niche concept would seem timely, given the increasing interest of philosophers of biology in the use of the function concept in ecology and in how this use can be related to theories of function developed in the philosophy of biology (see, e.g., Odenbaugh 2010, sec. 3; Nunes-Neto et al. 2014; Dussault and Bouchard 2017; Dussault 2018; Millstein forthcoming; and for a review, see Cooper et al. 2016).

In this article, I will analyze the notion of function that Elton implicitly tied to his niche concept. I will do so in part by situating Elton’s concept of the niche in the broader context of his approach to ecology and in relation to his views on the relationship between ecology and evolution. More specifically, I will situate his niche concept in relation to his theory of ecological communities and in relation to his ideas about the level(s) at which natural selection customarily operates. Against claims sometimes made that Elton’s idea of species as fulfilling functional roles within ecological communities committed him to an idea of communities as units of selection (e.g., Kimler 1986, p. 223), I will argue that Elton in fact rejected the idea that natural selection could operate on ecological communities as a whole, and that he accordingly adopted a nonselectionist understanding of the function concept. Hence, I will maintain that Elton’s understanding of function did not align with the *selected-effects* theory advocated by many philosophers of biology (e.g., Wright 1973; Millikan 1989; Neander 1991), and that it better accorded with alternative nonselectionist philosophical theories of function, such as the *causal-role*, *goal-contribution*, and *organizational* theories (e.g., Cummins 1975; Boorse 1976; Mossio et al. 2009).²

My discussion will be organized as follows. In the second section, I will introduce Elton’s niche concept as a species’ *function* or *functional role* within its community. I will highlight how Elton’s concept contrasted with Grinnell’s earlier concept, which focused on a species’ *ecological requirements*, and which, I will highlight, is essentially the concept that has been adopted by subsequent ecologists. I will also situate Elton’s

¹ For historical discussions of the niche concept, see David Cox (1979, chap. 4), Thomas Schoener (1989), James Griesemer (1992), Mathew Leibold (1995), and Arnaud Pocheville (2015).

² For reviews of philosophical theories of function, see, e.g., Peter McLaughlin (2001), Arno Wouters (2005), Denis Walsh (2008), Christian Saborido (2014), and Justin Garson (2016).

concept in the context of what I will call his “functionalist-interactionist” approach to community ecology. In the third section, I will discuss Elton’s theory of animal communities and analyze what he generally envisioned species to achieve by occupying their niche. This will make more precise the sense in which Elton construed species to fulfill functions or functional roles within ecological communities by occupying their niches. In section four, I will discuss Elton’s views on the relationship between ecology and evolution, and, in particular, his ideas on the organizational level at which natural selection customarily operates. I will argue that, given his rejection of the idea that natural selection can operate on an ecological community as a whole, Elton could not possibly understand ecological functions in a way that aligns with the selected-effects theory of function. In the fifth section, I will draw on discussions of the function concept in the philosophy of biology to offer an alternative interpretation of Elton’s implicit understanding of ecological functions. I will maintain that Elton’s analogy between niches and “trades or professions or jobs in a human community” suggests an understanding of those functions as *use* and *service* functions rather than as *design* functions (sensu Achinstein 1977), which, I will argue, is the type of function that the selected-effects theory purports to analyze. I will also argue that, in significant respects, Elton’s implicit understanding of function aligned with the *causal-role*, *goal-contribution*, and *organizational* theories of function developed in the philosophy of biology as alternatives to the selected-effects theory (e.g., Cummins 1975; Boorse 1976; Mossio et al. 2009). In the last section, I will conclude with some observations about the influence that Elton’s nonselectionist understanding might have had on subsequent ecologists’ use of the function concept.

Elton’s Functional Niche in Theoretical Context

The concept of ecological niche is usually taken to have been introduced independently by animal ecologists Joseph Grinnell (1917, 1924, 1928) and Charles Elton (1927, 1929, 1933).³ For both ecologists, the niche concept served to group species on the basis of similarities that are independent of taxonomic and phylogenetic considerations, but which are deemed important for our understanding of the ecological world. As Elton emphasized, “the idea of a niche is a purely ecological one, not taxonomic” (Elton 1933, p. 28). Grinnell and Elton thus both emphasized the possibility of phylogenetically unrelated species occupying similar niches (see, e.g., Grinnell 1924, p. 227; Elton 1927, p. 65; 1929, p. 921; 1933, pp. 28–29). Elton, for instance, observed that

in the arctic regions we find the arctic fox which, among other things, subsists upon the eggs of guillemots, while in winter it relies partly on the remains of seals killed by polar bears. Turning to tropical Africa, we find that the spotted hyæna destroys large numbers of ostrich eggs, and also lives largely upon the remains of zebras killed by lions. The arctic fox and the hyæna thus occupy the same two niches—the former seasonally, and the latter all the time. (Elton 1927, p. 65)

Beyond this important aspect of convergence, however, Grinnell’s and Elton’s niche concepts differed significantly (see Alley 1985, pp. 414–415; Leibold 1995, pp. 1372–1373). Grinnell’s concept emphasized cross-species similarities pertaining to the species’

³ As Elton himself reports, he and Grinnell “independently started using the term” (see Elton and Miller 1954, p. 477).

ecological *requirements*—that is, to the biotic and abiotic environmental factors that enable them to survive in a given location. Grinnell thus used the niche primarily to study species distribution, as well as the phenomenon of speciation (Griesemer 1992, pp. 233–234; Pocheville 2015, p. 550). The niche was for him the “ultimate distributional unit, within which each species is held by its structural and instinctive limitations” (Grinnell 1928, p. 435). In contrast, as we shall see, Elton’s concept emphasized cross-species similarities pertaining to the species’ ecological *impacts*, and the way in which those impacts led them to fulfill *functions* or *functional roles* within their communities (see Cox 1979, p. 99; McIntosh 1985, p. 92; Kimler 1986, p. 223; Griesemer 1992, p. 234; Hagen 1992, pp. 52–53; Looijen 2000, pp. 204–206; Jax 2010, p. 79; Gay 2013, p. 108; Birkhead et al. 2014, p. 357). This understanding of the niche implied an idea of ecological communities as *functionally organized systems*.

Before any further analysis of Elton’s concept, it is relevant to note that his “functional” niche is *not* the niche concept that has become paradigmatic in scientific ecology. Indeed, in popular talk about ecology, niches are still often depicted as species’ *functions*, or *functional roles*, within communities. However, in contemporary scientific ecology, niches more typically denote species’ ecological *requirements* (in line with Grinnell’s concept). Notably, Evelyn Hutchinson’s (1957, 1978) very influential “*n*-dimensional hypervolume” concept construes a species’ (fundamental) niche as all the possible environmental states that (theoretically) permit it to persist indefinitely. Hutchinson’s concept is therefore focused on the environmental conditions (biotic and abiotic) that a species *requires* for its survival, and, as such, better aligns with Grinnell’s concept than with Elton’s. The same is true of Robert MacArthur and Richard Levins’s (1967) “resource utilization” concept, which has become central in “niche theory,” an important body of work in community ecology devoted to the study of coexistence between species using similar resources. MacArthur and Levin’s concept construes a species’ niche mainly as the *resources* it commonly uses (and may compete for).⁴ Resources, to be sure, are something that a species *requires*, and hence the “resource utilization” concept also better aligns with Grinnell’s concept than with Elton’s. Elton’s “functional” concept has nevertheless been important in the historical development of the niche concept, and, as I will highlight below, it seems to have played an important role in shaping subsequent ecologists’ thinking about ecological functions.

Elton’s functional understanding of the niche is in part reflected in the parallel he made between niches and *socioeconomic roles* humans might be thought to fulfill within their societies (as they are often thought to do by functionalist-leaning social theorists). Elton defined the niche as “what [an animal] is *doing* in its community, ... its place in the biotic environment, *its relations to food and enemies*” (Elton 1927, pp. 63–64; italics in original).⁵ In line with his construal of ecological science as “the sociology and economics of animals” (Elton 1927, p. vii), Elton stated that the niche concept was “used in ecology in the sense that we speak of trades or professions or jobs in a human community” (Elton 1933, p. 28). For instance, small herbivores, which consume basic plant food and convert it into forms that can be assimilated by carnivores, could be

⁴ For reviews of niche theory, see, e.g., Schoener (1989, pp. 97–102) and Pocheville (2015, sec. 1.4).

⁵ His focus on animals reflects only the fact that he developed the concept in the context of *animal* ecology.

viewed analogically as a community's "key industries" (Elton 1927, pp. 64, 69). Hence, Elton stated: "There are in each animal community a great many different occupations, jobs, or *niches* (just as there is in a human community)" (Elton 1929, p. 921; italics in original), such that "when an ecologist says 'there goes a badger' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said 'there goes the vicar'" (Elton 1927, p. 64). Those sociological analogies suggest an idea of niches as *functional roles* fulfilled by species within their communities, those communities in turn being conceived analogously to societies or economic systems (Anker 2001, pp. 101–102; Jax 2010, p. 79; Gay 2013, p. 108).⁶

Elton's "functional" niche was tied to what can be referred to as Elton's newly introduced "functionalist-interactionist" approach to community ecology (Cox 1979, p. 32; McIntosh 1985, pp. 88–93; Cooper 2003, pp. 42–47; Gay 2013, pp. 29–30). This approach emphasized feeding (or trophic) interactions among species and the ensuing organization of animal communities in *food chains*. These food chains involved successive layers of predators in relation to their prey and of parasites in relation to their hosts, and all the food chains in a community formed what Elton called a *food cycle* (what ecologists now call a *food web*). As historians of ecology have remarked, Elton's functionalist-interactionist ecological approach departed from the more compositional and biogeographical focus of previous animal ecologists (e.g., Shelford 1913; Grinnell and Storer 1924; see, e.g., Cox 1979, p. 32). Those previous animal ecologists were primarily concerned with studying the *differences* pertaining to species composition that distinguished one community from another, and with showing how those differences (purportedly) made it possible to develop classification schemes for communities. Elton's approach, in contrast, emphasized cross-community *similarities* pertaining to their food-web architectures (see Cox 1979, pp. 24–25, 31–33, 86–87; McIntosh 1985, pp. 88–93; Sheail 1987, p. 87; Haak 2000, pp. 23–24). Food relations among species imposed constraints on their populations' relative abundance, and thus explained the tendency of animal communities to exhibit a relatively invariant architecture. Studying the (relative) architectural invariance of communities would enable ecologists to formulate general principles about the organization of animal communities (Hagen 1992, pp. 52–53; Pocheville 2015, pp. 549–550). Thus, for Elton, studying niches was important in that it helped expose "the tendency...for animals in widely separated parts of the world to drift into similar occupations" (Elton 1927, p. 65). Exposing this tendency would in turn enable ecologists "to see how very different animal communities may resemble each other in the essentials of organisation" (Elton 1927, p. 64).

As I mentioned, Elton's notion of niches as functional roles fulfilled by species within their communities is in part reflected in his analogy between niches and "trades or professions or jobs in a human community." When interpreting Elton's sociological-

⁶ Elton's analogies between animal communities and human societies were presumably influenced in part by sociologist Alexander Carr-Saunders (1886–1966), who is known to have acted as Elton's mentor at Oxford (together with zoologist Julian Huxley). Elton's construal of ecology as "the sociology and economics of animals" is explicitly linked to Carr-Saunders's (1922) study of the "sociology and economics" of humans in the preface of *Animal Ecology* (Elton 1927, p. vii). On the relationship between Elton and Carr-Saunders, see Sheail (1987, p. 90), Hagen (1992, pp. 56–57), and Anker (2001, Chap. 3). On functionalism in sociology in general, see Munch (1976), Moore (1978), and Bigelow (1998).

economic parallels, however, we should bear in mind that those parallels, as he used them, were “simply intended as analogies and nothing more” (Elton 1927, p. viii). Elton did not mean that animal communities were *literally* like human societies (or even socioeconomic systems); in his works, sociological analogies seem to have served more for *communicative* than for *theoretical* purposes. Nevertheless, as I will argue below, an idea of species as fulfilling functional roles within their communities by occupying their niches can clearly be discerned in Elton’s theory of animal communities. Moreover, I will maintain that his parallel with socioeconomic roles, rather than with traits and parts within individual organisms, was central to his functional understanding of the niche. Admittedly, the correspondence between niches and ecological functions fulfilled by species within their communities remains implicit in Elton’s works (see Munch 1976, p. 199n6). To be sure, in some works, Elton explicitly associates the terms “niche” and “function.” This is the case, for instance, in his review of the first edition of Eugene Odum’s *Fundamentals of Ecology*, where Elton complains that Odum mischaracterized the contrast between his and Grinnell’s niches (see Odum 1953, pp. 15–16). Rectifying Odum’s rendering of this contrast as one between a food-focused notion (Elton) and a habitat-focused notion (Grinnell), Elton specifies that, for him, the niche involved “the notion of *functional place* in a dynamic community—mainly but *not exclusively in regard to food-habits*” (Elton 1954, p. 383; italics in original). Moreover, in other publications, Elton sometimes uses the terms “niche” and “function” interchangeably, thus suggesting that he took the concepts to be close to equivalent (see, e.g., Elton and Miller 1954, pp. 477–478, 492; Elton 1966, pp. 108, 124). But even in those passages, the context does not make it clear what he meant exactly by “function.”

In the next section, I will situate Elton’s use of the niche concept in the context of his theory of animal community as he developed it in his early works. This will give us a clearer sense of what he might have meant when depicting species’ niches as analogous to “trades or professions or jobs in a human community,” and a species’ niche as its “*functional place* in a dynamic community.”

Communities as Functionally Organized Systems

According to Elton, species involved within communities collectively achieved two main things by occupying their niches: first, they maintained and regulated each other’s numbers, and, second, they collectively realized community-level properties (the invariants of community architecture alluded to in the previous section). Moreover, individual species contributed to those collective achievements in two main ways: first, by providing food to each other and, second, by regulating each other’s numbers.

Species’ Mutual Maintenance and Regulation

Elton’s theory of animal communities emphasized *interdependencies* among animal species. Those interdependencies were constituted, first, by the fact that all animal species depended upon other species for food (and ultimately on organic matter produced by plants). Such food interdependencies led animal species to be involved in predator-prey and parasite-host *food chains* (Elton 1927, pp. 55–59; 1933, pp. 30–32). In general, species at higher levels in food chains depended on species at lower levels for food, such

that by occupying their niches, species supported the lives of species that fed upon them (i.e., their predators and parasites) and those of species at higher levels in the *food chain*.

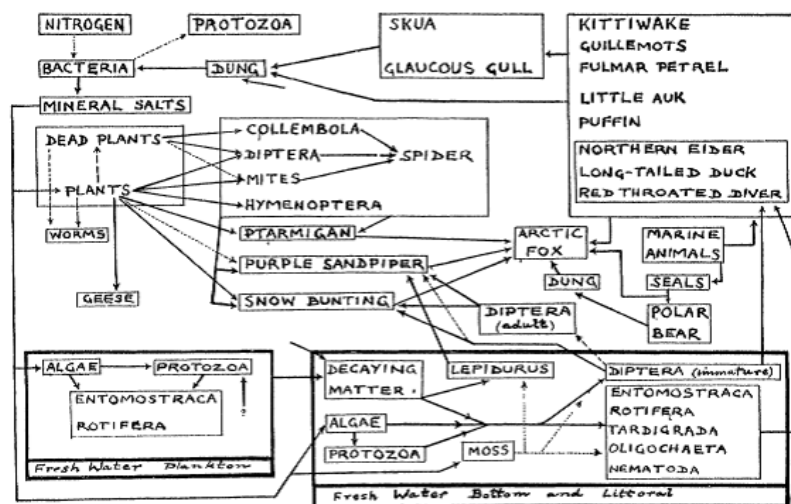


Fig. 1: Diagram of “nitrogen cycle” or “food-cycle” on Bear Island (from Elton 1927, p. 58, reproduced from Summerhayes and Elton 1923, p. 232)

But, as Elton highlighted, particular food chains were rarely isolated from each other and “usually several preys and several predators interact at each stage” (Elton 1933, p. 30). This led food chains to be organized into what he called a *food cycle*—a notion that referred to “all the food-chains in a community” (Elton 1927, p. 56) (see Fig. 1). In reality, a community’s food cycle could be exceedingly complex, and especially so given the usual interconnection of prey-predator and parasite-host food chains. As Elton observed, parasites have a tendency to get transferred from preys to their predators, and some parasites have “free-living” stages during which they can be preyed upon by other animals and thus become involved in predator-prey food chains (Elton 1927, pp. 76–77, 80–81). Hence, as Elton summarized, “when the food-relations of parasites and carnivores to other species are combined into a common food-cycle scheme, the amazingly complex nature of animal interrelations is seen” (Elton 1927, p. 80). By occupying its niche, a species therefore indirectly supported the lives of multifarious other species, and possibly (to various degrees) those of all the other species involved in its community.

Interdependencies among animal species were also constituted by the fact that, by feeding upon one another, animal species contributed to the *regulation* of each other’s numbers (Elton 1927, Chaps. 8–9). For Elton, animal populations had optimal abundances ultimately determined by the availability of the food they consumed. On a general basis, optimal abundance decreased from lower to higher levels of prey-predator food chains, a phenomenon Elton described as the *pyramid of numbers*. Because of their smaller sizes, animals at lower levels of the food chain tend to grow faster than animals at higher levels, and are therefore able to support more abundant populations of predators than those at higher levels (Elton 1927, pp. 68–70). Also, at each higher level of a food chain, less of the organic matter originally produced by plants remains available to support further levels (Elton 1933, p. 31). The pyramid of numbers is inverted in host-

parasite food chains, given that an individual host can usually support numerous individual parasites (Elton 1927, p. 78).

Elton, however, noted that animal populations have great powers of increase, and would therefore easily be able to exceed their food supply if not subject to some controlling factors. Much of his work was therefore devoted to the study of factors that regulate the abundance of animal populations. Unlike prominent population ecologists of his time (notably Nicholson 1933), and despite the relation he saw between optimal abundance and food availability, Elton did *not* consider populations to be regulated through primarily intraspecific competition. As he stated, “it is plain enough that the amount of food available sets an ultimate limit to the increase of any animal; but in practice, starvation seldom acts as a direct check upon numbers” (Elton 1927, p. 118).⁷ As he saw it, population regulation was more properly conceived as an effect of the food cycle as a whole:

How do animals regulate their numbers so as to avoid over-increase on the one hand and extinction on the other? The manner in which animals are organised into communities with food-cycles and food-chains to some extent answers the question. As a result of the existence of progressive food-chains, all species except those at the end of a chain are preyed upon by some other animals. Snails are eaten by thrushes, the thrushes by hawks; fish are eaten by seals, seals by sea leopards, and sea leopards by killer whales; and so on through the whole of nature.... Every species has also a set of parasites living in or on it, which are often capable of becoming dangerous when they are very numerous. So, in a general way, the food-cycle mechanism is in itself a fairly good arrangement for regulating the numbers of animals. (Elton 1927, pp. 117–118)

Hence, according to Elton, animal populations were largely controlled by their predators and parasites (i.e., what he called their “enemies”), and, by occupying its niche, a species *directly* contributed to the regulation of the population upon which it fed. But in fact the regulatory effects that a species had by occupying its niche usually reached far beyond the species it directly fed upon, such that, in practice, population regulation could be viewed as an overall effect of the food cycle as a whole. As Elton explained, “no species in a community, unless it happens to live a very isolated life or be very rare, is without its effect upon numbers of the rest of the community” (Elton 1927, p. 122). This entailed that, in practice, “in order to understand the way in which any animal is affected in its numbers or distribution by other animals living with it, it is necessary to study the *whole* animal community living on one habitat” (Elton 1929, p. 920; italics in original).⁸

Collective Realization of Community Architecture

Elton’s theory of animal communities also emphasized how species, by occupying their niches, collectively realized *invariants of community architecture* (i.e., a food-web architecture that was relatively similar across communities). Specifically, Elton identified three main invariants of community architecture collectively realized by species by

⁷ Elton, however, acknowledged the importance of intraspecific competition as a regulative factor in later publications (e.g., Elton 1958, p. 131; see Haak 2000, p. 30). On Elton’s ideas on population regulation, see also Cox (1979, pp. 50–64), Sheail (1987, sec. 2.5.2), and Hagen (1992, pp. 56–60).

⁸ For the sake of comprehensiveness, it should be mentioned that Elton considered animal populations to be regulated not only through the intracommunity factors just described, but also through climatic factors (Elton 1927, pp. 119, 123), and through the migration of animals from more populated to less populated areas (Elton 1930, pp. 61–62; 1933, pp. 70–72).

occupying their niches: *size relations between animals*, the *pyramid of numbers*, and the *limit on the length of food chains*. The *size-relations* aspect concerned the tendency of animals to be increasingly bigger from lower to higher levels of predator-prey food chains, and increasingly smaller from lower to higher levels of parasite-host food chains. This tendency resulted from the fact that a predator or a parasite can consume food only of an appropriate size. A predator can only consume prey that is small enough to be reasonably easy to catch and sufficiently big to supply enough food (Elton 1927, pp. 59–63); a parasite must be small enough to be able to exploit its host without harming it too severely or making it die prematurely (Elton 1927, pp. 72, 77–78). Thus, constraints on the size of the food animals could eat led animal communities to be relatively similar as regards size relations between animals at each level of the food chain.

The *pyramid of numbers* concerned the fact (already alluded to above) that the numbers of animals tend to decrease from lower to higher levels of prey-predator food chains, and to increase from lower to higher levels of host-parasite food chains. Constraints on the number of individual prey required to support each individual predator and on the number of individual parasites that can be supported by an individual host led animal communities to be relatively similar as regards the relative numbers of animals at each level of the food-chain.

The *limit on the length of food chains* concerned the observation that a food chain can normally contain only a limited number of levels, usually less than five (Elton 1927, p. 61). According to Elton, this resulted from the fact that predators at higher levels in food chains become too large for some even larger predators to exist and to be able to prey upon them, as well as from the fact that the population numbers at top levels of food chains are usually too small to be able to support any further levels (Elton 1927, pp. 61, 69).

Hence, the feeding habits of animals led them to collectively realize a food-web architecture that Elton hypothesized to be relatively invariant across communities. Besides maintaining and regulating each other, species, by occupying their niches, also contributed to the realization of this relatively invariant community architecture.

I submit that the above observations about species interdependencies and their collective realization of invariant community architecture conveys a picture of animal communities as functionally organized systems and, by association, of species as fulfilling *functions* or *functional roles* within those systems by occupying their niches. The above discussion suggests two broad types of functions fulfilled by species within animal communities:

Trophic functions: Contributions to the transfer of organic matter through the food cycle, necessary for supporting the lives of animal species that form the community.

Regulative functions: Contributions to the regulation of animal populations involved within the community.⁹

Elton on Community Selection

The two ideas discussed in the previous section—namely, Elton’s understanding of niches as *functions or functional roles* fulfilled by species in their communities, and his resultant view of ecological communities as *functionally organized systems*—may seem to commit one to an idea of communities as *units of natural selection* (i.e., units that are subject to natural selection as a whole). For many evolutionary biologists and philosophers of biology, the notions of *function* and *functional organization* are properly conceptualized in relation to evolution by natural selection, and the concept of function is essentially equivalent to the Darwinian concept of *adaptation* (e.g., Williams 1966). For these thinkers, functions, in other words, are *selected effects*—that is, effects for which some biological items (traits, parts, behaviors, etc.) have been preserved under past natural selection (Wright 1973; Millikan 1989; Neander 1991). They contrast with mere evolutionary *by-products*, traits that become fixed in a population because they are correlated with traits that are selected for.

Through the prism of a selection-based understanding of function such as this, the very idea that species fulfill functional roles within communities may seem to imply community selectionism. Elton’s construal of ecological niches as ecological functional roles may thus seem to entail an idea of whole ecological communities as subject to natural selection, as well as the corollary idea that species are adapted by natural selection in view of the functions that they fulfill within those communities. Such ideas are sometimes attributed to Elton by historians of ecology. According to William Kimler (1986, p. 223), for instance, Elton was a community selectionist for whom “adaptedness became a broad concept, including the community’s fitting of roles, or niches, into stable assemblages.”¹⁰ Along similar lines, Joel Hagen (1992, p. 60) states that, “Elton considered natural selection to be a general process operating at all levels of organization from cells to communities.”¹¹

The attribution of community selectionist ideas to Elton may seem to be reinforced by the fact that multilevel selectionist ideas were held by some of his well-known close collaborators. Notably, such ideas were held by Elton’s two mentors at Oxford, sociologist Alexander M. Carr-Saunders and evolutionary biologist Julian Huxley (Carr-Saunders 1922, pp. 223, 416–417; Julian Huxley 1942, pp. 479–480; see Angner 2009, pp. 80–85). Huxley even explicitly spoke of *communities* as subject to natural selection in

⁹ Elton’s occasional description of some animals’ niches in relation to *abiotic* factors evokes the possibility of complementary ecological functions based on species’ impacts on *abiotic* factors (see Schoener 1989, p. 86; Griesemer 1992, p. 234; Leibold 1995, p. 1373). For instance, he described land crabs living in burrows on coral islands and earthworms elsewhere as occupying the same (soil-burrowing) niche (Elton 1927, p. 67). This suggests the possibility of ecological functions associated with what we would now call *ecosystem engineering* (Jones et al. 1994; Berke 2010). This idea, however, is not fully developed in Elton’s works.

¹⁰ Kimler bases this reading partly on personal communication with Elton (see Kimler 1986, p. 224).

¹¹ At variance with Kimler and Hagen, and more in line with what I will maintain below, David Cox (1979, pp. 5–6) interprets Elton as an individual-level selectionist (see also Haak 2000, p. 32).

the ecology chapter of his book *The Science of Life* (a survey of the life sciences for a popular audience, coauthored with novelist H. G. Wells and his son) (Wells et al. 1931, p. 581).¹² Moreover, at Oxford, from 1925 to 1929, Elton was the tutor of none other than Vero C. Wynne-Edwards, probably the most illustrious advocate of group selection (Wynne-Edwards 1962). Wynne-Edwards credits Elton with recommending to him Carr-Saunders's book *The Population Problem* (1922), where group-selectionist ideas are exposed, and, more generally, with sparking his life-long interest in population ecology (Wynne-Edwards 1985, pp. 490–491; see Angner 2009, pp. 87–88; Borrello 2010, pp. 43–44; Gay 2013, p. 114). Partly based on such observations, historians of biology Birkhead et al. (2014, pp. 358–359) portray Elton's discussions of animal populations and, in particular, his notions that populations have optimal numbers and are subject to regulative factors, as the “seeds of the group selectionists ideas Wynne-Edwards later developed.”

The attribution of community selectionist views to Elton may also find support in the fact that later ecologists who incorporated Elton's ideas on food cycles and population regulation into their views often linked those ideas to ones of communities as units of natural selection. Notably, this is the case with community ecologists Warder C. Allee, Alfred E. Emerson, and colleagues (Allee et al. 1949). Allee et al. (1949, p. 728) maintained that, “natural selection operates upon the whole interspecies system, resulting in a slow evolution of adaptive integration and balance.” Hence, they claimed: “The interspecies system has also evolved...characteristics of the organism,” such as division of labor, integration, and homeostasis, “and may thus be called an ecological supraorganism.”

In fact, however, as we soon shall see, Elton explicitly rejected the idea of whole communities as subject to natural selection. He did so most forcefully in a small book called *Animal Ecology and Evolution*, published three years after his *Animal Ecology* (Elton 1930). Elton's rejection of community-selectionist ideas must, I think, be read in the broader context of the general views on the relationship between ecology and evolution expressed in this book, as well as in the context of his criticism of the *balance of nature* idea (also expressed in that book).¹³

The aim of *Animal Ecology and Evolution*, as Elton stated in its first pages, was to propose a middle way between the stances of some ecologists of his day who regarded the topic of evolution as vain theorizing, of little use for the concrete study of the lives of animals, and that of older naturalists whom, he believed, entertained “too rigid” and even “fanatical” beliefs about how evolution takes place (see Elton 1930, pp. 7–8). This aim led him to develop views on evolution that are strikingly anticipatory of ideas further explored decades later by biologists, some of which are now prominent themes in the works of advocates of an “extended evolutionary synthesis” (West-Eberhard 2003;

¹² Historian of ecology Peder Anker (2001, p. 112) notes that Wells et al.'s ecology chapter was entirely reviewed by Elton before publication.

¹³ For discussions of Elton's ideas on the relationship between ecology and evolution, see Scudo (1984, pp. 41–44), Kingsland (1985, pp. 53–55), Hagen (1992, pp. 59–61), Haak (2000, pp. 31–32), Cooper (2003, pp. 47–48), and Holt (2005, pp. 242–245).

Pigliucci and Müller 2010).¹⁴ Elton, for instance, criticized what some later biologists famously dismissed as a “Panglossian” or “pan-adaptationist” evolutionary paradigm (Gould and Lewontin 1979), according to which, in Elton’s terms, “every structure, reaction, and habit that an animal possesses is of use to its owner in the struggle for life,” and which regards natural selection as “producing the best possible world for each species” (Elton 1930, pp. 8, 17; see also 1927, pp. 181–184). He also emphasized the importance of drift for the initial spread of novel (potentially adaptive) traits (Elton 1930, pp. 70–75; see also 1927, p. 187). He moreover criticized the common view of animals as “stationary units,” or “helpless bundles of flesh,” passively “acted upon by a number of selective eliminating agents” (Elton 1930, p. 50). In contrast, he insisted on the ability of animals to change their habits and/or migrate when faced with unfavorable environmental conditions; hence, he drew attention to “a process which may be called the SELECTION OF THE ENVIRONMENT BY THE ANIMAL, as opposed to the NATURAL SELECTION OF THE ANIMAL BY ITS ENVIRONMENT” (Elton 1930, p. 51; capital letters in original).¹⁵ In general, what Elton sought to make plain in this book was that “the real life of animals...is the end result of a number of fundamentally different processes,” natural selection being just one of those processes (although indeed an important one) (Elton 1930, p. 88).¹⁶

In this book, Elton also relativized the importance of natural selection as a factor shaping ecological interactions among populations of animals. This led him to criticize (a version of) the classical *balance of nature* idea. He stated: “‘The balance of nature’ does not exist, and perhaps never has existed” (Elton 1930, p. 17). For Elton, “balance of nature” referred to the idea that natural selection acted so as to generate harmony among populations forming animal communities. On this view, natural selection would have equipped animals with a set of “definite and fixed reactions” that governed their responses to changes in their environment, including fluctuations in the numbers of the populations with which they interacted. This view is primarily what Elton rejected when criticizing the balance-of-nature idea. He thought it implausible that the responses of interacting animal populations to fluctuations in each other’s numbers might have been nicely coordinated by past natural selection so as to promote the overall persistence of the community (see Elton 1930, pp. 26–28).¹⁷

¹⁴ Elton also develops some of those ideas in the final chapter of *Animal Ecology* (Elton 1927, chap. 9), as well as in papers published before and after *Animal Ecology and Evolution* (Elton 1924, 1931).

¹⁵ Contemporary ecologists study this latter phenomenon under the term “habitat selection” (see, e.g., Morris 2003), and niche construction theorists refer to it as “relocational niche construction” (see Odling-Smee et al. 2003, pp. 44–47, 123–124).

¹⁶ In a later paper, Elton even drew attention to the phenomenon of *cultural evolution*, arguing that “among the higher animals we can perceive a method of evolution along a mental plane, unconnected with the spread of new mutations, a method which leads on a small scale to the production of customs, cultures, and gregarious habits, similar to those found in man” (Elton 1931, p. 134; quoted in Hagen 1992, pp. 60–61).

¹⁷ It is important to note that Elton’s rejection of this particular explanation for community stability did not amount to a wholesale rejection of the idea that communities achieved some kind of stability. Elton fully admitted that communities have “some power of regulation, of compensating here for a disturbance there,” and he remarked that “the species composition of most communities remains very much the same over long periods” (Elton 1930, pp. 38, 25). His main point was that community stability is achieved through other factors, such as the migration of animals from more to less populated areas. This is partly why, above, I say that Elton rejected “a version of” the balance of nature idea. This is meant to leave open the possibility that

The discussion of community selection in *Animal Ecology and Evolution* unfolds over a few pages and is at times a little fiddly, so it is worth quoting Elton at length. His discussion begins with a summary of how he understands natural selection to act on individual organisms (e.g., a deer) so as to promote cooperation among their cells and larger parts:

Let us...take the example of the deer. The cells of the deer's body are to a certain extent in competition for food, and the weaker cell will 'go to the wall'; yet groups of cells co-operate to produce tissues. They co-operate because a higher grade of competition is taking place between different organs in the body.... These organs which are in a state of balanced competition yet co-operate to make the body efficient. (Elton 1930, p. 28)

Elton then considers how natural selection may be thought to similarly operate on *groups* of deer and lead them to form larger evolutionary units (i.e., herds): "Each individual deer competes with its neighbours, yet co-operates to form a larger and also efficient unit—the herd" (Elton 1930, pp. 28–29). He proceeds by considering how natural selection could perhaps be envisioned as operating on interactions among populations of deer and their common enemy, the mountain lion:

Without mountain lions to control its numbers the deer is in danger of shooting *above* its optimum density and suffering a sudden reduction in numbers from disease and starvation.... Without the deer the mountain lions might be in danger of extermination, or at any rate serious reduction in numbers through starvation, or through disease induced by under-feeding. The competition between enemy and prey still remains, but co-operation also plays its part in forming a higher biological unit, analogous to the herd, the individual, the organ, and the cell. (Elton 1930, p. 29; italics in original)

Elton finally ponders how a similar reasoning could be applied to animal communities as a whole:

But why should we draw the line at these two species? The deer is also preyed on by wolves. When deer are scarce the wolves must starve or turn to other food.... In some parts of Canada, owing to the destruction of deer by man, the wolf has found in the snowshoe rabbit a staple source of food. But when the rabbits are scarce the wolves will turn suddenly to cattle and even horses. And when the wolves are dying from mange, induced by food shortage, the horses are said to catch the mange and die also. An animal community consists of such an inseparably interwoven set of parts that we cannot draw a line at any point. We must therefore follow our train of argument to its logical conclusion. We must admit that the whole of an animal community can act as a biological unit, operated upon by natural selection so as to bring about the best compromise in the way of optimum populations for all. Thus the whole of the northern coniferous forest of Canada forms a biological unit, covering some two million square miles of country. (Elton 1930, pp. 29–30)

From the passages just quoted, Elton may seem to have been rather sympathetic to multilevel selectionist ideas, including the idea that natural selection operates on communities as a whole. Attention to those passages may partly explain the frequent attribution of community-selectionist ideas to him. It must be remembered, however, that, in those passages, Elton is only exploring multilevel selection as a theoretical possibility.

his views may be ones that other ecologists would interpret as aligning with the balance-of-nature idea. For discussions of Elton's ideas on community stability and the balance of nature, see Hagen (1992, pp. 56–60), Haak (2000, pp. 26–29), and Dussault (forthcoming, sec. 4.3). For an analysis of the various views that ecologists have associated with the balance-of-nature idea, see Jansen (1972).

Moreover, on the page immediately following the latter passage, he explicitly and downrightly rejects the idea of community selection:

We started with the cell and we have ended up with the animals of two million square miles of spruce forest. But we have also seen that an efficient system of co-operating parts can only be produced by natural selection if this system is competing with some other unit of the same size and nature. The fauna of the whole northern coniferous belt of Canada has no competitor in this sense, unless it be the fauna of the coniferous belt of Siberia. We appear to have started with a perfectly sound argument, which has, however, landed us in an absurdity. (Elton 1930, p. 31)

Elton repeats this criticism at the beginning of the next chapter: “The animal community...cannot have been evolved solely by natural selection in the ordinary sense, as it has no competitors” (Elton 1930, p. 39). He expresses similar skepticism about community selection elsewhere, including in his entry on animal ecology written for the *Encyclopædia Britannica* (Elton 1929, p. 923), and, notably, in his review of Allee et al.’s book (where, as mentioned above, Elton’s ideas on food cycles and population regulation are linked to community-selectionist ideas). In this review, Elton complained that Allee et al.’s treatment of community (and ecosystem) selection was “rather discursive,” and “that it rather missed its opportunity of coming to grips with the very subtle question of whether any large ecosystem can be selected as a whole” (Elton 1950, p. 78). Similar skepticism about multilevel selectionist ideas is also expressed in Elton’s review of Wynne-Edwards’s book defending group selection (Elton 1963; see Chitty 1996, p. 148; Borrello 2010, pp. 86–87; Birkhead et al. 2014, p. 366).

It now becomes clear that, although, as seen above, Elton construed the niches of species as *functions* or *functional roles* that they fulfill within ecological communities, this construal could *not* have involved commitments to community-selectionist ideas. The understanding of *function* underlying his conception of the niche could therefore not possibly align with the *selected-effects* theory alluded to above.¹⁸

On the face of it, the *trophic* and *regulative* functional roles that, according to Elton, were fulfilled by species by occupying their niches (see the previous section) would not seem very plausibly interpreted as selected effects. It would seem quite implausible to assert that, on a general basis, prey and hosts (or their traits) have been selected for serving as food for their predators and parasites, or even that, conversely, predators and parasites (or their traits) have been selected for exerting regulative control on their prey and hosts. Prey and hosts more likely evolve traits that help them cope with the challenges they face in their environments, challenges that include *escaping* predators and parasites; the fact that they also evolve tissues that happen to be an appropriate and

¹⁸ This implication may seem to be challenged by Roberta Millstein’s (forthcoming) recent defense of the possibility of selected-effects ecological functions based in coevolution rather than community or ecosystem-level selection. Millstein’s discussion is of particular relevance here, given its focus on Aldo Leopold and given Elton’s known influence on Leopold. Millstein’s discussion, however, seems implicitly focused on a different notion of function than the one I am focusing on here. As she recognizes (footnote 1), her discussion is focused on function as a type of *activity* achieved by organisms across communities (e.g., predation, parasitism). In contrast, I am here concerned with function as a type of contribution to the capacities or activities of a larger system (e.g., as highlighted above, the transfer of organic matter through the food cycle, the regulation of animal populations involved within the community). Notwithstanding Millstein’s arguments, a selected-effects interpretation of the latter functions would still seem to require community-level selection.

attractive source of food for other animals seems more reasonably interpreted as a mere *by-product* from an evolutionary perspective. Similarly, predators and parasites more likely evolve traits that enable them to exploit their prey and hosts in view of their own survival and reproduction; the fact that this leads them to exert some regulative control on their prey and hosts seems better construed as a mere *by-product* from an evolutionary perspective.

In the next section, I will turn to the question of how exactly Elton could have understood the notions of ecological function and of community-functional organization if not in selectionist terms.

Functionalism without Selectionism

The understanding of function underlying Elton's niche concept and its contrast with the understanding of function operative in the *selected-effects* theory can, I think, be illuminated by situating Elton's concept in relation to philosopher Peter Achinstein's (1977, pp. 350–356) three ordinary-language notions of function: *design*, *use*, and *service* functions. An item's *design* function is what this item was *designed* or *created* to do (e.g., the function of a mouse trap is to catch mice). In contrast, an item's *use* function consists in what it is *used for* (e.g., this table is being used as a seat), and an item's *service* function consists in what it *serves as* (e.g., a watch's second hand serves as a dust sweeper). Thus, unlike *design* functions, *use* and *service* functions are functions that items fulfill in some interactive contexts, but which they need not have been designed or created to fulfill. Items bearing such functions do so by virtue of their *relations* or *interactions* with other items to which they are useful or serviceable, rather than by virtue of a design or design-like process from which they result.¹⁹

The association commonly made between selected-effects functions and the notion of natural or biological *design* (i.e., design by natural selection) suggests that the selected-effects theory of function aims to provide an analysis of Achinstein's *design* functions (on this association, see, e.g., Williams 1966, p. 9; Wright 1973, pp. 164–165; Millikan 1984, p. 17). The selected-effects theory, in other words, is concerned with cases where asserting that an item has a function amounts to asserting that, in a biologically relevant sense, it has been created and/or shaped in view of this function. In this respect, the selected-effects theory applies well to many paradigmatic cases of functions borne by traits and parts within individual organisms, given that many of organisms' function-bearing traits and parts are known (or can be presumed) to have been shaped by natural selection in view of their functions. For instance, hearts do not merely happen to serve as blood pumps within animals with circulatory systems; they were designed by natural selection in view of this function.

In contrast, I submit that the implicit notion of function underlying Elton's niche concept aligns with Achinstein's *use* and *service* functions. Ecological functions as

¹⁹ Other philosophers (e.g., Wright 1973, pp. 147–148; Boorse 1976, p. 76) make essentially the same contrast by distinguishing the notion of what *the function of x is* (Achinstein's *design* functions) from the notion of what *x functions as* (Achinstein's *use* and *service* functions). Wright, however, restricts the legitimate sense of function to the first notion, which, as regards *biological* functions (as opposed to *technical* functions), he analyzes in selected-effects terms.

understood by Elton, I suggest, are functions that species fulfill in particular ecological contexts by virtue of their (direct or indirect) interactions with other species to which they are useful or serviceable. Thus, prey and hosts, which, according to Elton's theory of animal communities (see the third section, above), fulfill *trophic* functions within ecological communities, fulfill those functions by virtue of the ecological contexts in which they find themselves, where they are *used* as food by some predators, or as food and shelter by some parasites. Such *use* interactions are what gives them their trophic functions; no design by natural selection in view of those functions needs to be involved. Likewise, predators and parasites, which, according to Elton's theory of animal communities, fulfill *regulative* functions within ecological communities, fulfill those functions by virtue of the ecological contexts in which they find themselves, where their limiting effects on prey and host populations is *serviceable* to those populations themselves and/or to the community as a whole. In line with what has been seen above, predators and parasites can acquire such service functions, for instance, by preventing the populations they exploit from overconsuming their food supply. Such service interactions are what gives them their regulative functions; again, no design by natural selection in view of those functions needs to be involved.

Hence, in short, I suggest that Elton could conceive of species as fulfilling functions within ecological communities while rejecting community-selectionist ideas because he implicitly appealed to a notion of function that is distinct from the one that the selected-effects theory purports to analyze. By using a notion of function that is context-based or relationally-based, rather than design-based, Elton could ascribe ecological functions to species without implying that they were shaped by natural selection in view of those functions. This enabled him to use the function concept in a way that is much more flexible than what the selected-effects theory would allow, and, in particular, to ascribe, as seen above, functions to species partly on the basis of traits that are (in all likelihood) evolutionary by-products.

Some support for this interpretation can, I think, be found in the parallel Elton makes between ecological niches and "trades or professions or jobs in a human community" (see the second section, above). This parallel, as I remarked, suggests an understanding of species' ecological functions as analogous to *socioeconomic roles* fulfilled by individuals within human societies (in line with Elton's construal of ecological science as "the sociology and economics of animals"; see also above). In a sense, Elton's use of such a sociological analogy is surprising, in that traits and parts within individual organisms, or artifacts and their parts, are more obvious and more commonly discussed cases of function-bearing entities. One might thus have expected Elton to introduce his functional understanding of the niche by way of analogies with traits and parts within individual organisms, or with artifacts and their parts, rather than by way of an analogy with humans envisioned as socioeconomic agents. Elton's choice of analogy is even more surprising considering the fact that it was quite common for ecologists at his time to draw analogies between ecological communities and individual organisms or machines (i.e., artifacts).²⁰

²⁰ As some historians of ecology have noted, 20th-century ecologists tended to use organicist and mechanistic analogies interchangeably (see Hagen 1992, pp. 11–14; Marshall 2002, Chap. 7). Elton, for his part, at times criticized the mechanistic analogy (see Elton 1930, p. 30) and, as far as I am aware of, never committed to the organicist analogy.

Why then did Elton describe species' niches, and hence their functions within communities, by analogy with "trades or professions or jobs," rather than by analogy with functions borne by traits and parts within individual organisms or functions borne by artifacts and their parts?

An important difference between the way in which human individuals can be construed as fulfilling socioeconomic functions within societies, on the one hand, and the way in which traits and parts within individual organisms or artifacts and their parts can be construed as bearing functions, on the other hand, lies in the context-based and relational character of socioeconomic functions. As remarked above, many paradigmatic functions of traits and parts within individual organisms are *design* functions (e.g., a heart is evolutionarily designed to pump blood). And, similarly, conscious design seems to be the source of the functions of most artifacts and their parts (e.g., Achinstein's mouse trap designed to catch mice). In contrast, individuals in human societies (at least in societies as we know them) seem to bear their socioeconomic functions in a much more context-based and relational manner.²¹ Unlike fictitious characters in dystopian societies like the one depicted by Aldous Huxley in *Brave New World*, human individuals are not (at least not in societies as we know them) *designed* to fulfill particular socioeconomic functions in a way comparable to the way in which traits and parts are designed to fulfill their functions within individual organisms. In this regard, I submit that the socioeconomic functions conceivably borne by individuals within human societies (e.g., their "trades or professions or jobs") and the ecological functions attributed by Elton to species within communities are closely similar to each other. Both are borne largely by virtue of the interactive context in which their bearers find themselves. Commenting on Elton's analogy between niches and human socioeconomic roles, philosopher and historian of ecology Kurt Jax (2010, p. 79) captures this commonality between socioeconomic and ecological functions very aptly:

In contrast to parts of an organism, a particular species has no clearly defined role within an ecosystem: a bird may have the function of being prey to other animals—but only if these carnivorous animals are parts of the specific system. If there are no predators in the system, the same species or even individual will not have the role "prey." Even if we can say that the bird actually has the role of being prey, we can also find other roles, e.g. its role to distribute seeds and nutrients, to be predator for insects, etc. That is, like a person within a human society, who may be teacher, spouse, child, politician, etc., either at the same time or at different times, it can have several roles. Roles can change and the same person as well as the same species can even take opposing roles in time.... "The" one and only role of a species does not exist. Roles are strongly context-dependent.

Hence, I submit that the context-based and relational character of ecological functions is essentially what Elton's parallel between ecological niches and "trades or professions or jobs in a human community" was meant to convey.

An important implication of this context-based character of the function concept as used by Elton concerns the kind of *functional organization* his ecological approach implicitly attributed to ecological communities. The implication is that Elton's implicit

²¹ I leave it open whether, from a functionalist sociological perspective, humans can soundly be depicted as fulfilling social functions within their societies. See note 6 above for references on functionalism in sociology.

understanding of community functional organization did not entail a view of communities as tightly integrated *superorganisms*, similar to the view espoused by subsequent ecologists such as Warder C. Allee et al. (1949) (see the previous section).²² On an understanding of community functional organization based on an idea of communities as units of natural selection, communities would be conceived as functionally organized in the sense that they are composed of parts (their components species) that have been shaped by natural selection in view of their function within the whole. Just like parts and traits within individual organisms, species within ecological communities would bear their ecological functions as *design* functions. In this respect, ecological communities would thus exhibit a degree of part-whole integration comparable to that exhibited by paradigmatic individual organisms, which would make it reasonable to regard them as *superorganisms* (for a discussion, see Wilson and Sober 1989). In contrast, on Elton's understanding, ecological communities exhibit a much weaker degree of part-whole integration than that exhibited by paradigmatic individual organisms. Since, as I just observed, his functional approach depicted species as fulfilling *use* and *service* functions within communities (as opposed to *design* function), this approach did not entail a view of communities as formed of species shaped by natural selection in view of their function within the community. Hence, as construed by Elton, ecological communities were functionally organized not in the sense that they were tightly integrated superorganisms, but in a much weaker sense. They were functionally organized in the sense that they consisted in complex webs of use and service interactions among species.²³

The notion of function underlying Elton's niche concept can be further illuminated in light of theories of function that philosophers of biology have offered as alternatives to the selected-effects theory. Prominent among these alternatives are the *causal-role* theory, the *goal-contribution* theory, and the *organizational* theory (e.g., Cummins 1975; Boorse 1976; Mossio et al. 2009). It is relevant to note that these theories draw no conceptual relation between an item's function and what it is or was selected for. They focus more on the part-whole organization of biological systems, as well as on ways in which the parts of biological systems contribute to the overall functioning of those systems.

In key respects, the understanding of function associated with Elton's niche concept aligns with understandings conveyed by those nonselectionist theories of function. It aligns in some respects with the *causal-role* theory (e.g., Cummins 1975; Craver 2001). The causal-role theory focuses on how the parts of a system contribute to that system's realization of some system-level capacities. Such an understanding of function seems at play in Elton's discussions of how species that form communities, by occupying their niches, (purportedly) collectively realize and maintain *invariants of community architecture* (i.e., a food-web architecture that is relatively invariant across communities;

²² For a more detailed comparison of Elton's ideas on ecological communities and those of ecologists who construed communities by close analogy with organisms, see Dussault (forthcoming).

²³ In more contemporary parlance we could say that ecological communities were, for Elton, functionally organized entities by virtue of being *niche-construction networks*—that is, networks of species that, by their simple presence or their effect on the environment, provide key conditions of existence to each other (see Odling-Smee et al. 2003; Barker and Odling-Smee 2014).

see above). In other respects, Elton's implicit understanding of function aligns with the understanding of function conveyed by the *goal-contribution* and the *organizational* theories of function. The goal-contribution theory focuses on how the parts of a system contribute to its ability to achieve some kind of *self-regulation* (e.g., Boorse 1976; Nagel 1977); the organizational theory focuses on how the parts of a system collectively maintain each other and, in so doing, contribute to the whole system's ability to *maintain itself* (e.g., Schlosser 1998; Mossio et al. 2009).²⁴ Such understandings of the function concept seem at play in Elton's discussions of how species that form communities, by occupying their niches, maintain each other and regulate each other's numbers (see above).

Although the selected-effects theory is arguably still the most influential theory of function among philosophers of biology, many of them have, in recent years, embraced a pluralistic stance on the function concept (e.g., Millikan 1989; Neander 1991; Godfrey-Smith 1993; Amundson and Lauder 1994). This pluralistic stance recognizes the complementary relevance of selection-based and non-selection-based theories of function for our understanding of the biological world. The selected-effects theory focuses on the *teleological* dimension of the function concept—that is, on the intuitive idea that functions help explain *why* some biological item is present in some biological context and *why* it has the features it has. In contrast, the nonselectionist theories focus more on the *systemic* dimension of the function concept—that is, on the intuitive idea that functions delineate *how* some biological item contributes to the functioning of a more encompassing systemic entity of which it is part (on the contrast between biological explanatory projects centered on *why* and *how* questions, see Mayr 1961).²⁵

When situated in the broader context of the pluralism in regard to function, Elton's use of the function concept in a way that diverges from the selected-effects theory turns out to be in no way peculiar or idiosyncratic. The understanding of function associated with his niche concept aligns with explanatory projects focused on *how* rather than *why* questions. As seen above, Elton's primary aim was to explain *how* species, by occupying their niches, contributed to their communities' ability to maintain themselves, to regulate the numbers of populations within them, and to realize what he thought to be invariants of community architecture.²⁶

²⁴ For an application of the organizational theory of function to the context of ecology, see Nunes-Neto et al. (2014).

²⁵ For the sake of exactness, it should be mentioned that one of the nonselectionist theories mentioned above—namely the organizational theory—is intended to account as much for the teleological (the *why*) as for the systemic (the *how*) dimensions of the function concept (see, e.g., Mossio et al. 2009, sec. 4.1). Nevertheless, what has primary relevance for my purposes is how, by accounting for the systemic dimension, the organizational theory, like other nonselectionist theories, can shed light on Elton's nonselectionist use of the function concept.

²⁶ On Mayr's contrast between *why* and *how* questions and its relationship to the use of the function concept in ecology in general, see Hagen (1992, pp. 150–151).

Conclusion: Ecological Functions after Elton

Above, I offered an analysis of the notion of function that underlies Elton's niche concept. I argued that Elton's ideas of species as fulfilling *functions* or *functional roles* within ecological communities does not entail a view of ecological communities as units of natural selection, and, hence, that his implicit understanding of ecological functions does not align with the *selected-effects* theory of function advocated by many philosophers of biology. I observed how a selected-effects interpretation of Elton's implicit understanding of function would lie in tension with his rejection of community selection. Moreover, I maintained that Elton's analogy between niches and "trades or professions or jobs in a human community" suggests an understanding of ecological functions as *use* and *service* functions rather than as *design* functions (sensu Achinstein 1977), and that the notion of function that the selected-effects theory purports to analyze is a *design* notion of function. I explained that, according to Elton's theory of animal communities, what species mainly achieve by occupying their niches consists in maintaining and regulating each other and collectively realizing purported invariants of community architecture. I argued that Elton's theory of animal communities thus suggests an understanding of function that aligns with alternative theories of function focused on the part-whole organization of biological systems. In particular, I observed how Elton's understanding aligns with the *causal role*, the *goal-contribution* and the *organizational* theories of function in significant respects (e.g., Cummins 1975; Boorse 1976; Mossio et al. 2009).

In closing, I would like to broaden the focus from the particular case of Elton and consider the influence that his nonselectionist understanding might have had on subsequent ecologists' notions of ecological function. Remarkably, some prominent subsequent ecologists, such as community ecologist Lee R. Dice (1952) and ecosystem ecologist Eugene Odum (1959), seem to have shared Elton's nonselectionist understanding. According to Dice (1952, p. 353),

any service that 1 species of plant or animal renders to an associate may from the standpoint of community organization be considered an ecologic function. Thus, the green plants, which are the ultimate source of food for almost all the other organisms, perform an important food function in the community. The herbivorous animals in their turn perform the ecologic functions of controlling the abundance of their food plants and of providing food for carnivores. The light-tolerant plants perform the ecologic function of providing shade and shelter and often breeding places for many kinds of animals and for shade-loving plants. An important function in community regulation is performed by parasites and predators through their destruction of surplus individuals of their host and prey species. Many particular kinds of insects perform the ecological function of pollinating the flowers of particular kinds of plants. The ecologic function of soil enrichment is performed by practically all terrestrial organisms.

Noticeable in this passage is Dice's mention of ecological functions performed by *plants*, which expands on Elton's focus on animals. Also noticeable is his recognition of ecological functions associated with *nontrophic* interactions (i.e., pollination and shade and shelter provision), which expands on Elton's focus on trophic and regulative functions (see above). Dice's use of the function concept nevertheless seems to accord with Elton's nonselectionist understanding. Like the cases discussed by Elton, some cases of ecological functions mentioned by Dice are more plausibly interpreted as evolutionary by-products than as selected effects (e.g., it would seem implausible to assert that, on a

general basis, light-tolerant plants are selected for providing shade and shelter to other species). Moreover, Dice's discussion of ecological functions makes no mention of natural selection and explicitly links ecological functions to *services* that species provide to one another (in line with my above interpretation of Elton's implicit understanding of them as *use* and *service* functions; see the previous section). As he asserts, "each species performs various *services* for its associates and, therefore, simultaneously performs a number of diverse kinds of ecologic functions in the community" (Dice 1952, p. 353; italics added; see also previously quoted passage).²⁷

Along similar lines, Odum states, while discussing the ecological function of decomposers:

Decomposition, of course, is the result of the process by which bacteria and fungi obtain food for themselves. It is an absolutely vital function, nevertheless, because, if it did not occur, all the nutrients would soon be tied up in dead bodies, and no new life could be produced. (Odum 1959, p. 20)

Odum then explains that the chemical substances produced by bacteria and fungi through their decomposing activities either are used as food by organisms from other species or regulate their growth by having inhibitory or stimulatory effects on them (Odum 1959, pp. 20–25). Odum's statement in this passage that decomposition occurs as a "result of the process by which bacteria and fungi obtain food for themselves" indicates that he does not construe decomposition and its production of substances that are useful to other species as *selected effects* of bacteria and fungi. Decomposition instead occurs as a by-product of the feeding activities of bacteria and fungi, activities that were presumably selected because of how they contribute to the survival and reproduction of bacteria and fungi themselves. Hence, following Elton, ecologists Dice and Odum seem to have construed ecological functions in nonselectionist terms.

Closer to us, contemporary functional ecologists also seem to have a nonselectionist understanding of the function concept. Like Elton, contemporary ecologists do not tend to conceive communities and ecosystems as customary units of natural selection. This, as commonly remarked by philosophers of ecology who have discussed the ecological function concept, entails that the selected-effects theory of function has limited applicability when it comes to organisms or species envisioned as function bearers within communities or ecosystems (see Maclaurin and Sterelny 2008, p. 114; Odenbaugh 2010, pp. 250–251; Nunes-Neto et al. 2014, p. 124).²⁸ Moreover, contemporary functional ecologists do not usually ground their claims about species' ecological functions in claims about those species' selective history (see Dussault 2018). Hence, it seems that the nonselectionist understanding of function that Elton initiated while introducing his functional niche concept tends to have been the prevailing one in the work of subsequent ecologists.

²⁷ It should be noted, however, that, although Dice seems to have shared Elton's nonselectionist understanding of function, he did not associate the niche concept itself with functions fulfilled by species within communities (see Dice 1952, p. 227). Like most ecologists, he followed Grinnell in adopting a niche concept focused on species' ecological *requirements* (in his case, mainly the *resources* that species require) (for a discussion, see Hurlbert 1981).

²⁸ See however Millstein (forthcoming) for a dissenting view.

In the second section, I noted that Elton's functional understanding of the niche diverged from Grinnell's earlier understanding focused on species' ecological *requirements*, and that subsequent ecologists have generally adopted an understanding that stands more in line with Grinnell's concept than with Elton's. The above discussion and the observations made in this section about post-Elton ecologists' use of the function concept indicate that Elton's functional niche has nevertheless had an indirect but lasting influence on subsequent ecologists' thinking. Subsequent ecologists may not have adopted Elton's functional understanding of the niche, but many of them have nevertheless followed him in describing species as fulfilling functional roles within ecological communities and ecosystems. And those who have, have also typically followed him in adopting a nonselectionist understanding of the function concept.

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