Neither Superorganisms nor Mere Species Aggregates: Charles Elton's Sociological Analogies and His Moderate Holism about Ecological Communities

Antoine C. Dussault

Collège Lionel-Groulx; Centre interuniversitaire de recherche sur la science et la technologie (CIRST)

Abstract

This paper analyzes community ecologist Charles Elton's ideas on animal communities, and situates them with respect to the classical opposition between organicist-holistic and individualistic-reductionist ecological views drawn by many historians of ecology. It is argued that Elton espoused a moderate ecological holism, which drew a middle way between the stricter ecological holism advocated by organicist ecologists and the merely aggregationist views advocated by some of their opponents. It is also argued that Elton's moderate ecological holism resonated with his preference for analogies between ecological communities and human societies over more common ones between communities and individual organisms. I discuss, on the one hand, how the functionalistinteractionist approach to community ecology introduced by Elton entailed a view of ecological communities as more or less self-maintaining functionally organized wholes, and how his ideas on this matter were incorporated into their views by organicist ecologists Frederic Clements, Victor Shelford, and Warder C. Allee et al. On the other hand, I identify some important divergences between Elton's ecological ideas and those of organicist ecologists. Specifically, I show (1) how Elton's ideas on species distribution, animal migrations, and ecological succession entailed a view of animal communities as exhibiting a weaker degree of part-whole integration than that attributed to them by Clements and Shelford; and (2) how Elton's mixed stance on the balance of *nature* idea and his associated views on community stability attributed to communities a weaker form of self-regulation than that attributed to them by Allee et al.

1. Introduction

Historical discussions of early ecologists' views on the nature of ecological communities (and ecosystems) commonly paint a polarized picture opposing proponents of *organicist-holistic* views to proponents of *individualistic-reductionist* ones (see, e.g., Simberloff 1980; Tobey 1981; Shrader-Frechette 1986; Worster 1990; Barbour 1996; Callicott 2003; Trepl and Voigt 2011). According to this picture, early ecologists were divided into two main camps: a first one espousing a notion of communities as tightly

integrated and functionally organized superorganisms, often conceived as subject to community-level natural selection, and a second camp espousing a view of communities as arbitrarily defined aggregates formed of species only weakly (if at all) dependent upon one another.

A prominent early twentieth-century ecologist whose ideas do not fit well within this polarized picture is animal-community ecologist Charles Elton (1900–1991). Elton is well known for his popularization of concepts now central to ecological theorizing, such as those of *food chains*, the *pyramid of numbers*, and the *ecological niche*. He is also known for having been the protégé of zoologist and protagonist of the Darwinian synthesis Julian Huxley (1887–1975) and for having been the editor of the *Journal of Animal Ecology* from 1933 to 1950 (see, Cox 1979, Chapter 1; Anker 2001, Chapter 3), as well as for his influence on prominent environmentalists such as Aldo Leopold (1887–1948) and Rachel Carson (1907–1964) (see Newton 2006, Chapters 4, 6; Davis 2012). Despite this influence, Elton's ideas on the nature of ecological communities have been only scarcely examined by philosophers and historians of ecology.¹

The aim of this paper is to contribute to filling this gap by discussing Elton's ideas on animal communities and by situating them with respect to the above described opposition between organicist-holistic and individualistic-reductionist ecological views. Specifically, I will argue that Elton's theory of animal communities, which he exposed mainly in three of his early books and two encyclopedia entries (Elton 1927, 1929, 1930, 1933, 1936), offered what can be regarded as a middle way between strict organicist and steeply aggregationist views of ecological communities. Elton's middle way, I will argue, combined ideas from both sides of the holism/reductionism polarity, in a picture that was consistent overall despite its seemingly hybrid character. In particular, I will maintain that Elton's ecology reconciled two individualistic-reductionist ideas, namely, that species that form communities are independently distributed across landscapes and that they have mostly independent evolutionary histories (Curtis and McIntosh 1951; Whittaker 1967) with two holistic-organicist ideas, namely, that those species are functionally dependent upon one another and that the communities they collectively form constitute (more or less) self-regulating functionally organized wholes. As we shall see, those views led Elton to express commitments to ideas commonly associated with the individualisticreductionist side of the holism/reductionism polarity, but to also repeatedly insist that animal communities are more than mere aggregates. Elton stated, for instance, that "animal communities... are not mere assemblages of species living together, but form closely-knit communities or societies comparable to our own" (Elton 1927, p. 5); or, in slightly different terms, that "animal communities are not simply unorganized assemblages of animals which happen to live in the same habitat," but "are intimately connected together in a most complex manner" (Elton 1929, p. 920).

My discussion will thus substantiate the statement, made in a review of the 2001 republication of Elton's first book, *Animal Ecology* (2001), that his perspective on

¹ It is noteworthy that the two most detailed treatments of Elton's ideas on communities (and his related ideas on population regulation) are found in unpublished doctoral dissertations (i.e., Cox 1979; Haak 2000). The below discussion owes a lot to those treatments, as well as to the more succinct ones offered by McIntosh (1985), Sheail (1987), and Hagen (1992).

ecological communities "struck a balance between what emerged as a half-century debate on communities as superorganisms or random species assemblages" (Yunger 2003, p. 1479). It will do so in part by linking Elton's middle way between ecological organicismholism and individualism-reductionism with his repeated use of analogies between ecological communities and *human societies* (or economic systems). I will contend that Elton's preference for those analogies over ones between communities and *individual organisms* reflect his espousal of a moderate form of ecological holism.

My discussion will be organized as follows. In section 2, I will expose how Elton's ecology involved a significant departure from the approach of previous animal ecologists, introducing what can be described as a functionalist-interactionist approach to community ecology. In section 3, I will discuss how this functionalist-interactionist approach and its focus on feeding and regulatory interactions among animal species led Elton to espouse a view of those species as being *functionally interdependent* and as collectively forming *functionally organized wholes*. Moreover, I will show how those ideas held by Elton were incorporated by prominent organicist ecologists Frederic Clements and Victor Shelford (1939) and Warder C. Allee et al (1949) into their views. In section 4, I will argue that Elton's views on ecological communities nevertheless diverged significantly from those of organicist ecologists, and I will explain how these points of divergence reflected his preference for sociological over organicist ecological analogies. I will maintain this, first, with regards to Elton's and Clements and Shelford's contrasting ideas on the part-whole integration of ecological communities, and second, with respect to Elton's and Allee et al.'s divergent takes on the classical balance of nature idea.

2. Elton's functionalist approach to community ecology

As commonly remarked by historians of ecology (e.g., Egerton 1968, p. 225; Cox 1979, Chapter 1), Elton's approach to animal ecology involved a significant departure from the approach of his predecessors (e.g., Shelford 1913; Grinnell and Storer 1924). This was a shift from a more classificatory and habitat-centered approach that focused on differentiating communities by their species composition to a more functionalist and interactionist approach that focused on showing similarities among communities by finding resemblances in their food-web architecture (see, Cox 1979, pp. 24–25, 31–33, 86–87; Haak 2000, pp. 23–24; McIntosh 1985, pp. 88–93; Sheail 1987, p. 87).² Paralleling the work of plant ecologists of the time, animal ecologists prior to Elton centered their investigations on the relationship between the composition of animal communities and local environmental factors.³ One of their aims was to develop classification schemes for animal communities, similar to those that had been developed for plant communities, and to show how the distributional boundaries of animal communities mapped onto those of plant communities (which were themselves thought to

^{2} For Elton's own account of how he was brought to this shift, see Elton and Miller (1954, pp. 461–462).

³ As pointed out to me by Kurt Jax, an exception to this general observation is Karl August Möbius (1825–1908), whose picture of ecological communities closely anticipates Elton's functionalist and interactionist picture. Möbius is best known for his work on oyster banks (Möbius 1883), where he introduced the term "biocenosis" to denote ecological communities. On Möbius's ideas on ecological communities, see Glaubrecht (2008, pp. 17–18), van der Valk (2017, pp. 115–116), Schwarz and Jax (2011, pp. 242–244), and Potthast (this issue).

coincide with differences in habitats) (see Wake et al. 2009, pp. 19631–19632).⁴ Elton's early field work (reported in Summerhayes and Elton 1923), had made him hesitant about this classificatory approach. His observations had shown that many animals move between habitats and plant communities (e.g., feed in water and nest on land), such that the boundaries of plant and animal communities rarely coincide.

The new approach introduced by Elton, which he portrayed as a "sociology and economics of animals" (Elton 1927, p. vii), shifted the attention from classification and species-habitat relations to *feeding interactions* among animal species. He stated: "Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply" (Elton 1927, p. 56). Elton's approach to community ecology was thus articulated around food-related concepts, such as those of *food chain* and what he called the *food cycle* (i.e., essentially what ecologists now call food webs) (see Elton 1927, Chapter 5, 1933, Chapter 3). Food chains and food cycles had been discussed in previous ecological works, notably Victor Shelford (1913), from whom Elton took the notions, but Elton made them central to his understanding of communities (see Leibold and Wootton 2001, p. xxxii).⁵ Also central to Elton's functionalist-interactionist approach was the study of population dynamics. In Elton's view, as he stated in an early paper discussing population fluctuations in relation to climate, "the study of the regulation of animal numbers forms about half the subject of ecology, although it has hitherto been almost untouched" (Elton 1924, p. 154; see Kingsland 1985, p. 53). Elton's interest in population dynamics originated from his early reading of books on population fluctuations suggested to him by his mentor Julian Huxley (Cox 1979, pp. 10–15), and was further explored in his studies of the Hudson's Bay Company's fur-return data (reported in Elton and Nicholson 1942a, 1942b). This research interest also led him to participate to the "Matamek Conference on Biological Cycles" (1931), which took place at the estuary of the Matamec River on the North Shore of the Gulf of St. Lawrence in northeastern Québec (see Cox 1979, Chapter 5; Anker 2001, pp. 107–108; Hébert 2006, pp. 403–404), as well as to found the Oxford-based Bureau of Animal Populations in 1932, in which he was involved until his retirement in 1967 (see Cox 1979, Chapter 6; Sheail 1987, pp. 103-104; Gay 2013, pp. 108-111; and Crowcroft 1991 for a book-length discussion).⁶

Pivotal to Elton's functionalist-interactionist ecological approach was his concept of *ecological niche*, which he conceived in part as the *functional role* of a species within a community. The niche concept had already been used by Joseph Grinnell (1917, 1924, 1928) in work that aligned with the above-described classificatory and habitat-focused ecological approach, and Elton's use partly lined up with that of Grinnell.⁷ Like Grinnell, Elton used the niche concept to highlight the possibility that phylogenetically unrelated

⁴ For detailed discussions of this earlier classificatory and habitat-focused approach, see Griesemer (1990) and Neumann (2017).

⁵ For a detailed history of ideas on food chains and food webs, see Egerton (2007).

⁶ The Matamek conference gathered scientists from various fields and was organized by wealthy fisheries trader and nature lover Copley Amory on his private estate (for report and proceedings, see Huntington 1932).

⁷ For historical discussions of the niche concept, see Cox (1979, Chapter 4), Schoener (1989), Griesemer (1992), Leibold (1995), and Pocheville (2015).

species be "equivalent" as regards their ecologically relevant features (Grinnell 1924, p. 227; Elton 1927, pp. 64–68, 1933, pp. 28–29). Moreover, like Grinnell, Elton used the niche concept primarily in relation to the *feeding habits* of animals. Accordingly, Elton defined an animal's niche as "its place in the biotic environment, *its relations to food and enemies*" (Elton 1927, p. 64; italics in the original) and acknowledged that, in a sense, niches were simply "smaller subdivisions of the old conceptions of carnivore, herbivore, insectivore, etc." (Elton 1927, p. 64)

For Elton, however, niches were more than that. In contrast to Grinnell's niche concept, Elton's niche concept was concerned not only with the food *requirements* of animals, but also with their *impacts* on the environment and with the way in which those impacts affected the lives of other species (Alley 1985, pp. 414–415; Leibold 1995, pp. 1372–1373; see also Patten and Auble 1980).⁸ Elton was moreover interested in how, through affecting each other's lives, interacting species came to collectively form more or less self-maintaining communities, which all exhibited a relatively invariant food-web architecture (see Hagen 1992, pp. 52–53; Pocheville 2015, pp. 549–550). Hence, in line with his construal of ecology as "the sociology and economics of animals" (Elton 1927, p. vii), Elton portrayed an animal's niche as its "status...in its community, ...what it is doing" (Elton 1927, p. 64; italics in the original). The niche concept, as he explained, "is 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 that feed upon basic plant food and convert it into forms that can be consumed by larger animals can be construed as a community's "key industries" (Elton 1927, pp. 64, 69). So understood, the niche concept, as Elton maintained, helped make manifest "the tendency which exists for animals in widely separated parts of the world to drift into similar occupations" (Elton 1927, p. 65). It also helped highlight the fact that "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 the original). Accordingly, Elton advised: "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).

As commonly remarked by historians of ecology, Elton's parallel between niches on the one hand and jobs, occupations and professions on the other, read in the context of his general parallels between ecological communities and human societies (or economic systems), conveys the idea of *functional roles* fulfilled by species within their communities (Anker 2001, pp. 101–102; Jax 2010, p. 79; Gay 2013, p. 108). Those functional roles are somewhat analogous to socioeconomic roles fulfilled by human individuals within their societies (as they are often conceived in functionalist-leaning sociological works).⁹ The idea of the niche as denoting functional ecological roles, in

⁸ In this respect, Elton's niche somewhat anticipated the concept of niche construction (Odling-Smee et al. 2003). Elton, however, in contrast to niche construction theorists, seems to have conceived the niche not so much as what is constructed by organisms (the result of construction), but rather as the constructing activity itself.

⁹ A most likely inspiration for Elton's parallels between animal communities and human societies is sociologist Alexander Carr-Saunders (1886–1966), who, together with Julian Huxley, is considered to have acted as his mentor at Oxford. In the preface of his *Animal Ecology*, Elton explicitly links his understanding

turn, suggests a notion of ecological communities as *functionally organized wholes*—that is, of communities as composed of parts (i.e., their component species) that are interdependent in a way similar to the way in which social agents in a complex human society are interdependent (or to the way in which organs in an individual organism are, though I will argue below that the sociological analogy better reflects Elton's views). To be sure, Elton cautioned that his parallels between animal communities and human societies were "simply intended as analogies and nothing more" (Elton 1927, p. viii) and, importantly, he seems to have used those parallels for *communicative*, not *theoretical*, purposes. Nevertheless, as I will argue in the following sections, Elton's preference for sociological over organicist ecological analogies is significant in that it reflects important aspects of his understanding of ecological communities. As he himself stated, those parallels, for him, were important partly in that they helped "to drive home the fact that animal interrelations ... are very complicated, but at the same time subject to definite economic laws" (Elton 1927, p. viii). They also highlighted the fact that "it is impossible to treat any one species as if it were an isolated unit, when we are studying its distribution and numbers" (Elton 1927, p. 190).

In the next section, I will show that Elton's consideration of the "very complicated" interrelations alluded to in the above passage led him to paint a somewhat holistic picture of ecological communities. By shaping each other's environments, animal species that form communities became *functionally interdependent*—that is, dependent upon one another for the achievement their life activities (and consequently for their survival). Moreover, they came to collectively realize and maintain exceedingly complex and intricate webs of ecological interactions, which, for Elton, were essentially what ecological communities consisted in.

3. Elton's functional holism

As conceived by Elton, species that form communities were functionally interdependent in two important ways: they depended upon each other (1) for *food provision* and (2) for the *regulation of their numbers*.¹⁰ A basic fact about animal species is that they are all reliant upon other species for food (and ultimately upon supplies of organic matter and energy from plants) (Elton 1927, Chapter 5, 1933, Chapter 3). This, as Elton observed, led animal species to be involved in several predator-prey and parasite-host *food chains*. The formation of food chains resulted from the fact that predators and parasites can consume food only of appropriate size. A predator can consume only prey that is sufficiently small to be reasonably easy to catch and big enough to meet its nutritional needs (Elton 1927, pp. 59–63). Similarly, a parasite must be small enough to be able to live off its host without harming it too much or killing it too quickly

of ecology as "the sociology and economics of animals" to Carr-Saunders's (1922) study of the "sociology and economics" of humans (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, Chapter 3). For general discussions of functionalism in sociology, see, e.g., Munch (1976) and Moore (1978).

¹⁰ For detailed discussions of Elton's ideas on animal communities, see Cox (1979, pp. 51–54, Chapter 3) and Hagen (1992, pp. 51–62).



Figure 1: Diagram of "nitrogen cycle" or "food-cycle" on Bear Island. From Summerhayes and Elton 1923, p. 232 (the same diagram is reproduced in Elton 1927, p. 58).

(Elton 1927, pp. 72, 77–78). The organization of species into food chains entailed that, by occupying its niche, a species contributed to supporting the lives of all species located at higher links of the chain.

But there is more. Although Elton recognized that it is sometimes useful for analytic purposes to study particular food chains in isolation, he insisted that, in reality, "foodchains are seldom simple and self-contained," and "usually several preys and several predators interact at each stage" (Elton 1933, p. 30). This observation led him to introduce his concept of the food cycle-which encompassed "all the food-chains in a community" (Elton 1927, p. 56). In practice, a community's food cycle could be very complex, and even more so when one takes into consideration the usual interconnection of prey-predator and parasite-host food chains (see the example in figure 1). As Elton explained, parasites often get transferred from prey to their predators, and some parasites have "free-living" adult stages during which they can be consumed as food by other animals. These animals, in turn, often themselves serve as prey in other food chains (Elton 1927, pp. 76–77, 80–81). Such observations entailed that, according to Elton, "the food-relations of animals are extremely complicated and form a very closely and intricately woven fabric—so elaborate that it is usually quite impossible to predict the precise effects of twitching one thread in the fabric" (Elton 1927, p. 79). Thus, by occupying its niche, a species indirectly contributed to supporting the lives not only of species at higher links of its food chain, but also of countless other species. Hence, in practice, a species could be considered to participate in supporting its whole community's food cycle. Food interdependencies among animal species, he stated, entailed that "every animal community is knit into a more or less interconnected whole" (Elton 1936, p. 1033).

A second way in which, as conceived by Elton, species that form communities were functionally dependent upon one another concerns how feeding interactions between them contributed to the *regulation* of their numbers (Elton 1927, Chapters 8–9, 1933, Chapters 5–6). Like many other ecologists at the time, Elton construed populations of

animal species as having optimal abundances ultimately determined by the availability of their food, and, at the same time, as having great powers of increase that would enable them to quickly exceed their food supply if allowed to grow unchecked. On a general basis, optimal abundances decreased from lower to higher links of prey-predator food chains, a phenomenon Elton described as the *pyramid of numbers*. Because of their smaller sizes, animals at lower links of the food chain tend to grow faster than animals at higher links, such that the former are able to support more abundant predator populations than the latter (Elton 1927, pp. 68–70). In host-parasite food chains, Elton remarked, the pyramid of numbers is inverted. Given that an individual host can usually support a large number of individual parasites, optimal numbers generally increase from lower to higher links of host-parasite food chains (Elton 1927, p. 78). This, of course, was a very broad picture, and Elton noted that, in reality, species' optimal abundances are always changing and are by no means always achieved (Elton 1927, p. 114).

Although Elton considered the optimal numbers of species to be ultimately determined by the availability of their food, he did not consider intraspecific competition for food as the primary factor regulating populations (his views, in this respect, contrasted with those of prominent population ecologists of the time, notably Nicholson 1933).¹¹ 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, although the possibility of it is always present. Instead we find that other factors, such as enemies of all kinds, usually keep numbers down well below the point which would bring the population in sight of starvation. (Elton 1927, p. 118)

Hence, in Elton's view, animal populations were on a general basis regulated first and foremost by their predators and parasites (which he jointly referred to as their "enemies"). The regulation of animal populations was thus, for him, an *interspecific* rather than *intraspecific* phenomenon. This interspecific mode of regulation, as Elton further explained, had the advantage of preventing species from living "all the time up to the extreme limits of their food-supply," leaving themselves no margin for times when food would become scarcer (such as winters). It also prevented entire populations from being destroyed as a result of exceeding their food supply (Elton 1927, pp. 118–119). The organization of species in food chains hence entailed that, by occupying its niche, an animal species contributed to the regulation of the populations it fed upon.

But, again, there is more. Given the complex organization of the food cycle, populations within animal communities were in fact, according to Elton, interdependent as regards their regulation with *many* other populations. As he 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) and, conversely, "no animal can be said [as regards its distributions and numbers] to be dependent upon

¹¹ Interestingly, Elton's ideas, in this respect, aligned with those of Carr-Saunders, who criticized strict Malthusian views on population regulation (see Carr-Saunders 1922, Chapter 9; and for discussions, see Sheail 1987, p. 90; Angner 2009, p. 81). It should be noted, however, that, in later publications (Elton 1958, p. 131), Elton recognized a more important regulative role to intraspecific competition (see Haak 2000, p. 30). For general discussions of Elton's ideas on population regulation, see Cox (1979, pp. 50–64), Sheail (1987, sec. 2.5.2), Hagen (1992, pp. 56–60), and Haak (2000, pp. 26–30, 43–44).

only one other species, since all are bound together by food connections into one complex organization" (Elton 1929, p. 920). Those observations entailed that, in practice, population regulation was more properly construed as an overall effect of the food cycle as a whole. Hence, by occupying its niche, a species did more than simply regulate the abundance of the population it directly fed upon; it also indirectly contributed to regulating the numbers of many other species (and perhaps of all those involved in the community). At the methodological level, such observations had important implications. They implied, as Elton stated, that "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 the original). Hence, as he tellingly asserted: "It is clear that the study of the *autecology* of the numbers of any species involves inevitably a study of the *synecology* of the community in which it lives" (Elton 1933, pp. 68–69; italics added).¹²

For completeness, it must be remarked that Elton acknowledged complementary modes of population regulation, besides those involving interspecific feeding interactions. Among them were the intrinsic ability of some species (mostly top predators) to limit their reproduction (Elton 1927, pp. 119–120, 123–124), the controlling effects of climate (Elton 1927, pp. 119, 123), and, importantly, as we shall see in more detail in section 4, the migration of animals from overpopulated areas to less populated ones (Elton 1930, pp. 61–62, 1933, pp. 70–72). It must also be mentioned that, as will also be discussed further in section 4, Elton's ideas on population regulation were significantly qualified by his awareness that, in reality, the numbers of animal were subject to important fluctuations.

Those qualifications notwithstanding, it remains the case that, according to Elton, species that form communities were functionally interdependent in two main ways: (1) with regards to food provision and (2) with respect to the regulation of their numbers. This functional interdependence of species that form communities, I contend, was what Elton's parallels between ecological communities and human societies were essentially meant to convey. Ecological communities that formed through the multifariously intertwined interactions of animal species exchanging organic matter with each other were, in his view, analogous (though not identical) to the economic component of human societies (which formed through the complexly interwoven interactions of socioeconomic agents exchanging goods and services with each other). Moreover, just like socioeconomic agents, when viewed as constituents of networks of socioeconomic interactions, could be conceived as fulfilling socioeconomic roles within their societies; species, when viewed as constituents of networks of ecological interactions, could be construed as fulfilling complementary functional roles within their ecological communities.

¹² Elton restated this idea in later publications (e.g., Elton and Miller 1954, p. 463). The distinction between *autecology* and *synecology* invoked by Elton in the latter passage was from Swiss ecologists Schröter and Kirchner (1902) and draws a contrast between ecological studies focusing on single species in relation to their environment (autecology) and studies concerned with ecological communities as a whole (synecology). Elton presumably took this distinction from his Oxford colleague Arthur Tansley (1923, p. 20).

4. A moderate ecological holism

4.1 Elton and organicist ecologists

Elton's view of species within communities as functionally interdependent suggests an idea of ecological communities as *functionally organized wholes*. This idea, in turn, invites an association of his views with those of early twentieth-century ecologists who maintained that ecological communities were properly construed as *organism-like* entities, or *superorganisms* (see, e.g., Sagoff 1988, p. 127).¹³ Such an association with organicist ecological views may find support in the fact that key aspects of Elton's functionalist-interactionist ecologist, such as Frederic Clements and Victor Shelford (1939), as well as Warder C. Allee et al. (1949). Such an association may moreover find support in the fact that this incorporation of Eltonian aspects often involved the extension of *physiological* concepts (concepts customarily used in relation to organisms) to ecological communities.¹⁴

Prior to Elton's publications, Frederic Clements's organicist perspective on plant communities had primarily been centered on the idea that ecological succession mimicked the development of an individual organism (e.g., Clements 1905, 1916; see Gibson et al. 2013, pp. 515–516).¹⁵ However, Clements's later book attempting a synthesis of plant and animal ecology, written in collaboration with animal ecologist Victor Shelford, incorporated Elton's ideas on food chains and the food cycle (Clements and Shelford 1939). Clements and Shelford ascribed to feeding interactions between organisms—in their own terminology "food coactions"—a central role in "the integration of plant and animal relations to constitute an organic complex" (Clements and Shelford 1939, pp. 107, 115–116). As Simberloff illuminatingly remarks: "Elton's description of the food chain as a conduit for community energy flow...provided such a diagrammatic analogy to the *physiology* of an individual organism that it was readily incorporated as an integral part of the superorganism, in fact, one of the forces giving it organismic cohesion" (Simberloff 1980, p. 14; italics added). In a paper that antedated the publication of his book coauthored with Clements, Shelford had referred to the transfer of organic matter and energy through food cycles—in his own terminology, the "food interrelations of animals"—as a "processes comparable to *metabolism*" (Shelford 1931, pp. 456–457; italics added).

¹³ For historical discussions of organicist views in early ecology, see Bodenheimer (1957), Acot (1987), McIntosh (1998), and Bergandi (1999).

¹⁴ Additional indirect support may be found in the fact that the idea of communities as superorganisms was espoused by Elton's mentor Julian Huxley, along with novelist H. G. Wells, in the ecology chapter of their book *The Science of Life*, a huge book that surveyed life sciences for a popular audience. In this book, Wells and Huxley asserted that "it is not altogether fanciful to compare all [the world's] various [ecological] communities, each one to a sort of super-organism, and in practice much of the thought and work of the ecologist involves that idea" (Wells et al. 1931, p. 578). According to historian of ecology Peder Anker (2001, p. 112), Wells et al.'s chapter on ecology was entirely reviewed by Elton prior to its publication.

¹⁵ For further discussions of Clements's ideas on ecological succession, see Whittaker (1974), McIntosh (1980, 1985, pp. 76–82), Hagen (1988, 1992, Chapter 2), and Eliot (2007, 2011).

A physiological parallel between the transfer of organic matter and energy through food cycles and the *metabolism* of individual organisms can also be found in the work of Warder C. Allee, Alfred E. Emerson, and colleagues (Allee et al. 1949). In a chapter entirely devoted to the topic of "community metabolism," Allee et al. asserted that "the sum total of the organismal nutritional and assimilative responses of the community may be considered to be the metabolism of the community, just as the sum total of the physicochemical processes in the organism is thought of as the metabolism of the individual" (Allee et al. 1949, p. 495). Interestingly, they described the effects of bacteria on organic and inorganic matter and the photosynthetic activity of plants as "anabolic processes" within the community, and the effects of the feeding activities of herbivores and carnivores as the "catabolism of a community" (Allee et al. 1949, pp. 496, 508). Allee et al. also incorporated Elton's idea of population numbers as being regulated by the community as a whole and linked this idea to the physiological notion of homeostasis.¹⁶ They described the "development of balance between populations of different species" as "to some degree...similar to the dynamic equilibrium characteristic of individual organisms and intraspecies populations" and stated that this "equilibrium in interspecies systems often constitutes ecological homeostasis" (Allee et al. 1949, p. 710; italics added). That Allee et al. took their ideas about transfers of organic matter and energy through food cycles and about population regulation is partly supported by their high praise for Elton's work on animal communities. They stated: "Since Elton's treatment of communities seems without question the best of the decade, we can do no better than examine the state of this phase of ecology as seen through his eyes" (Allee et al. 1949, p. 58).

The association between Elton's ecological ideas and those of organicist ecologists may moreover find support in the fact that Elton seemingly espoused Clements and Shelford's analogy between ecological succession and the *development* of an individual organism. He stated:

There is a...process known as the *development* of plant communities. Development is a term used by plant ecologists in a special technical sense, to include changes in plant communities which are solely or largely brought about by the activities of the plants themselves. Plants, like many animals, are constantly moulting, and the dead leaves produced accumulate in the soil below them and help to form humus. This humus changes the character of the soil in such a way that it may actually become no longer suitable for the plants that live there, with the result that other species come in and replace them. (Elton 1927, p. 20; italics in the original)

Elton referred to this successional developmental process as "extremely important" and most "interesting since its movements are orderly and often predictable." His discussion of ecological succession includes references to Clements and Shelford's earlier works (Shelford 1907; Clements 1916). In a later publication, Elton's treatment of ecological succession even included a brief allusion to the organicist analogy:

Some ecologists are so impressed by the definiteness and regularity of the sequence of change in a "sere"—the series of communities that grow during [ecological] succession—that they compare the sere [i.e., a successional unit] to a *new and higher kind of organism*. Other ecologists do not

¹⁶ The concept of *homeostasis* was coined by Walter B. Cannon (1932) and denoted organisms' characteristic ability to maintain their state in response to external perturbations. It was inspired by the work of the French physiologist Claude Bernard (1879).

agree with this idea, or will only admit that it is a "quasi-organism." Whatever philosophical view one takes of the phenomenon, there is no doubt at all about the importance and regularity. (Elton 1936, p. 1032; italics added)¹⁷

Despite these striking affinities, I will argue in the remainder of this section that Elton's ideas on communities and those of the above-mentioned ecological organicists in fact significantly diverged. Moreover, I will illustrate that they did so in ways that were consistent with Elton's repeated use of analogies between ecological communities and human societies, and with the related fact that he rarely (if ever) compared ecological communities to individual organisms (on the face of it, Elton remains fairly neutral with regards to the organicist analogy in the passage just quoted). I will illustrate this, first, with regards to Elton's ideas on species distribution, animal migrations, and ecological succession (which will set his views in contrast to those of Clements and Shelford), and, second, with respect to his nuanced stance on the classical *balance of nature* idea (which will set his views in contrast to those of Allee et al.).

4.2 Individualistic distribution, migrations, and polyclimactic succession

Even if from a sociological perspective it sometimes seems relevant to describe human societies as functionally organized wholes, similar in some respects to individual organisms, a remaining seeming difference between human societies and organisms concerns their comparative degrees of part-whole integration. Unlike organs and subsystems with respect to the organisms they are part of, human individuals seem to retain a relatively high degree of autonomy with respect to the societies in which they are involved (see Jax 2010, pp. 79–80). In particular, individual humans can routinely be involved in more than one society (e.g., live on one country and do business in another), often have the possibility of moving between societies (e.g., spend time in another country or emigrate there), and largely pursue their own ends (although they can of course sometimes become engaged in the pursuit of societal ends). In contrast, organs and subsystems within organisms normally belong to only one single organism, cannot freely move from one organism to another, and achieve their biological activities for the sake of the organism as a whole (e.g., hearts are present and pump blood within organisms because this contributes to the organism's survival).

When Elton started working on animal communities, such differences between individual organisms and human societies had been recurring themes in debates over the legitimacy of organicist analogies in the social sciences (see, e.g., Ferrière 1915, Chapters 1–2; Child 1924, Chapter 16). Differences of this kind had also been highlighted (in a discussion of Clements's ideas) by Elton's Oxford colleague and plant ecologist Arthur Tansley (1920, pp. 123–124), whose work Elton knew very well.¹⁸ Whether or not Elton was influenced by those discussions, we will now see that his views on species distribution, animal migrations, and ecological succession attributed to animal species a significant degree of autonomy with respect to the ecological communities in which they are involved—one similar to that typically enjoyed by human individuals with respect to

¹⁷ The "quasi-organism" notion alluded to here was from plant ecologist Arthur Tansley (1920, 1935).

¹⁸ Elton and Tansley and are known to have been in relatively close contact with each other (see Anker 2001, Chapter 3). Moreover, Elton's *Animal Ecology* cites two books by Tansley, and the discussion of ecological succession in chapter 3 of that book draws heavily on Tansley's works. Hence, I take it that Elton was likely aware of Tansley's remarks on the organicist analogy.

their societies. Moreover, we shall see that Elton's attribution of such a degree of autonomy to animal species with respect to their communities entailed a view of ecological communities partly congruent with that of Clements's theoretical opponent Henry Gleason (1917, 1926).

Central to Clements and Shelford's ecological ideas was the view that species that form ecological communities are so strongly interdependent that their ranges of geographical distribution largely coincide. This distributional coincidence entailed that communities had relatively uniform species compositions, which made it possible for ecologists to delineate community boundaries on the basis of compositional contrasts between them. According to Clements and Shelford, species' distributional coincidence resulted primarily from the influence of what they called *dominants* within communities. Dominants are species that are relatively abundant within a community and that exert a high degree of control on the community's general composition. They do so by shaping the community's environmental conditions, either by their simple presence or by the physical changes they bring to the environment. In so doing, they determine the ability of other species, called the *subordinates*, to persist within the community (see Clements and Shelford 1939, Chapter 7).¹⁹ According to Clements and Shelford, this strong dependency of subordinate on dominant species was mainly a result of the (alleged) fact that species that form communities had shared coevolutionary histories (which, for Clements, involved Lamarckian adaptive mechanisms).²⁰ Such coevolutionary histories entailed that subordinate members of a community were, on a general basis, more finely adapted to the conditions created by the dominants than potentially immigrating species.

Gleason (1917, 1926), in contrast, advocated what he called an "individualistic concept" of communities, which he explicitly conceived as an alternative to Clements's organicist view. According to this "individualistic concept," species were independently distributed across landscapes. It entailed, in Gleason's view, that the particular species composition of a given community was largely contingent, a "coincidence," as he famously suggested (see, e.g., Gleason 1917, p. 473).²¹

As already seen in section 2, Elton was doubtful of previous animal ecologists' idea that plant and animal species found in a particular habitat had coinciding ranges of distribution (in part because of the ability of animals to move between communities). Elton recognized that, indeed, some animal species were "exclusive" to or "characteristic" of some plant communities (e.g., game birds found in Great Britain and long-tailed mice in Oxford woods). However, such "exclusives" and "characteristics," he insisted, "form only a comparatively small section of the whole community." As he

¹⁹ For discussions of this aspect of Clements and Shelford's ecology, see Whittaker (1957, pp. 197–198), and Kirchhoff (this issue).

²⁰ On Clements's Lamarckianism, see Hagen (1983).

²¹ In the interest of not misrepresenting Gleason's ideas, it must be remarked that, despite his emphasis on contingency, he did not deny that species interactions were important factors in the organization of communities. He regarded interactions between species as important determinants of their ability to establish and maintain themselves in particular locations. Hence, although, for him, the composition of communities was largely contingent, communities nonetheless remained, to a significant extent, interactive systems. His views, in this respect, were very close to those I am attributing to Elton. On Gleason's ecological ideas, see McIntosh (1975, 1995), Nicolson (1990), and Nicolson and McIntosh (2002).

moreover insisted, "there are many species of animals that range freely over several zones of vegetation, either because they are not limited by the direct or indirect effects of the vegetation, or because they can withstand a greater range of environment than the others" (Elton 1927, pp. 11–12, see also p. 18). In a later work, Elton also challenged the idea that the distributional ranges of subordinate *plant* species coincided with those of dominants (see Elton 1936, pp. 1032–1033). Hence, despite the above-observed affinities between his views and those of Clements and Shelford, Elton's ideas on species distribution in fact better aligned with their theoretical opponent Gleason's "individualistic concept."²²

Elton also rejected Clements and Shelford's idea that species that form communities had shared coevolutionary histories. In his small book on the relationship between ecology and evolution (Elton 1930), follow-up to his Animal Ecology, Elton criticized the common construal of animals as "stationary units" passively acted upon by natural selection, and insisted on the ability of animals to select their environments besides being selected by them (a phenomenon referred to by today's ecologists as "habitat selection"; see Morris 2003). This latter ability, he maintained, explained much of the observable fit between animal species and their local environmental conditions (see McIntosh 1985, p. 167; Sheail 1987, pp. 92–93; Haak 2000, p. 32). As Elton argued, individual animals had an "awareness...of their harmonious adjustment with [their] environment," which enabled them to select "new environments by irregular migration away from unharmonious conditions" (Elton 1930, p. 51). This ability of animals, he maintained, greatly increased "the range of environments with which [their] hereditary variations [could] be brought into contact with consequent increase in adaptive radiation" (Elton 1930, p. 52). Those observations imply that, for Elton, animal communities were, to a significant degree, formed of species that had evolved their adaptive traits prior to being involved in their current communities, rather than formed of species that had become finely adapted to each other through a long coevolutionary history. Many species had become part of their community simply as a result of opportunistically immigrating to habitats and local communities that offered (biotic and abiotic) conditions to which they were preadapted (a phenomenon that is commonly referred to as "ecological fitting" by contemporary ecologists; see, e.g., Janzen 1985; Agosta and Klemens 2008). Hence, Elton's ideas on species evolution and community formation, just like his ideas on species distribution, better aligned with Gleason's than with Clements and Shelford's ecological ideas.

Relatedly, although Elton, as mentioned above, seems to have embraced the Clementsian analogy between ecological succession and the *development* of individual organisms, his particular views on ecological succession significantly departed from those of Clements and Shelford. As is well known, Clements considered the normal endpoint of ecological succession—the climax—to be primarily determined by the climate of a region (rather than by other possible factors such as the soil composition). This implied that, in all communities located in the same climatic region, succession normally—i.e., when no impeding factors were at play—tended to realize the same

²² Revealingly, in a later work where he reminisces on the development of his views on species distributions, Elton explicitly acknowledges the relevance of Gleason's "individualistic concept" (Elton and Miller 1954, p. 479; see McIntosh 1995, p. 319).

climax. This view held by Clements is sometimes referred to as the *monoclimax* view of ecological succession, and it was, in Clements's works, tied to a sophisticated vocabulary (which included terms such as "subclimax," "disclimax," etc.) that served to classify cases where normal succession did not in fact occur.²³ With respect to animal species, Elton rejected the monoclimax view of succession. Discussing a case of animal succession documented by Shelford and which seemingly aligned with the monoclimax view (one involving tiger beetles of the genus *Cicindela*), Elton insisted that cases of this kind are "rather unusual" because Shelford's case involved "a genus of animals which tends to form species that are exclusive or confined to one or two plant associations" (Elton 1927, p. 26). For Elton, the direction of succession occurring in animal communities was more commonly determined by a combination of factors, and sometimes more by the food and shelter provided by some species to others than by the regional climate (as Clements maintained) (see Elton 1927, pp. 26–27).

Hence, despite Elton's seeming espousal of Clements's analogy between succession and the development of an individual organism, his particular views on ecological succession in fact better aligned with Arthur Tansley's (1920, 1935) more flexible *polyclimax* view (according to which succession tends to result in a mosaic of compositionally divergent climaxes rather than a single, climate-determined one). As is well known, Tansley was, besides Gleason, an important critic of Clements's organicist ecological ideas.²⁴

In sum, Elton's views on species distributions, animal migrations, and ecological succession indicate that, although, as seen above, he conceived ecological communities as functionally organized wholes, in partial agreement with organicist views of ecological communities, he also, in partial agreement with Gleason's "individualistic concept," attributed to species a significant degree of autonomy with respect to the communities in which they are involved. The observations made in this section thus illustrate that Elton espoused a *moderate* kind of ecological holism, one which, I suggested, reflects his preference for sociological over organicist ecological analogies, and which attributes to ecological communities a weaker degree of part-whole integration than that attributed to them by ecological organicists.

As we shall see in section 4.3, Elton's espousal of a moderate ecological holism, more in line with sociological than with organicist ecological analogies, is also reflected in his views on community regulation and stability.

4.3 The imbalance of nature

Even if it is sometimes relevant, from a sociological (or economic) perspective, to describe human societies as achieving some kind of self-regulation, to some degree similar to that which occurs in individual organisms, important differences undeniably remain between the types of regulative processes that can conceivably be attributed to each kind of entity. Specifically, a noticeable difference between societies and individual

²³ For discussions of Clements's ideas on ecological succession, see the references in note 15 above.

²⁴ For a discussion of the contrast between Clements's and Tansley's ideas on succession, see Whittaker (1974) and van der Valk (2014); for further discussion of Elton's ideas on ecological succession, see Leibold and Wootton (2001, pp. xxv–xxvii).

organisms is that regulative processes in the latter are usually coordinated by a centralized control system (e.g., the central nervous system), whereas no comparable centralized control is at play in human societies. Even when the most severe and repressive, regulative controls imposed on socioeconomic agents by centralized states arguably remain much less stringent than those operative in individual organisms (for discussions, see Canguilhem 2002, p. 584, 2012; d'Hombres 2012).

When Elton started working on ecological communities, such differences between human societies and individual organisms, just like those mentioned above concerning the autonomy of human individuals with respect their societies, had been central topics in debates over the legitimacy of organicist analogies in the social sciences (see, e.g., Huxley 1911 [1871]; Spencer 1916 [1871]; and d'Hombres 2012 for a discussion). Whether or not Elton was influenced by those debates, we shall now see that his mixed stance on the classical *balance of nature* idea entails a view of ecological communities as realizing only a *weak* form of self-regulation. This weak form of self-regulation, I will argue, is closer to that in which human societies can conceivably be construed as self-regulating than to self-regulation as it typically occurs within individual organisms.²⁵ The contrast between strong and weak forms of self-regulation, I will also argue, helps highlight an important way in which Elton's views on ecological communities departed from those espoused by organicist ecologists Allee et al. (1949).

An idea commonly associated with the organicist view of ecological communities is that of the *balance of nature* (see McIntosh 1985, Chapter 3; Simberloff 2014, pp. 1–2). This idea antedates the development of ecology as a self-conscious science and can be traced back to the work of ancient and modern thinkers such as Herodotus, Cicero, and Carl von Linnaeus (Egerton 1973; Simberloff 2014). In contemporary ecology, this idea has been associated with diverse ecological phenomena involving various kinds of stability or equilibrium (compare, for instance, what "balance of nature" denotes when used by Nicholson 1933; Allee et al. 1949; and C. B. Williams 1964). The balance of nature was a key component of Allee et al.'s (1949) analogy between ecological communities and individual organisms. In their work, "balance of nature" referred mainly to the regulative processes exerted on populations by the food cycle as a whole previously characterized by Elton (which they incorporated into their views under the concept of community *homeostasis*, as seen above).

Although Elton, as seen above, conceived animal populations as controlled by their enemies and the community's food cycle as a whole, it is important to note that, for him, the regulative processes occurring in ecological communities remained far from perfect ones. Elton repeatedly emphasized that animal populations, although indeed regulated, were nonetheless subject to important, and sometime violent, fluctuations.²⁶ He stated: "It is not a rare or exceptional thing for a species to break out of control of its normal checks; ... [such] 'plagues' of animals are an inevitable consequence of the way in which animal

²⁵ Historian of ecology Joel Hagen (1992, p. 59) ventures that, living at the time of the 1929 Great Depression and having himself, in that context, lost his job at the Hudson's Bay Company, Elton could not but be aware that self-regulative processes occurring in human societies were at best imperfect ones compared to those occurring within organisms.

²⁶ On Elton's ideas on population regulation and fluctuations, see references in footnote 11.

communities are arranged and of the great instability of the environment" (Elton 1927, p. 111). As indicated in this passage, Elton considered population instabilities to be, in some respects, an inherent effect of the internal organization of communities. This internal organization did not prevent the occurrence of epidemics caused by parasites, or that of capricious changes of habits on the part of animals in response to changes in food availability. Population instabilities were also an effect of the instability of the environment. For instance, a warmer summer could stimulate the growth of a herbivore population to such a degree that its usual predators—whose populations cannot grow as fast—remain unable to control it. A third cause of population instabilities, which he discussed elsewhere, was the migration of animals between communities (see Elton 1930, pp. 23–24).

In his 1930 book *Animal Ecology and Evolution*, Elton's appreciation of the ubiquity of population fluctuations led him to criticize the classical *balance of nature* idea. He stated:

"The balance of nature" does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying... and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers the resultant confusion is very remarkable (Elton 1930, p. 17)

Elton expressed similar criticism in his *Encyclopædia Britannica* entry, there stating that "the 'balance of nature' hardly exists, except in the minds of scientists" (Elton 1929, p. 923), as well as in his Matamek conference paper (Elton 1932, p. 12).

It is worth considering in more detail what, exactly, Elton was rejecting when criticizing the *balance of nature* idea, and, relatedly, how, precisely, his stance on that idea differed from Allee et al.'s. For, importantly, Allee et al. readily acknowledged the fact of population fluctuations, but considered it compatible with the *balance of nature* idea. And, conversely, Elton fully acknowledged that "the community possesses some power of regulation, of compensating here for a disturbance there," and that "the species composition of most communities remains very much the same over long periods" (Elton 1930, pp. 38, 25). In this context, one may wonder whether, as Allee et al. themselves suggested, the disagreement between them and Elton on this matter was not simply terminological: "Elton's concept of balance seems to be constancy, while we refer rather to long-term relations of numbers that include many regular and irregular periodicities as well as dispersal" (Allee et al. 1949, p. 710). At variance with Allee et al.'s suggestion, I think that the disagreement at issue here between them and Elton concerned more than the appropriateness of the phrase "balance of nature" in reference to regulated but fluctuating populations. This disagreement concerned, more fundamentally, the *explanation* for how animal communities achieve their relative degree of stability.

What Elton specifically rejected when criticizing the *balance of nature* idea was the view—a view later advocated by Allee et al.—of natural selection as a factor generating some kind of harmony within animal communities. What he rejected, in other words, was the view of natural selection as a factor that nicely coordinated the responses of interacting animal populations to each other's fluctuations in a way that would significantly reduce the risks of community collapse resulting from those fluctuations.

For Allee et al., natural selection had such a coordinating ability because it operated not only at the level of individual organisms and populations, but also at that of communities as a whole (see Allee et al. 1949, pp. 705–710). Elton rejected both the view that animal fluctuations were nicely coordinated by past natural selection and the view that natural selection operated at the community level. The former view, Elton stated, "has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue" (Elton 1930, p. 16). As he explained, such a view would imply that an animal's ability to adjust itself to environmental fluctuations is underlain by a preevolved set of "definite and fixed reactions." This, he argued, was made implausible by the typically irregular and heterogeneous character of environmental fluctuations. As he humorously illustrated, this would require every animal "to have so many different reactions, some of which would only be used at intervals of many years, or perhaps never at all, that it would have to resemble the conjuror's magic kettle which poured out any drink that you asked for" (Elton 1930, p. 28). Elton thus concluded that ecologists should "abandon the simple idea of the balance of nature, which was supposed to be produced by the natural selection of more or less fixed instincts, physiological reactions, and structures" (Elton 1930, p. 24). He also rejected the view of natural selection as operating on ecological communities as a whole: "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," and communities have "no competitors in this sense" (Elton 1930, p. 31; see also 1929, p. 923). It is notable that he criticized Allee et al. (1949) for their poorly supported commitment to this view (see Elton 1950, p. 78).²⁷

Elton's rejection of the (community-selectionist) balance of nature led him to consider what alternative explanations could be given for the observable relative stability of animal communities (which, as noted above, he fully recognized). In his view, what called for explanation, specifically, was "the combination of a fairly constant composition of species and of constantly changing numbers which we find in most animal communities." This combination, Elton thought, indicated the presence of some "internal regulating factor in the animal community" that confers them some "necessary elasticity and regulative power" and "safeguards them from ecological disaster" (Elton 1930, pp. 32–33). According to Elton, this "elasticity" of communities resulted in large part from the above-discussed ability of animals to migrate from unfavorable to favorable conditions (i.e., the phenomenon of *habitat selection*). Such migrations, Elton contended, act as "a sort of safety-valve" buffering the otherwise possibly reverberating effects of population fluctuations throughout the community (Elton 1930, p. 61).²⁸ He explained:

When the population increases seriously far above its optimum, there is a shifting of the animals to other places, so that the abnormal density is relieved.... If the population is less than it might be, the gaps soon fill from the outside by similar process of adjustment. Migration in response to an innate sense of harmony with the habitat makes possible a solution to the animal population problem. (Elton 1930, p. 61)

²⁷ For a more detailed presentation of Elton's critique of community selection, see Dussault (forthcoming, sec. 4).

²⁸ This mode of regulation is commonly referred to by contemporary ecologists as "source-sink dynamics" (see, e.g., Pulliam 1988).

Another mode of community regulation (discussed in *Animal Ecology*) was what he called the "switch arrangement" of feeding.²⁹ Elton explained:

Most carnivores do not confine themselves rigidly to one kind of prey; so that when their food of the moment becomes scarcer than a certain amount, the enemy no longer finds it worth while to pursue this particular one and turns its attention to some other species instead.... This switch arrangement is common enough in animal communities, and is probably an important factor in preventing the complete extermination of animals (Elton 1927, p. 113; see also p. 144).

Elton's search for explanations of community stability indicates that his stance on the balance of nature idea amounted more to a rejection of one particular way of explaining this (relative) stability than to an outright denial of the view that communities were somehow regulated. I submit that the contrast between Elton's and Allee et al.'s views on what explains community stability-migrations and "switch arrangement" versus coordination by past natural selection—is reflective of their preferences for sociological and organicist ecological analogies, respectively. Allee et al.'s explanation, I submit, entails a view of community regulation as more closely similar to regulation as it occurs in individual organisms. By conceiving ecological communities as formed of populations whose responses to each other's fluctuations are coordinated by past natural selection, Allee et al. attribute to them a kind of regulative unity similar to that which characterizes individual organisms. On their view, an important similarity between ecological communities and individual organisms was that the ability of their internal regulating factors to maintain the stability of the whole resulted from the coordination of those factors by past natural selection operating on the whole. In contrast, Elton's explanation of community stability as a somewhat incidental combined effect of animal migrations and the "switch arrangement" of predators attributes no comparable regulative unity to ecological communities. Animal communities "regulate themselves" only in the sense that a somewhat incidental, although quite regular, result of their component organisms' (uncoordinatedly) achieving their life activities is the achievement of some relative degree of stability at the community level. Animals' eating food that is more abundant and their migrating when food becomes scarce incidentally lead them to buffer (to some degree) the possible effects of fluctuations in the populations they feed upon on their own populations. At the level of whole communities, the combined buffering effects of those animal behaviors (to some degree) prevent fluctuations that unavoidably and unpredictably affect populations within a community from reverberating throughout the community and causing its collapse. Community-level (relative) stability is therefore largely a product of the self-serving behaviors of individual animals. This kind of "invisible hand" explanation for community stability indeed recalls theorizations of market economies as achieving some kind of self-regulation. As remarked by critics of those theorizations, this kind of self-regulation can plausibly be only weak, one which contrasts with the kind of self-regulation that characteristically occurs in individual organisms (Huxley 1911 [1871]; d'Hombres 2012).³⁰

²⁹ This mode of regulation is commonly called "switching" or "prey switching" by contemporary ecologists (see, e.g., Murdoch 1969).

 $^{^{30}}$ The contrast between strong and weak regulation I am evoking here is partly inspired by d'Hombres (2012, sec. 4). Unlike d'Hombres, however, I do not restrict *strong* regulation to regulation involving some kind of centralized control exerted on the parts by the whole. I instead cast the contrast as one between

Hence, Elton's views on community self-regulation, like his views on communities' part-whole integration discussed in section 4.2, illustrate his espousal of a *moderate* ecological holism, one reflective of his preference for sociological over organicist ecological analogies.

5. Conclusion

In the preceding sections, I argued that Elton's ideas on animal communities led him to espouse a moderate ecological holism, one that reflects his preference for sociological over organicist ecological analogies, and which offers a middle way between the stricter ecological holism advocated by organicist ecologists and the merely aggregationist views to which they are commonly opposed. First (in section 2), I discussed Elton's introduction of a functionalist-interactionist approach to animal ecology, which shifted away from the more classificatory and habitat-focused approach of his predecessors. Second (in section 3), I showed how this functionalist-interactionist approach and its focus on feeding and regulatory interactions between populations of animals led Elton to espouse a view of communities as *functionally organized wholes* formed of *functionally* interdependent populations. Third (in section 4), I discussed how Elton's views on communities must be situated with respect to those of prominent twentieth-century organist ecologists. I showed (in section 4.1) how Elton's ideas on populations' functional interdependence were incorporated by organicist ecologists Clements and Shelford (1939) and Allee et al. (1949) into their views, but then (in sections 4.2 and 4.3), I exposed how Elton's views nevertheless significantly diverged from theirs. Specifically, I argued that Elton's ideas on species distribution, animal migrations, and ecological succession entailed a view of animal communities as exhibiting a degree of part-whole integration more in line with the views of Clements and Shelford's "individualistic" opponent Henry Gleason (1917, 1926). Moreover, I argued that Elton's mixed stance on the balance of nature idea and his explanations of community stability based on uncoordinated animal interactions attributed to communities a weak form of selfregulation that diverged from the stronger form attributed to them by Allee et al. (1949). In parallel to this, I maintained that, in line with Elton's preference for sociological over organicist analogies, the weak degree of part-whole integration and the weak kind of selfregulation he attributed to ecological communities were more consistent with analogies between ecological communities and human societies than between them and individual organisms.

In closing, I wish to highlight a possible implication of the above discussion for the more general interpretation of the history of the holism/reductionism opposition in ecology. This implication concerns the significance of the demise of Clements's and Allee et al.'s organicist ecological ideas in the 1950s and 1960s. As documented by historians of ecology, ecologists of the second part of the twentieth century became skeptical about organicist ecological ideas. Their skepticism, as historians report, resulted, in part, from John Curtis's continuum and Robert Whittaker's gradient analyses of species distributions, which seemed to confirm Gleason's ecological ideas (see

regulation achieved by regulative factors whose behavior has been coordinated by past natural selection, on the one hand, and regulation that arises from the uncoordinated behavior of a system's freely interacting parts, on the other.

McIntosh 1975, pp. 264–266; Nicolson 1990, pp. 149–151), and, in part, from George Williams's (1966) influential critique of multilevel selection (see Gibson et al. 2013, pp. 518–520; Huneman, this issue). Although it is true that ecologists' use of organicist analogies waned in the second part of the twentieth century, the above discussion suggests that Curtis and Whittaker's analyses (Curtis and McIntosh 1951; Whittaker 1967) and Williams's critique of multilevel selection did not downrightly disqualify holistic ecological ideas.³¹ As seen above, Elton's moderate ecological holism readily acknowledged the Gleasonian idea that species are, for the most part, independently distributed across landscapes. Moreover, Elton's holism was *not* grounded in community-selectionist ideas. The kind of ecological holism held by Elton thus seems to remain untouched by Curtis and Whittaker's analyses and Williams's critique of multilevel selection.

It is often observed that, in the second part of the twentieth century, ecosystem ecologists like Eugene Odum conceived their ecological approach as holistic and advocated views of ecosystems as functionally organized wholes (as Elton did). At the same time, it is also often questioned whether their approach was truly holistic, in part given the marked differences between their views and those of earlier organicist ecologists (see Hagen 1992, Chapters 6–7; Bergandi 1995, 2011). Elton's known influence on the development of ecosystem ecology invites the conjecture that the seeming ambivalence of Odum and other early ecosystem ecologists' ideas as regards the holism/reductionism polarity may in part be explained by their endorsement of a hybrid kind of ecological holism similar to Elton's. The full exploration of this conjecture, however, must be deferred to future works.

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³¹ It should also be mentioned that, although I here grant, for the sake of the argument, that Curtis and Whittaker's studies and Williams's critique of multilevel selection disqualified the kinds of ecological holism respectively endorsed by Clements and Allee et al., one may question whether this really is the case. For criticisms of Whittaker, see Leibold and Mikkelson (2002) and Wilson et al. (2004); for a partial rehabilitation of community-level selection, see Wilson and Sober (1989).

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