

# Functional Ecology's Non-Selectionist Understanding of Function

---

Antoine C. Dussault (CIRST, Collège Lionel-Groulx)

## Abstract

This paper reinforces the current consensus against the applicability of the selected effect theory of function in ecology. It does so by presenting an argument which, in contrast with the usual argument invoked in support of this consensus, is not based on claims about whether ecosystems are customary units of natural selection. Instead, the argument developed here is based on observations about the use of the function concept in functional ecology, and more specifically, research into the relationship between biodiversity and ecosystem functioning. It is argued that a selected effect account of ecological functions is made implausible by the fact that it would conflict with important aspects of the understanding of function and ecosystem functional organization which underpins functional ecology's research program. Specifically, it would conflict with (1) Functional ecology's adoption of a context-based understanding of function and its aim to study the functional equivalence between phylogenetically-divergent organisms; (2) Functional ecology's attribution to ecosystems of a lower degree of part-whole integration than the one found in paradigm individual organisms; and (3) Functional ecology's adoption of a physiological or metabolic perspective on ecosystems rather than an evolutionary one.

**Keywords:** functional biodiversity; function; biodiversity; ecosystem function; biological individuality; superorganism.

## 1. Introduction

In the recent years, the notion of *functional biodiversity* has become increasingly important in ecology. This is particularly the case in the *biodiversity and ecosystem function research* program (or BEF research, for short), a field of ecological research which studies the effects of biodiversity on the functioning of ecosystems (Chapin et al., 1997, 2000; Naeem, 2002; Hooper et al., 2005; Loreau, 2010a, 2010b; Tilman, Isbell, & Cowles, 2014). BEF research aims to achieve a synthesis of the two traditionally isolated ecological subfields of *community* and *ecosystem* ecology, and of their respective concerns for the distribution and abundance of species interacting in particular environments (i.e. biodiversity) and for the ecosystem processes (e.g. biomass productivity, cycles of nutrients and flows of energy) which arise from those interactions (i.e. ecosystem functioning). To this aim, BEF researchers develop ways to classify organisms into *functional groups* or *types*, on the basis of similarities of potential contributions to ecosystem processes. Many BEF researchers claim that this synthesis, besides being a significant scientific achievement, is of critical societal importance given the many benefits that humans derive from well-functioning ecosystems (Naeem, 2002, p. 1540; Loreau, 2010b, p. 51; Laureto, Cianciaruso, & Samia, 2015, p. 113).

A key concept at the interface of these domains of inquiry, and which underlies the classification of organisms into *functional groups* or *types*, is that of *ecological function* (e.g. K. W. Cummins, 1974; Lavorel & Garnier, 2002; Hooper et al., 2002). In BEF research, the ascription of functions to organisms and other biodiversity items serves as a conceptual bridge between the traits of those biodiversity items and their contribution to ecosystem processes (Petchey & Gaston, 2006, pp. 750–752; Nunes-Neto, Do Carmo, & El-Hani, 2016, p. 299). BEF research thus looks at how the particular traits (structural, phenological, behavioral, etc.) of organisms explain their potential contributions to ecosystem processes, such as biomass productivity, nutrient cycling, energy flows, and so on (Naeem, 2002, p. 1539; Loreau, 2010b, p. 51). Such a linkage of traits to ecosystem processes aims to improve upon the more abstract “black box” approach characteristic of classical ecosystem ecology, which tended to disregard the identity of the species involved in ecosystem processes on the assumption that most ecological functions could be performed by many different species (Hagen, 1992, pp. 90–98, 103–106; Cooper, 2003, pp. 48–49).<sup>1</sup>

While the concept of function has been widely discussed in the philosophy of biology (for reviews, see McLaughlin, 2001; Wouters, 2005; Garson, 2016), only a few recent discussions have been devoted to the concept as it is used in ecology (Maclaurin & Sterelny, 2008, sec. 6.2; Odenbaugh, 2010, sec. 3; Gayon, 2013, sec. 5; Nunes-Neto, Moreno, & El-Hani, 2014; Dussault & Bouchard, 2017; Cooper, El-Hani, & Nunes-Neto, 2016). Nonetheless, a consensus emerges in those discussions, according to which one of the most advocated philosophical theories of function, namely the *selected effect* theory, is poorly suited for accounting for the concept of function as it is used in ecology (see Nunes-Neto, Moreno, & El-Hani, 2013). The commonly invoked argument in support of this view is the following: insofar as, on the one hand, the selected effect theory of function can only apply to the traits or parts of entities which are targets of natural selection, and on the other hand, ecosystems are not customary units of natural selection, then the selected effect theory cannot account for the ascription of functions to organisms conceived as parts of ecosystems. This argument thus draws on the well-known criticism of group selection (Maynard-Smith, 1964; Williams, 1966) and contemporary biology’s ensuing adoption of an individualistic take on natural selection.

The aim of this paper is to reinforce the current consensus by presenting an additional, and I think more fundamental, argument against the applicability of the selected effect theory of function in ecology. This argument is based on the theoretical practice of functional ecologists and more particularly on that of BEF researchers. I maintain that a selected effect account of ecological functions would be at odds with the very understanding of the function concept as it is used in ecology and BEF research.<sup>2</sup>

---

<sup>1</sup> In this paper, I will assume an understanding of the notions of ecological community and ecosystem as characterizing complementary *perspectives* on the same (multispecies) level of organization rather than as denoting *distinct* levels (see Hutchinson, 1978, pp. 214–215; Hagen, 1989; Callicott, Crowder, & Mumford, 1999, pp. 23–25). As I will argue in section 3.3, the *functional* perspective which ascribes functions to organisms within multispecies assemblages is more characteristic of ecosystem ecology than of community ecology. Thus, in what follows, my primary focus will be on the ascription of functions to organisms within *ecosystems*.

<sup>2</sup> It should be noted that, in the present paper, I will focus on the notion of function underlying what functional ecologists refer to as *functional effect traits*, in contrast to *functional response traits* (Catovsky,

While, as I will later highlight, the usual argument against the applicability of the selected effect theory of function in ecology is ultimately an empirical one which hinges upon the empirical question of whether natural selection customarily operates at the level of ecosystems, the argument I develop below is conceptual. What I argue is that the epistemic aims for which the function concept is used in ecology and the view of ecosystem functional organization associated with this use involve an understanding of function with which a selected effect account would conflict.

Importantly, as I will emphasize, my argument does not hinge on whether or not ecosystems are customary units of natural selection. This independence from issues regarding levels of natural selection is significant, given the fact that, as I will highlight, the view that natural selection can operate at supraorganismic levels has been partly rehabilitated in the last decades. This partial rehabilitation results mainly from Wilson and Sober's collaborative work on multilevel selection, which identifies environmental conditions under which natural selection can realistically occur at the level of groups and multispecies assemblages (see e.g. Wilson & Sober, 1989; Sober & Wilson, 1998). Thus, in contrast to the usual argument against the adoption of a selected effect account of ecological functions, the argument I develop below does not hinge on issues regarding levels of selection and would retain its cogency no matter how prevalent community and ecosystem selection may turn out to be.

My discussion will be organized as follows. In section 2, I will discuss the usual argument against the adoption of a selected effect account of ecological functions. I will contend that this argument is less straightforwardly compelling than has been assumed when one considers Wilson and Sober's partial rehabilitation of the idea that natural selection can operate at the level of multispecies assemblages. In section 3, I will develop an alternative argument against the adoption of a selected effect account of ecological functions, which is based on the practice of functional ecologists rather than on claims about levels of selection. First, I will argue (in section 3.1) that a selected effect account of ecological functions would conflict with the context-based understanding of function adopted by functional ecologists and BEF researchers and with their aim of studying the functional equivalence between phylogenetically and taxonomically divergent organisms. Second, I will argue (in section 3.2) that a selected effect account of ecological functions would entail a view of ecosystems as exhibiting a degree of part-whole integration comparable to that found in paradigm individual organisms (i.e. a view of ecosystems as superorganisms), which conflicts with functional ecologists' more communitarian picture of ecosystem-level functional organization. Third, I will argue (in section 3.3) that a selected effect account of ecological functions would entail a view of ecosystems as evolutionary individuals (i.e. as units of natural selection), which conflicts with functional ecologists' more metabolic understanding of the individuality of ecosystems. In section 4, I will turn to the suggestion made by many proponents of the usual argument against the adoption of a selected effect account of ecological functions that the ecological function concept should instead be interpreted through the prism of

---

1998; Hooper et al., 2002; Jax, 2010, pp. 54–55). Insofar as the former are concerned with the *roles* that organisms fulfill within ecosystems, they are the ones most directly relevant to BEF research. The latter underlie classifications of organisms in terms of their ability to thrive in various environmental contexts and so are more directly relevant to community ecology's aim of explaining species distributions.

Cummins's (1975) alternative *causal role* theory of function. The extent to which the observations made in section 3 reinforce this suggestion will be briefly discussed.

## 2. The usual argument against selected effect ecological function

As mentioned in the introduction, a consensus has emerged among philosophers of ecology to the effect that the selected effect theory of function cannot adequately account for ecological functions. The commonly invoked argument in support of this view is that insofar as the selected effect theory of function can only be applied to the parts or traits of biological entities which are units of natural selection, a selected effect account of ecological functions would require that some of the traits of organisms within ecosystems be shaped by natural selection operating at the level of ecosystems (Maclaurin & Sterelny, 2008, p. 114; Odenbaugh, 2010, pp. 250–251; Gayon, 2013, pp. 76–77; Cooper et al., 2016, pp. 111–112). A selected effect account of ecological functions would therefore rest on the assertion that ecosystems are customary units of natural selection. Yet, although many classical community and ecosystem ecologists explicitly committed to the view that natural selection commonly operates at community and ecosystem levels (e.g. Tansley, 1935; Allee, Emerson, Park, Park, & Schmidt, 1949, Chapter 35; Dunbar, 1960, 1972; Odum, 1971), this view has lost favor among contemporary biologists and ecologists (see e.g. Whittaker, 1975, Chapter 8; Harper, 1977; May, 1978). This loss of favor, partly results from Maynard-Smith (1964) and Williams's (1966) influential critiques of group selection, which have convinced many biologists and ecologists that natural selection primarily operates at the level of individual organisms (see Hagen, 1992, Chapter 8; DeLaplante & Picasso, 2011, p. 184). Accordingly, MacLaurin and Sterelny (2008, p. 114) observe:

[L]ocal [ecological] assemblages do not have selective histories. They are not part of lineages. Communities are not elements of a population of competing communities, and they do not have daughter communities that resemble their parents. If a selective history is necessary for communities to have organization or structure [as stated by the selected effect theory], then most assemblages of populations are not [functionally organized] ecological systems.

On those grounds, MacLaurin and Sterelny, as well as other philosophers of biology and ecology, propose that ecological functions should be interpreted through the prism of Cummins's (1975) alternative *causal role* theory of function (Maclaurin & Sterelny, 2008, pp. 114–115; Odenbaugh, 2010, pp. 251–252; Gayon, 2013, pp. 76–77).

At first glance, this argument appears compelling. If the selected effect theory of function can only be applied to the parts or traits of entities which are units of natural selection, and if natural selection primarily operates at the level of individual organisms (rather than that of groups, communities or ecosystems), then the selected effect theory of function seems inapplicable to organisms envisioned as parts of ecosystems. However, it must be remarked that the issue of whether natural selection does or does not customarily operate at the level of ecosystems is ultimately an empirical one. This remark is made particularly important by the fact that significant work has been done in defense of natural selection at supraorganismic levels since the publication of Maynard-Smith and Williams's criticism. In particular, David Sloan Wilson and Elliott Sober have shown, in their collaborative work on multilevel selection, that the classical arguments against supraorganismic selection rested on an unrealistic assumption (Wilson & Sober, 1989;

Sober & Wilson, 1998; see also Wilson, 1980, 1992, 1997). Specifically, the assumption is that individual organisms within populations interact randomly with each other such that they have equal chances of mating with any other member of their population. In practice, however, Wilson and Sober emphasize, the heterogeneity of many environments makes it the case that individual organisms regularly interact only with a subset of their population. Such population structure, they persuasively explain, creates conditions which make it likely for populations and multispecies assemblages to evolve as unified wholes.

According to Wilson and Sober (1989, pp. 348–349), a paradigm case of community-level natural selection made possible by environmental heterogeneity is that of *phoretic associations*: communities formed by a winged insect and many wingless organisms (such as mites, nematodes, fungi and microbes) that are transported from one resource patch to another by it. When the winged insect reaches a resource patch (e.g. carrion, dung, or stressed timber), it carries a whole community of phoretic associates, which then pursue their free-living existence within the patch. Such a phenomenon, they emphasize, creates conditions that make it possible for natural selection to operate at the level of phoretic communities as a whole (Wilson & Sober, 1989, pp. 348–9). And besides phoretic communities, Wilson (1997, pp. 2020–2022) discusses other likely cases of community selection made possible by environmental heterogeneity, as well as a likely case of natural selection operating on populations of micro-ecosystems forming at the surface of lakes and oceans.<sup>3</sup> In the recent years, Wilson and Sober’s take on community and ecosystem selection has been embraced by many prominent ecologists (e.g. Johnson & Boerlijst, 2002; Loreau, 2010a, Chapter 8), which indicates that community and ecosystem selection are no longer anathema in the field.

Wilson and Sober’s work on multilevel selection seems to make the selected effect theory of function more easily applicable to organisms envisioned as parts of communities and ecosystems than is commonly assumed (see Basl, 2017). Wilson and Sober themselves speak as if their work on multilevel selection also legitimizes the view that at least some communities and ecosystems (those which meet the conditions for being units of natural selection) constitute *functionally organized* entities (Wilson & Sober, 1989, pp. 345, 349; see also Wilson, 1997). They even conceive their work as rehabilitating (to some extent) the view that some multispecies constitute genuine *superorganisms* (Wilson and Sober 1989, p. 349). To be sure, Wilson and Sober (1989, pp. 343, 351–352) also caution that they conceive their approach to multilevel selection as vindicating only a moderate form of ecological functionalism. And accordingly, they distance their work from the claims made by classical ecosystem ecologists and Gaia theorists (e.g. Odum, 1969; Lovelock, 1979; Margulis, 1981) who ascribe “functional design” to ecosystems in general and even to the biosphere as a whole. Nevertheless, a key implication of Wilson and Sober’s work is that community and ecosystem selection are no longer utterly improbable for theoretical reasons, and are even likely to occur (mixed with some degree of individual selection) in heterogeneous environments.

---

<sup>3</sup> See also Swenson, Arendt and Wilson (2000), and Swenson, Wilson and Elias (2000) for discussions of artificial ecosystem selection experiments.

Those observations make the usual argument against the applicability of the selected effect theory of function in ecology less straightforwardly compelling. On the assumption that natural selection could only very rarely operate at ecosystem levels, adopting a selected effects account of ecological functions would have had implausibly revisionist implications. It would have implied that the practice of ecologists which consists in ascribing functions to organisms within ecosystems is for the most part misguided, given the fact that only few of the function ascriptions formulated by ecologists could be expected to involve traits of organisms that result from natural selection operating at the ecosystem level. I take it that such revisionism would make a selected effect account of ecological functions a non-starter. However, if community and ecosystem selection can be presumed to be more common, a selected effect account of ecological functions seems less unwarrantedly revisionist. This is because if community and ecosystem selection are more common, then adopting a selected effect account of ecological functions (i.e. an account which maintains that such functions can be ascribed only on the basis of organismic traits which result from community or ecosystem-level selection) would require one to exclude less of the function ascriptions formulated by ecologists. This would make it more conceivable for proponents of a selected effect account of ecological functions to maintain that among the function ascriptions formulated by ecologists, only those which involve traits that were shaped by ecosystem-level selection must be embraced while others must be excluded. Thus, although Wilson and Sober's work on multilevel selection does not in itself constitute a vindication of a selected effect account of ecological functions, I contend that it substantively weakens the usual argument against such an account.

For this reason, I think that it is relevant to consider an alternative, and I think more fundamental, argument against adopting a selected effect account of ecological functions. This argument rests on observations about the practice of functional ecologists, which indicate that a selected effect account of ecological function would be at odds with the understandings of the concepts of ecological function and ecosystem functional organization that underpins this practice. This argument is thus *conceptual*—in contrast to the usual argument, which, as seen above, hinges on the ultimately empirical question of whether natural selection customarily operates at the level of ecosystems. It focuses on the *meaning* of the function concept as it is used in functional ecology and BEF research. If sound, this argument entails that the question of whether natural selection does or does not customarily operate at the level of communities and ecosystems has little bearing on the question of whether a selected effect account of ecological functions should or should not be adopted.

Thus, in section 3, I will review salient aspects of the use of the function concept in functional ecology and BEF research. I will argue that this use involves an understanding of the concept which conflicts with central implications of a selected effect account.

### **3. The concept of function as used in ecology**

#### ***3.1 Ecological functions as contextual properties***

The origin of the standard ecological understanding of function can be traced back to the renowned community ecologist Charles Elton's (1927) picture of biotic interactions

in ecological communities as being analogous to economic exchanges in human societies. More specifically, this use derives from Elton's concept of *ecological niche*, which he defined as "the status of an animal in its community, [...] what it is *doing*," (Elton, 1927, p. 63, italics original), and which is often depicted as an organism's "profession" within a community or ecosystem (e.g. Odum, 1953, p. 15). This concept is commonly referred to as an organism's "functional niche" to emphasize its focus on an organism's *ecological role* and to contrast it with Grinnell's (1917) "habitat niche" concept which focuses on an organism's requirements.<sup>4</sup>

For Elton and his followers, the main theoretical import of the niche concept lay in how it allowed ecologists to identify similarities between organisms from the perspective of their "*relations to food and enemies*" rather than on the basis of similarities pertaining to their "appearance, names, affinities, *and past history*." (Elton, 1927, p. 64, italics added) In other words, the niche concept served to study how phylogenetically divergent organisms could occupy similar places in communities (primarily conceived as food webs). For instance, Elton remarked that the arctic fox, which subsists on guillemot eggs and seal remains left by polar bears, occupies the same niche as the spotted hyæna in tropical Africa, which feeds upon ostrich eggs and zebra remains left by lions.

Contemporary functional ecologists and BEF researchers refer to such niche similarities between species as their *functional equivalence*—thereby characterizing what organisms do within their community or ecosystem as their *function* within it. BEF researchers' interest in functional equivalence, however, is motivated by a research program different from the one pursued by Elton. For Elton, the study of niche similarities between phylogenetically divergent organisms was tied to the aim of identifying invariances of structure among communities composed of organisms belonging to different species (see Pocheville, 2014, pp. 549–550). In BEF research, in contrast, the notion of functional equivalence is more primarily associated with the project of explaining and comparing the various contributions of organisms to the functioning of the ecosystems they are part of (see e.g. K. W. Cummins, 1974; Lavorel & Garnier, 2002; Hooper et al., 2002). Thus, BEF researchers group organisms according to how their traits enable them to achieve particular contributions to ecosystem processes (e.g. biomass productivity, the cycling of carbon, nitrogen and other nutrients, etc.). In doing so, they aim to develop ways to explain and predict how changes in the species composition of ecosystems may affect the various dimensions of their functioning. Nevertheless, as was the case for Elton, those classifications are not conceptually based on phylogeny and may, in practice, significantly diverge from phylogeny-based ones (see Blondel, 2003, pp. 226–227).

The dissociation of the ecological concept of function from evolutionary history is made explicit by many BEF researchers. For instance, Grimm (1995, p. 8) notes that although the use of the concept of function in ecology may foster miscommunication among ecologists owing to the fact that "a term such as 'function' implies to some an evolutionary origin, which must therefore imply operation of natural selection at supraorganismic levels," the term "remains a useful term for describing what a system

---

<sup>4</sup> For discussions of ecological niche concepts, see Schoener (1989), Griesemer (1992), Leibold (1995), and Pocheville (2015).

does in the context of its surroundings.” Likewise, Petchey and Gaston (2006, p. 742) state that “[f]unctional diversity [in ecology] generally involves understanding communities and ecosystems based on what organisms do, rather than on their evolutionary history” (see Nunes-Neto et al., 2013, p. 50, for a discussion).

This grounds a first important observation about the ecological understanding of function. The notion of functional equivalence at play in functional ecology involves an understanding of ecological functions as *contextual* properties which depend upon an organism’s *actual* or *potential* interactions with other organisms. This contrasts with evolutionary biology’s understanding of functions as *historical* properties which depend on an organism’s selective history as in the selected effect account (see Brennan, 1988, Chapter 8). Functional ecology’s context-based understanding of functions is aptly captured by Jax (2010, p. 79):

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.

It is easy to see that a selected effect account of ecological function would conflict with this context-based understanding of function and the associated aim of studying functional equivalence, in that it would imply that two organisms can be functional equivalents only to the extent that their functional traits evolved in similar selective contexts.

The above indicates that, functional ecology ties the function concept to a different epistemic aim than the one pursued by evolutionary biology. Whereas evolutionary biology primarily uses the function concept as a conceptual tool for distinguishing genuine adaptations—i.e. selected effects—from selectively neutral traits which are “mere by-products” of naturally selected traits (Williams, 1966; Gould & Vrba, 1982), such a distinction does not matter for functional ecology. If two organisms have traits that enable them to contribute in a similar way to some ecosystem process, while the first organism’s trait was selected for this contribution and the second organism’s trait was not, the two organisms will still count as functional equivalents from the perspective of functional ecology. It simply does not matter for the purposes of functional ecology whether a trait is a selected effect or whether it is an evolutionary by-product. Thus, insisting on ascribing ecological functions to organisms strictly on the basis of traits that are selected effects would impose upon functional ecology an understanding of function which is at odds with its research program. It would impose an understanding of function which, on the one hand, is tied to an epistemic aim that is foreign to its research program (i.e. that of distinguishing adaptations from evolutionary by-products); and which, on the other hand, is incompatible with the epistemic aim that is central to its research program (i.e. that of studying functional equivalence between taxonomically divergent organisms).

Functional ecology's context-based understanding of function can be illuminated by considering Achinstein's (1977, pp. 350–356) delineation of three distinct function notions in ordinary language: *design*, *use* and *service* functions. An entity's *design* functions consist in what this entity was *designed* or *created* to do (e.g. the function of a mouse trap is to catch mice); whereas an entity's *use* and *service* functions consist, respectively, in what it is *used for* (e.g. this table is used for sitting) and what it *serves as* (e.g. a watch's second hand serves as a dust sweeper). Assuming that natural selection is what characteristically designs biological entities, the selected effect theory of functions can, in light of Achinstein's triad, be conceived as concerned with *design* functions.<sup>5</sup> In contrast, I submit that the concept of function as it is used in ecology more typically denotes *use* and *service* functions. For instance, in an ecological context, a rabbit can be *used as* food by a fox and so acquire a *use function* with respect to the fox. The fox may in turn, through such an interaction, acquire a *service function* with respect to the overall community as a regulator of the rabbit population. Insofar as those use and service interactions are what primarily determines the ways in which nutrients and energy will flow within the ecosystem formed through those interactions, those interactions also confer functions to the rabbit and the fox within their ecosystem. In contrast to *design* function ascriptions, such use and service function ascriptions neither imply that the rabbit has evolved to be food for the fox, nor that the fox has been designed by natural selection to regulate the rabbit population. Thus, Achinstein's triad illuminates how the ecological use of the function concept involves notions of function that are distinct from the one that the selected effect theory is meant to elucidate.

### **3.2 Ecosystems not as superorganisms**

The aforementioned clarifications about functional ecology's contextual use of the function concept lead to a second important observation about its understanding of the concept: that functional ecology's research program is underpinned by a view of communities and ecosystems as exhibiting a lower degree of part-whole integration than the one found in paradigm individual organisms. This is significant given the fact that since the 1950s, ecological theorizing has steered away from views of communities ecosystems in strong analogy with individual organisms (commonly associated with the work of Frederic Clements 1916, 1936) (see McIntosh, 1975; Barbour, 1996).<sup>6</sup>

An intuitive feature of paradigm individual organisms seems to be their remarkable *teleological integration*. That is, the fact that their parts seem, in some biologically relevant sense, to be *designed* for achieving their function within the organism as a whole and to achieve their functional activities *for the sake of* the organism as a whole (this feature of organisms is emphasized by Queller & Strassmann, 2009, p. 3144; see also Strassmann & Queller, 2007, p. 8619). For instance, saying that the function of the heart within organisms is to pump blood does not merely amount to saying that hearts typically contribute to the overall functioning of organisms by pumping their blood. It also involves asserting that, in some biologically relevant sense, hearts are biologically *designed* for pumping blood and that they achieve their pulsing activities within

---

<sup>5</sup> This suggestion is reinforced by some selected effect theorists' explicit association of function with design (see e.g. Williams, 1966, p. 9; Millikan, 1984, p. 17).

<sup>6</sup> See however Eliot (2007, 2011) for reexaminations of received interpretations of Clements's ecology.

organisms *for the purpose* of pumping blood. On prominent biological understandings, such teleological notions are understood in natural selectionist terms, such that being biologically designed for some function amounts to having been shaped by natural selection for fulfilling this function (i.e. to have this function as a *selected effect* function).

Functional ecology's picture of ecosystems as *functionally organized* (i.e. as composed of parts (mainly organisms) which achieve functions within them) does not entail a view of ecosystems as being *teleologically integrated* in the same way. The fact that ecological functions frequently are use and service functions (and that, accordingly, organisms may have ecological functions on the basis of traits that are evolutionary by-products) entails that organisms are not conceived by functional ecologists to do what they do within ecosystems *for the sake of* fulfilling ecological functions. This is made explicit by some BEF researchers. Schulze and Mooney (1993, p. 500), for instance, remark: "Species are not purposely "put" into a certain position of an ecosystem [...], but species become established in habitats or ecosystems if the conditions (including competition) are suitable for growth." Thus, as conceived by functional ecologists, organisms establish themselves within ecosystems as a result of the local environment's providing favorable biotic and abiotic conditions rather than because of the functions they are meant to fulfill within them. Once established, they may then acquire ecological functions through being involved in use and service interactions with other organisms.

In this respect and in contrast to what would be entailed by a selected effect account of ecological functions, functional ecology ascribes to ecosystems a lower degree of part-whole integration than the one found in paradigm individual organisms. In line with Elton's picture of biotic interactions in ecological communities as analogous to economic exchanges in human societies, functional ecology adopts a picture of ecosystem functional organization in stronger analogy with the interdependence of professions within human communities than with that of organs within individual organisms (see Jax, 2010, pp. 78–81, for a discussion). Thus, at variance with Wilson and Sober's linkage of multispecies-level functional organization with superorganismality, functional ecology's understanding of ecosystem-level functional organization does not entail a view of ecosystems in strong analogy with paradigm individual organisms.

### ***3.3 Functional ecology as ecosystem-level physiology***

This brings us to a third important observation about the ecological use of the function concept. This third observation concerns functional ecology's historical connection with the biological sub-discipline of *physiology*, and BEF research's epistemic aim of explaining ecosystem processes on the basis of the particular contributions of the organisms which participate in them. This observation has implications for the kind of "biological individuality" functional ecologists attribute to ecosystems.

The historical connection between functional approaches to ecology and the biological sub-discipline of *physiology* can be illuminated by considering how ecosystem ecology emerged (in the work of Hutchinson, Lindemen and the Odum brothers) through the combination of Elton's economic picture of ecological communities with elements of

Clements's (1916, 1936) and Tansley's (1935) ecological thinking. In contrast to Wilson and Sober's more recent superorganism theory discussed in section 2, Clements's analogy between ecological communities and individual organisms was motivated by a project to extend the methods of *physiology* to the study of communities (Hagen, 1988, 1992, Chapter 2). Clements sought to understand how communities as a whole have the ability to respond adaptively to the changes that occur in their environment (in a way similar to how individual organisms are able to physiologically accommodate environmental variations). As is well-known, the more rigid aspects of Clements's superorganismic thinking were criticized by his contemporaries Gleason (1926) and Tansley (1935), leading Tansley to introduce the less contentious term *ecosystem* to denote the alleged multispecies-level entities studied by Clements.

Tansley's terminological proposal made it possible for founding ecosystem ecologists Lindeman (1942) and Hutchinson (1948) to draw on Clements's idea of a community-level physiology while giving up its more rigid aspects. Lindeman and Hutchinson also moved from Clements's study of the *external* physiology of multispecies assemblages (i.e. the study of how they accommodate environmental variations) to the study of their *internal* physiology. As Hutchinson (1940, p. 268, italics added) reasoned, commenting on Clements's ideas, "[i]f, [...] the community is an organism, it should be possible to study the *metabolism* of that organism." Through the pioneering work of Hutchinson's student Lindeman (1942), whom historians acknowledge as the first ecologist to fully exploit the potential of Tansley's ecosystem notion (McIntosh, 1985, p. 196; Hagen, 1992, pp. 78–79), this metabolic study became the focus of the new sub-discipline of ecosystem ecology. Henceforth, ecosystem ecologists conceived their discipline as being oriented towards the study of the *metabolism* of multispecies assemblages (Hagen, 1992, Chapters 4–6).

As Hagen (1992, Chapters 4–5) highlights, Elton's economic picture of ecological communities ascribing functions to species within food webs was a key insight for founding ecosystem ecologists, in that their theories were essentially reformulations of this picture in terms of thermodynamics, biogeochemistry and cybernetics. In Eugene Odum's (1971, pp. 5, 33–35) later work, this metabolic approach came to also be linked to the physiological concept of *homeostasis*, coined by Walter B. Cannon (1926, 1932) and inspired by the French physiologist Claude Bernard (1879). This link emphasized the phenomenon of self-regulation within ecosystems and served as a conceptual basis for the study of the factors that determine it (Hagen, 1992, Chapter 7, 2014).

This physiological or metabolic perspective on multispecies assemblages is what ecologists commonly conceive as the *functional* (or holological) approach characteristic of ecosystem ecology (which was integrated to contemporary BEF research), in contradistinction with the more *compositional* (or mereological) approach adopted in population and community ecology (which is more concerned with explaining species distribution and abundance) (see Hutchinson, 1978, pp. 214–215; Hagen, 1989; Callicott, Crowder, & Mumford, 1999, pp. 23–25). Given the former approach's roots in physiology and the fact that natural selection is more typically relevant to the concerns of the latter, this functional/compositional contrast can, I contend, drawing on Hagen's (1992, pp. 150–151) suggestion, be understood in the broader context of Mayr's (1961)

classical distinction between functional and evolutionary perspectives in biology. As characterized by Mayr, *functional biology* (e.g. physiology, immunology, developmental biology) studies biological entities in a largely ahistorical way and focuses on the *proximal causes* of biological phenomena. It seeks to explain *how* biological entities operate on the basis of the interactions of their parts. In contrast, *evolutionary biology* studies biological entities as evolutionary products and focuses on the *ultimate* causes of biological phenomena. It is concerned with the historical-evolutionary causes that explain *why* organisms are the way they are. As Mayr emphasizes, those two domains of biological inquiry are complementary and, to some extent, autonomous. The functional perspective of ecosystem ecology, I submit, given its physiological take on multispecies assemblages, stands more along the lines of Mayr's *functional* branch of biology. In contrast, I submit that given community and population ecology's aims to explain species distribution and abundance (i.e. *why* species survive and fare well in some environments, but not in others), the compositional perspective on the ecological world adopted by those disciplines stands more along the lines of Mayr's *evolutionary* branch of biology.<sup>7</sup> Consequently, I contend that as studied from the functional perspective of ecosystem ecology, multispecies assemblages are more fundamentally *physiological*, or *metabolic*, entities than evolutionary ones.

This remains the case in the more contemporary approaches adopted in BEF research, which, in their aim to explain ecosystem processes in terms of the functional contributions of biodiversity items, reintroduce compositional considerations into functional ecology (Callicott et al., 1999, pp. 30–31; Naeem, 2002; Loreau, 2010a, 2010b). Although some BEF researchers (e.g. Loreau, 2010a, 2010b) envision a more ambitious synthesis also encompassing evolutionary biology, BEF research remains primarily concerned with explaining ecosystem processes (biomass productivity, nutrient cycling, energy flow) rather than ecosystem evolution. By linking the traits of organisms with potential ecological functions, BEF researchers seek to formulate a *mechanistic* understanding of ecosystem processes (Naeem, 2002, pp. 1540–1543; Petchey & Gaston, 2006), similar to the kind of explanation sought by physiologists. Just like physiologists seek to explain the functioning of the various subsystems of organisms through the ascription of functions to their parts, BEF researchers seek to explain ecosystem processes through ascribing functions to their component organisms. What primarily matters for the kind of mechanistic explanations sought by BEF researchers are the structural, phenological and behavioral properties of biodiversity items rather than their historical-phylogenetic ones. This ahistorical focus on the mechanistic link between community structure and ecosystem function, I submit, locates BEF research within the scope of Mayr's functional biology.

The ecological use of the function concept, therefore, is tied to an understanding of ecosystems as *physiological* rather than *evolutionary* entities. Thus, in contrast to what would be implied by the adoption of a selected effect account of ecological functions, the ecological understanding of function does *not* entail a view of ecosystems as units of natural selection.

---

<sup>7</sup> Though it should be noted that community ecology combines selectionist explanations with explanations that appeal to more proximal factors, such as those posited by niche theory and assembly rules theory (for reviews, see Schoener, 1989, pp. 96–105; Fox, 1999).

Functional ecology's non-evolutionary perspective on ecosystems can be illuminated by connecting it with Godfrey-Smith (2013) and Booth's (2014) recent discussions of biological individuality. Godfrey-Smith and Booth's take on biological individuality contrasts with that of many philosophers of biology who have treated the question of what a biological individual is as if there had to be *one* single answer (see Booth, 2014, pp. 9–10). Those philosophers usually assume that this answer is to be grounded in the theoretical framework of evolutionary biology (e.g. Hull, 1980; Clarke, 2011; Haber, 2013). Godfrey-Smith and Booth instead propose that philosophy of biology needs *two* individuality concepts: *evolutionary individuals* and *metabolic* or *physiological individuals* (see also Dupré & O'Malley, 2009; Pradeu, 2016; Smith, 2017).<sup>8</sup>

Evolutionary individuals delineate biological entities from the perspective of evolutionary biology's aim to explain how populations adapt to their environments through the process of natural selection. On standard understandings of that process, this requires either the identification of evolutionary interactors (i.e. entities which determine the evolutionary success of *replicators*) (Hull, 1980; Lloyd, 2012), or the delineation of *Darwinian individuals* (i.e. entities which are members of populations exhibiting variation and are capable of differentially transmitting their traits through reproduction) (Lewontin, 1970; Godfrey-Smith, 2009).

In contrast to evolutionary individuals, *metabolic individuals*, as conceived by Godfrey-Smith and Booth, delineate biological entities according to the purposes of *non-evolutionary* branches of biology. The main theoretical purpose of those biological subfields, as Godfrey-Smith (2013, pp. 25–26) and Booth (2014, pp. 14–15) specify, consists in formulating mechanistic understandings of the global capacities of biological entities on the basis of the contributions of their parts, along the lines of the recent work on mechanisms in the philosophy of science (Machamer, Darden, & Craver, 2000; Craver & Darden, 2013). Insofar as the mechanistic understandings formulated in those biological subfields can be elaborated without considering the evolutionary history of biological entities, those subfields' underlying notion of individuality is conceptually autonomous from evolution. Further discussion would be required to identify constitutive features of metabolic or physiological individuality—counterparts to replicator-interactor relation for replicators, or population membership, variation, and differential transmission of traits for Darwinian individuals—but plausible contenders Godfrey-Smith and Booth's discussions lean towards are: 1) Functional interdependence of parts; 2) homeostatic regulation; and 3) self-maintenance. Those features, I submit, apply to some relevant degree to ecosystems as conceived by functional ecology. Thus, I contend that functional ecology conceives ecosystems, *not* as *evolutionary individuals* (i.e. as units of selection), as would be implied by a selected effect account of ecological functions, but as *metabolic individuals*.

---

<sup>8</sup> It should be noted that Godfrey-Smith and Booth use the term “organism” to refer to biological individuals as understood from the theoretical perspective of functional ecology, and thus speak of a contrast between evolutionary individuals and *organisms*. For the sake of terminological consistency with my above restriction of the term “organism” to biological entities whose parts are teleologically integrated and my above observation that ecosystems as conceived by functional ecology do not exhibit such degree of part-whole integration (see section 3.2), I prefer using the terms “physiological individual” and “metabolic individuals” to refer to Godfrey-Smith and Booth's “organisms”.

To summarize, this section has made three important observations, which indicate that a selected effect account of ecological functions would conflict with the ecological understanding of the function concept and of the idea of ecosystem-level functional organization. Those observations are:

- 1) That functional ecology adopts a context-based understanding of the function concept, which is associated with the epistemic aim of studying ecological-functional equivalence between phylogenetically divergent organisms. This context-based understanding conflicts with the historical understanding implied by a selected effect account.
- 2) That functional ecology attributes to ecosystems a lower degree of part-whole integration than the one found in paradigm individual organisms, which is more comparable to that found in human economic communities. This communitarian picture conflicts with the superorganismic picture of ecosystems implied by a selected effect account.
- 3) That functional ecology adopts a metabolic perspective on ecosystems, which more appropriately locates ecosystem ecology and BEF research within the scope of Mayr's functional branch of biology than his evolutionary branch. This metabolic perspective entails a view of ecosystems as metabolic individuals, which conflicts with the view of ecosystems as units of selection implied by a selected effect account.

Importantly, those observations are reasons against adopting a selected effect account of ecological functions which do not hinge on the issue of whether or not ecosystems are customary units of natural selection. In this respect and in contrast to the usual argument discussed in section 2 (which, as I argued, is ultimately empirical), those observations offer a *conceptual* argument against the adoption of a selected effect account of ecological functions. The observations made above imply that even if ecosystems turned out to be more frequent targets of natural selection than has been assumed by critics of supraorganismic selection, adopting a selected effect account of ecological functions would still be ill-advised. A selected effect account would impose upon the legitimacy of ecological function ascriptions requirements that run counter to the epistemic aim in relation to which the function concept is used in ecology (i.e. that of studying the ecological-functional equivalence between phylogenetically divergent organisms), and would moreover impose upon functional ecology an evolutionary perspective on ecosystems that is foreign to its theoretical outlook.

#### **4. A causal role account?**

The observations made in section 3 partly reinforce the suggestion that the concept of function as used in ecology should be interpreted through the prism of Cummins's (1975) *causal role* theory of function (Maclaurin & Sterelny, 2008, sec. 6.2; Odenbaugh, 2010; Gayon, 2013). Those observations point to two function-related concepts used in ecology:

- [1] **Ecosystem functioning:** The processes constitutive of an ecosystem's *metabolism* (e.g. primary productivity, energy flow, nutrient cycling).

**[2] Ecological role functions:** The particular contributions of individual organisms and other biodiversity items to ecosystem functioning (as characterized by [1]).<sup>9</sup>

The relationship between those two concepts accords with the explanatory aim assigned to the concept of function in the causal role theory. According to that theory, the ascription of functions to the parts of a system serves to explain how those parts contribute to the activities or capacities of that system as a whole. In this respect, a part's function is its "causal role" with respect to an activity or capacity of the system. Moreover, as mechanism theorists have emphasized (e.g. Craver, 2001), the causal role understanding of functions is the one involved in the elaboration of mechanistic explanations of the activities of systems. Those aspects of the causal role theory concord with BEF researchers' aim to explain ecosystem processes (or ecosystem metabolism) in terms of the particular contributions of ecosystem components to those processes (i.e. explanations of [1] in terms of [2]); and with their hope that those explanations constitute *mechanistic* explanations of ecosystem processes.<sup>10</sup> The relationship between [1] and [2] moreover contrasts with the explanatory aim assigned to the function concept in the selected effect theory (according to which function ascriptions serve to explain the *presence* of their bearers and not the higher level activities of a system they are part of as in the causal role theory and BEF research).

Odenbaugh (2010, p. 251) offers the following formulation of the causal role account of ecological function (where *C* refers to capacities of the system *S* to achieve processes such as those characterized by [1] above):

*Causal role account of ecological function:* The function of *X* in a system *S* is to *F* if, and only if, *X* is capable of *F*-ing and *X*'s capacity to *F* in part accounts for *S*'s capacity to *C*.

For instance, the function of *Rhizobium*, a kind of soil bacteria, in a given ecosystem is to fix nitrogen if and only if *Rhizobium* are capable of fixing nitrogen, and this capacity in part accounts for that ecosystem's capacity to cycle nitrogen (Odenbaugh, 2010, pp. 251–252).

So formulated, however, the causal role account does not explicitly reflect a central theoretical interest of ecosystem ecology and BEF research. Specifically, the interest concerns the conditions by which ecosystems maintain themselves when subject to disturbing factors. This interest is what motivated early ecosystem ecologists' discussions of ecosystem *homeostasis* and the importance they ascribed to studying *feedback mechanisms* within ecosystems (for discussions, see DeAngelis, 1995; Hagen, 2014; Donhauser, 2016). In contemporary ecology, this interest motivates research into the factors that influence the *stability* or *resilience* of ecosystems (e.g. Holling, 1973, 1996; Gunderson & Holling, 2002; for a discussion, see Desjardins, Barker, Lindo, Dieleman, & Dussault, 2015).

---

<sup>9</sup> For an alternative interpretation of the ecological use of the function concept, see Jax (2010, pp. 62–65).

<sup>10</sup> For more details on how a causal role account of ecological function could be used to develop a mechanistic understanding of ecological systems, see Cooper et al. (2016, sec. 4).

In other words, the causal role theory of function focuses, at least explicitly, on how the parts of a system contribute to that system's capacities to *execute* its activities. Ecologists, however, use the function concept to also investigate how organisms conceived as parts of an ecosystem interact in ways that affect the *resilience* of that ecosystem's capacities to execute its activities (i.e. the resilience of ecosystem functioning). This interest in stability and resilience, I contend, would have to be reflected in an adequate account of ecological function. A full discussion of ecological functions in relation to stability and resilience, however, lies beyond the scope of this paper. Thus, I leave it open here whether the importance of stability and resilience could be integrated into the basic structure of a causal role account, or whether their integration requires the formulation of an alternative account.

## 5. Conclusion

In the preceding sections, I reinforced the current consensus against the adoption of a selected effect account of ecological functions by presenting a conceptual argument in favor of this consensus. In contrast to the usual argument invoked in support of this consensus, this conceptual argument does not hinge on the empirical question of whether natural selection customarily operates at the level of ecosystems. It instead identifies ways in which a selected effect account would convey an understanding of the ecological function concept which conflicts with the understanding at play in functional ecology. Specifically, I argued that:

- 1) Functional ecology adopts a context-based understanding of the function concept, which conflicts with the historical understanding implied by a selected effect account.
- 2) Functional ecology adopts a communitarian picture of ecosystem functional organization, which does not entail the kind of superorganismic teleological integration entailed by a selected effect account.
- 3) Functional ecology adopts a metabolic perspective on ecosystems, which conflicts with the view of ecosystems as units of selection implied by a selected effect account.

I then discussed the extent to which those observations support the adoption of a causal *role account* of ecological function. I argued that although the causal role account resonates with BEF researchers' use of the function concept to formulate mechanistic explanations of ecosystem processes in terms of the contributions of ecosystem components, it remains to be seen whether it can also adequately integrate BEF researchers' interest in the study of ecosystem resilience.

Besides reinforcing the current consensus against the adoption of a selected effect account of ecological functions, my hope is that the above discussion has contributed to a better understanding of the epistemic aims in relation to which the function concept is used in ecology.

## Acknowledgements

The author would like to thank Beatrix Beisner, Philippe Huneman, the DC/Maryland History and Philosophy of Biology discussion group, anonymous referees, and various audiences where earlier drafts of this paper have been presented for helpful comments. He also thanks O’Neal Buchanan for kindly polishing his written English. The work for this paper was supported by a postdoctoral grant from the Social Science and Humanities Research Council of Canada (SSHRC) and a research grant from the Fonds de Recherche du Québec – Société et Culture (FRQSC).

## References

- Achinstein, P. (1977). Function statements. *Philosophy of Science*, 44(3), 341–367.
- Allee, W. C., Emerson, A. E., Park, O., Park, T., & Schmidt, K. P. (1949). *Principles of animal ecology*. Philadelphia: Saunders Co.
- Barbour, M. G. (1996). Ecological Fragmentation in the Fifties. In W. Cronon (Ed.), *Uncommon Ground: Rethinking the Human Place in Nature*. New York; London: W. W. Norton & Company.
- Basl, J. (2017). A trilemma for teleological individualism. *Synthese*, 194(4), 1057–1074. <https://doi.org/10.1007/s11229-017-1316-0>
- Bernard, C. (1879). *Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux*. Paris: Baillière.
- Blondel, J. (2003). Guilds or functional groups: does it matter? *Oikos*, 100(2), 223–231. <https://doi.org/10.1034/j.1600-0706.2003.12152.x>
- Booth, A. (2014). On the theoretical roles of biological individuality. In A. Booth (Ed.), *Essays on Biological Individuality* (pp. 5–25). Cambridge, Mass.: Doctoral Dissertation, Harvard University. Retrieved from <https://dash.harvard.edu/handle/1/13070056?show=full>
- Brennan, A. (1988). *Thinking about nature*. Athens: University of Georgia Press.
- Callicott, J. B., Crowder, L. B., & Mumford, K. (1999). Current Normative Concepts in Conservation. *Conservation Biology*, 13(1), 22–35.
- Cannon, W. B. (1926). Physiological regulation of normal states. Some tentative postulates concerning biological homeostasis. In A. Rettit (Ed.), *A Charles Richet. Ses amis, ses collègues, ses élèves*. (pp. 91–93). Paris: Imprimerie des éditions médicales.
- Cannon, W. B. (1932). *The wisdom of the body*. New York: W. W. Norton & company, inc.
- Catovsky, S. (1998). Functional Groups: Clarifying Our Use of the Term. *Bulletin of the Ecological Society of America*, 79(1), 126–127. <https://doi.org/10.2307/20168223>
- Chapin, F. S., III, Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., & Tilman, D. (1997). Biotic Control over the Functioning of Ecosystems. *Science*, 277(5325), 500–504. <https://doi.org/10.1126/science.277.5325.500>
- Chapin, F. S., III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234–242. <https://doi.org/10.1038/35012241>
- Clarke, E. (2011). The Problem of Biological Individuality. *Biological Theory*, 5(4), 312–325.

- Clements, F. E. (1916). *Plant Succession: An Analysis of the Development of Vegetation*. Washington, D.C.: Carnegie Institution of Washington.
- Clements, F. E. (1936). Nature and Structure of the Climax. *Journal of Ecology*, 24(1), 252–284.
- Cooper, G. J. (2003). *The Science of the Struggle for Existence: On the Foundations of Ecology*. Cambridge; New York: Cambridge University Press.
- Cooper, G. J., El-Hani, C. N., & Nunes-Neto, N. (2016). Three Approaches to the Teleological and Normative Aspects of Ecological Functions. In N. Eldredge, T. Pievani, E. Serrelli, & I. Tëmkin (Eds.), *Evolutionary theory: a hierarchical perspective* (pp. 103–124). Chicago: University of Chicago Press.
- Craver, C. F. (2001). Role Functions, Mechanisms, and Hierarchy. *Philosophy of Science*, 68(1), 53–74. <https://doi.org/10.1086/392866>
- Craver, C. F., & Darden, L. (2013). *In search of mechanisms: discoveries across the life sciences*.
- Cummins, K. W. (1974). Structure and Function of Stream Ecosystems. *BioScience*, 24(11), 631–641. <https://doi.org/10.2307/1296676>
- Cummins, R. C. (1975). Functional analysis. *Journal of Philosophy*, 72(November), 741–764.
- DeAngelis, D. L. (1995). The Nature and Significance of Feedback in Ecosystems. In B. C. Patten & S. E. Jorgensen (Eds.), *Complex ecology: the part-whole relation in ecosystems* (pp. 450–467). Englewood Cliffs, N.J.: Prentice-Hall.
- DeLaplante, K., & Picasso, V. (2011). The Biodiversity–Ecosystem Function Debate in Ecology. In K. DeLaplante, B. Brown, & K. A. Peacock (Eds.), *Philosophy of Ecology* (pp. 219–250). Oxford; Amsterdam; Waltham: Elsevier.
- Desjardins, E., Barker, G., Lindo, Z., Dieleman, C., & Dussault, A. C. (2015). Promoting Resilience. *The Quarterly Review of Biology*, 90(2), 147–165.
- Donhauser, J. (2016). Theoretical ecology as etiological from the start. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 60, 67–76.
- Dunbar, M. J. (1960). The Evolution of Stability in Marine Environments Natural Selection at the Level of the Ecosystem. *American Naturalist*, 94(875).
- Dunbar, M. J. (1972). The ecosystem as a unit of natural selection. *Transactions of the Connecticut Academy of Arts and Sciences*, 44, 113–130.
- Dupré, J., & O'Malley, M. A. (2009). Varieties of Living Things: Life at the Intersection of Lineage and Metabolism. *Philosophy & Theory in Biology*, 1, 1–25.
- Dussault, A. C., & Bouchard, F. (2017). A Persistence Enhancing Propensity Account of Ecological Function to Explain Ecosystem Evolution. *Synthese*, 194(4), 1115–1145.
- Eliot, C. H. (2007). Method and Metaphysics in Clements's and Gleason's Ecological Explanations. *Studies in History and Philosophy of Science Part C*, 38(1), 85–109.
- Eliot, C. H. (2011). The Legend of Order and Chaos. In K. DeLaplante, B. Brown, & K. A. Peacock (Eds.), *Philosophy of Ecology* (pp. 49–107). Oxford; Amsterdam; Waltham: Elsevier.
- Elton, C. S. (1927). *Animal ecology*. New York: The Macmillan Company.

- Fox, B. J. (1999). The genesis and development of guild assembly rules. In E. Weiher & P. Keddy (Eds.), *Ecological Assembly Rules* (pp. 23–57). Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511542237.002>
- Garson, J. (2016). *A Critical Overview of Biological Functions*. Cham, Switzerland: Springer.
- Gayon, J. (2013). Does Oxygen Have a Function, or Where Should the Regress of Functional Ascriptions Stop in Biology? In P. Huneman (Ed.), *Functions: selection and mechanisms* (pp. 67–79). Dordrecht, Holland: Springer.
- Gleason, H. A. (1926). The Individualistic Concept of the Plant Association. *Bulletin of the Torrey Botanical Club*, 53, 7–26.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford; New York: Oxford University Press.
- Godfrey-Smith, P. (2013). Darwinian Individuals. In P. Huneman & F. Bouchard (Eds.), *From Groups to Individuals. Evolution and Emerging Individuality* (pp. 17–36). MIT Press.
- Gould, S. J., & Vrba, E. S. (1982). Exaptation—A missing term in the science of form. *Paleobiology*, 8(1), 4–15.
- Griesemer, J. R. (1992). Niche: Historical Perspectives. In E. F. Keller & E. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 231–240). Cambridge, Mass.: Harvard University Press.
- Grimm, N. B. (1995). Why link species and ecosystems? A perspective from ecosystem ecology. In C. G. Jones & J. H. Lawton (Eds.), *Linking species & ecosystems* (pp. 5–15). New York: Chapman & Hall.
- Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. *Auk*, 34, 427–433.
- Gunderson, L. H., & Holling, C. S. (2002). *Panarchy: Understanding Transformations in Human and Natural Systems*. Washington; Covelo; London: Island Press.
- Haber, M. (2013). Colonies are individuals: revisiting the superorganism revival. In P. Huneman & F. Bouchard (Eds.), *From Groups to Individuals. Evolution and Emerging Individuality* (p. 195). Mit Press.
- Hagen, J. B. (1988). Organism and Environment: Frederic Clements’s Vision of a Unified Physiological Ecology. In R. Rainger, K. R. Benson, & J. Maienschein (Eds.), *The American development of biology* (pp. 257–280). Philadelphia, Pa.: University of Pennsylvania Press.
- Hagen, J. B. (1989). Research perspectives and the anomalous status of modern ecology. *Biology and Philosophy*, 4(4), 433–455.
- Hagen, J. B. (1992). *An Entangled Bank: The Origins of Ecosystem Ecology*. New Brunswick, N. J.: Rutgers University Press.
- Hagen, J. B. (2014). Eugene Odum and the Homeostatic Ecosystem: The Resilience of an Idea. In D. P. Arnold (Ed.), *Traditions of systems theory: Major figures and contemporary developments* (pp. 179–193). New York, London: Routledge.
- Harper, J. L. (1977). The Contributions of Terrestrial Plant Studies to the Development of Ecological Theory. In C. E. Goulden (Ed.), *Changing Scenes in the Natural Sciences, 1776-1976* (pp. 139–157). Philadelphia: Academy of Natural Sciences.
- Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, 4(1), 1–23.

- Holling, C. S. (1996). Engineering Resilience versus Ecological Resilience. In P. C. Schulze (Ed.), *Engineering within ecological constraints* (pp. 31–44). Washington, D.C.: National Academy Press.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35.
- Hooper, D. U., Solan, M., Symstad, A., Diaz, S., Gessner, M. O., Buchmann, N., ... van Peer, L. (2002). Species diversity, functional diversity and ecosystem functioning. In M. Loreau, S. Naeem, & P. Inchausti (Eds.), *Biodiversity and ecosystem functioning: synthesis and perspectives* (pp. 195–208). Oxford: Oxford University Press.
- Hull, D. L. (1980). Individuality and Selection. *Annual Review of Ecology and Systematics*, 11(1), 311–332.
- Hutchinson, G. E. (1940). Review of BioEcology. *Ecology*, 21, 267–268.
- Hutchinson, G. E. (1948). Circular causal systems in ecology. *Annals of the New York Academy of Sciences*, 50, 221–246.
- Hutchinson, G. E. (1978). *An introduction to population ecology*. New Haven: Yale University Press.
- Jax, K. (2010). *Ecosystem Functioning*. Cambridge; New York: Cambridge University Press.
- Johnson, C. R., & Boerlijst, M. C. (2002). Selection at the level of the community: the importance of spatial structure. *Trends in Ecology & Evolution*, 17(2), 83–90. [https://doi.org/10.1016/S0169-5347\(01\)02385-0](https://doi.org/10.1016/S0169-5347(01)02385-0)
- Laureto, L. M. O., Cianciaruso, M. V., & Samia, D. S. M. (2015). Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, 13(2), 112–116. <https://doi.org/10.1016/j.ncon.2015.11.001>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Leibold, M. A. (1995). The Niche Concept Revisited: Mechanistic Models and Community Context. *Ecology*, 76(5), 1371–1382. <https://doi.org/10.2307/1938141>
- Lewontin, R. C. (1970). The Units of Selection. *Annual Review of Ecology and Systematics*, 1(1), 1–18.
- Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, 23(4), 399–417.
- Lloyd, E. (2012). Units and Levels of Selection. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy*. Retrieved from URL = <http://plato.stanford.edu/archives/win2012/entries/selection-units/>
- Loreau, M. (2010a). *From populations to ecosystems theoretical foundations for a new ecological synthesis*. Princeton: Princeton University Press.
- Loreau, M. (2010b). Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1537), 49–60. <https://doi.org/10.1098/rstb.2009.0155>
- Lovelock, J. (1979). *Gaia: a new look at life on Earth*. Oxford: Oxford university press.

- Machamer, P. K., Darden, L., & Craver, C. F. (2000). Thinking about mechanisms. *Philosophy of Science*, 67(1), 1–25.
- Maclaurin, J., & Sterelny, K. (2008). *What is biodiversity?* Chicago: University of Chicago Press.
- Margulis, L. (1981). *Symbiosis in cell evolution: life and its environment on the early Earth*. San Francisco: W.H. Freeman.
- May, R. M. (1978). The Evolution of Ecological Systems. *Scientific American*, 239(3), 160–175.
- Maynard-Smith, J. (1964). Group Selection and Kin Selection. *Nature*, 201(4924), 1145–1147. <https://doi.org/10.1038/2011145a0>
- Mayr, E. (1961). Cause and Effect in Biology. *Science*, 134(3489), 1501–1506.
- McIntosh, R. P. (1975). H. A. Gleason-"Individualistic Ecologist" 1882-1975: His Contributions to Ecological Theory. *Bulletin of the Torrey Botanical Club*, 102(5), 253.
- McIntosh, R. P. (1985). *The Background of Ecology: Concept and Theory*. Cambridge; New York: Cambridge University Press.
- McLaughlin, P. (2001). *What Functions Explain: Functional Explanation and Self-Reproducing Systems*. Cambridge; New York; Melbourne: Cambridge University Press.
- Millikan, R. G. (1984). *Language, Thought, and Other Biological Categories: New Foundations for Realism*. Cambridge, Mass. ; London: MIT Press.
- Naeem, S. (2002). Ecosystem Consequences of Biodiversity Loss: The Evolution of a Paradigm. *Ecology*, 83(6), 1537. <https://doi.org/10.2307/3071972>
- Nunes-Neto, N., Do Carmo, R. S., & El-Hani, C. N. (2016). Biodiversity and ecosystem functioning: an analysis of the functional discourse in contemporary ecology. *Filosofia e História Da Biologia*, 11(2), 289–321.
- Nunes-Neto, N., Moreno, A., & El-Hani, C. N. (2013). The implicit consensus about function in philosophy of ecology. In N. Nunes-Neto, C. N. El-Hani, & A. Moreno (Eds.), *The functional discourse in contemporary ecology* (pp. 40–65). Salvador, Bahia: Doctoral dissertation, Universidade Federal da Bahia.
- Nunes-Neto, N., Moreno, A., & El-Hani, C. N. (2014). Function in ecology: an organizational approach. *Biology and Philosophy*, 29(1), 123–141.
- Odenbaugh, J. (2010). On the Very Idea of an Ecosystem. In A. Hazlett (Ed.), *New Waves in Metaphysics* (pp. 240–258). Basingstoke, N. Y.: Palgrave Macmillan.
- Odum, E. P. (1953). *Fundamentals of ecology*. Philadelphia: Saunders. Available online at [catalog.hathitrust.org/api/volumes/oclc/880892.html](http://catalog.hathitrust.org/api/volumes/oclc/880892.html).
- Odum, E. P. (1969). The Strategy of Ecosystem Development. *Science*, 164(3877), 262–270.
- Odum, E. P. (1971). *Fundamentals of Ecology* (3rd ed.). Philadelphia, London, Toronto: W. B. Saunders Company.
- Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, 9(6), 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Pocheville, A. (2014). The ecological niche: history and recent controversies. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Eds.), *Handbook of evolutionary thinking in the sciences*. Springer.

- Pocheville, A. (2015). The Ecological Niche: History and Recent Controversies. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Eds.), *Handbook of Evolutionary Thinking in the Sciences* (pp. 547–586). Springer Netherlands. [https://doi.org/10.1007/978-94-017-9014-7\\_26](https://doi.org/10.1007/978-94-017-9014-7_26)
- Pradeu, T. (2016). Organisms or biological individuals? Combining physiological and evolutionary individuality. *Biology & Philosophy*, 31(6), 797–817. <https://doi.org/10.1007/s10539-016-9551-1>
- Queller, D. C., & Strassmann, J. E. (2009). Beyond society: the evolution of organismality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3143–3155. <https://doi.org/10.1098/rstb.2009.0095>
- Schoener, T. W. (1989). The Ecological Niche. In J. M. Cherrett & A. D. Bradshaw (Eds.), *Ecological concepts: the contribution of ecology to an understanding of the natural world* (pp. 79–114). Oxford, England: Blackwell Scientific Publications.
- Schulze, E.-D., & Mooney, H. A. (1993). Ecosystem Function of Biodiversity: A Summary. In E.-D. Schulze & H. A. Mooney (Eds.), *Biodiversity and ecosystem function* (pp. 497–510). Berlin; New York: Springer-Verlag.
- Smith, S. E. (2017). Organisms as Persisters. *Philosophy, Theory, and Practice in Biology*, 9(20171201). <https://doi.org/10.3998/ptb.6959004.0009.014>
- Sober, E., & Wilson, D. S. (1998). *Unto others: the evolution and psychology of unselfish behavior*. Cambridge, Mass.: Harvard University Press.
- Strassmann, J. E., & Queller, D. C. (2007). Insect societies as divided organisms: The complexities of purpose and cross-purpose. *Proceedings of the National Academy of Sciences*, 104(suppl 1), 8619–8626. <https://doi.org/10.1073/pnas.0701285104>
- Swenson, W., Arendt, J., & Wilson, D. S. (2000). Artificial selection of microbial ecosystems for 3-chloroaniline biodegradation. *Environmental Microbiology*, 2(5), 564–571.
- Swenson, W., Wilson, D. S., & Elias, R. (2000). Artificial ecosystem selection. *Proceedings of the National Academy of Sciences*, 97(16), 9110–9114. <https://doi.org/10.1073/pnas.150237597>
- Tansley, A. G. (1935). The Use and Abuse of Vegetational Concepts and Terms. *Ecology*, 16(3), 284–307.
- Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Whittaker, R. H. (1975). *Communities and Ecosystems* (2nd ed.). New York, London: Macmillan, Collier.
- Williams, G. C. (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, N.J.: Princeton University Press.
- Wilson, D. S. (1980). *The natural selection of populations and communities*. Menlo Park, Calif.: Benjamin/Cummings Pub. Co.
- Wilson, D. S. (1992). Complex Interactions in Metacommunities, with Implications for Biodiversity and Higher Levels of Selection. *Ecology*, 73(6), 1984–2000. <https://doi.org/10.2307/1941449>
- Wilson, D. S. (1997). Biological communities as functionally organized units. *Ecology*, 78(7), 2018–2024.

- Wilson, D. S., & Sober, E. (1989). Reviving the superorganism. *Journal of Theoretical Biology*, 136(3), 337–356.
- Wouters, A. (2005). The function debate in philosophy. *Acta Biotheoretica*, 53(2), 123–151.