

Chapter 14

Functional Biodiversity and the Concept of Ecological Function



Antoine C. Dussault

Abstract This chapter argues that the common claim that the ascription of ecological functions to organisms in functional ecology raises issues about levels of natural selection is ill-founded. This claim, I maintain, mistakenly assumes that the function concept as understood in functional ecology aligns with the selected effect theory of function advocated by many philosophers of biology (sometimes called “The Standard Line” on functions). After exploring the implications of Wilson and Sober’s defence of multilevel selection for the prospects of defending a selected effect account of ecological functions, I identify three main ways in which functional ecology’s understanding of the function concept diverges from the selected effect theory. Specifically, I argue (1) that functional ecology conceives ecological functions as *context-based* rather than *history-based* properties of organisms; (2) that it attributes to the ecological function concept the aim of explaining ecosystem processes rather than that of explaining the presence of organisms within ecosystems; and (3) that it conceives the ecological functions of organisms as *use* and *service* functions rather than *design* functions. I then discuss the extent to which the recently proposed causal role and organizational accounts of ecological functions better accord with the purposes for which the function concept is used in functional ecology.

Keywords Functional biodiversity · Function · Selected effect theory · Ecosystem selection · Superorganism

A. C. Dussault (✉)

Centre interuniversitaire de recherche sur la science et la technologie (CIRST),
Université du Québec à Montréal (UQAM), Montréal, QC, Canada

Département de philosophie, Collège Lionel-Groulx, Sainte-Thérèse, QC, Canada
e-mail: antoine.cdussault@clg.qc.ca

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14.1 Introduction

In the last decades, *functional biodiversity* has become a central focus in ecology and environmental conservation (e.g. Tilman 2001; Naeem 2002; Petchey and Gaston 2006; Nock et al. 2016). This follows from the recognition by an increasing number of ecologists of the explanatory and predictive limitations of more traditional “species richness” measures of biodiversity. This recognition has led ecologists and conservationists to consider, alongside the number of species present in a community, the particular features of organisms of those species and how those features determine their potential relationships with their environments (see Hooper et al. 2002, 195; DeLaplante and Picasso 2011, 173; Nunes-Neto et al. 2016, 296–297). Consideration of those features has fostered among ecologists an interest in the ways in which organisms can be grouped or classified on the basis of their *functional traits*, which are deemed to be of more direct ecological importance than those on which the more standard taxonomic measures of biodiversity are based.

Those functional groupings include:

Guilds: Groupings of organisms on the basis of similarities in resource use. Two organisms are members of a same guild if they tend to use a similar resource in a similar way (Simberloff and Dayan 1991; J. B. Wilson 1999; Blondel 2003).

Functional response groups: Groupings of organisms on the basis of similar expected response to environmental changes. Two organisms are members of the same functional response group if they tend to respond similarly to similar changes in environmental conditions (Catovsky 1998; J. B. Wilson 1999; Hooper et al. 2002; Lavorel and Garnier 2002)

Functional effect groups: Groupings of organisms on the basis of similar roles in ecosystem processes. Two organisms are members of the same functional effect group if they tend to contribute similarly to some important ecosystem process (e.g. nutrient cycling, primary productivity, energy flows) (Catovsky 1998; Hooper et al. 2002; Lavorel and Garnier 2002; Blondel 2003).¹

Among those three modes of functional classification, the first two—*guilds* and *functional response groups*—are commonly used to explain the assembly of ecological communities and how their species composition changes in response to changes in their environments. The third—*functional effect groups*—is commonly used to explain

¹It should be noted that functional ecologists have adopted various modes of functional classification with different emphases, and have used diverse terminologies to refer to them. For instance Wilson (1999) draws a contrast between *alpha guilds* and *beta guilds* which is essentially equivalent to the contrast made above between *guilds* and *functional response groups*. Similarly, Catovsky (1998), and Lavorel and Garnier (2002) draw a contrast between *functional response groups* and *functional effect groups* similar to the one made above, but define *functional response groups* also in reference to resource use (a basis for classification that I associated with *guilds*). And likewise, Blondel (2003) draws a contrast between *guilds* and *functional groups*, and his concept of *functional group* is essentially equivalent to the above concept of *functional effect group*. I think that my above identification of three main modes of functional classification adequately reflects the complementary epistemic aims in relation to which ecologists use functional classifications.

ecosystem processes through delineating the particular contributions of organisms of different species to those processes (see discussion in Sect. 14.3.2 below).

A particularity of the third mode of functional classification—*functional effect groups*—is that it involves the ascription of *roles* or *functions* to organisms within ecosystems (Catovsky 1998, 126; Symstad 2002, 23–24; Jax 2010, 54). As remarked by Jax (2010, sec. 4.2) and DeLaplante and Picasso (2011, sec. 3.2), such ascriptions of ecological functions to organisms within ecosystems raise important philosophical issues. One of them concerns the meaning of the *function* concept and its relationship to claims about natural selection. Given the association made by many biologists and ecologists between the concept of function and the evolutionary concept of *adaptation* (Williams 1966), the idea that organisms fulfil functions within ecosystems has been claimed to raise issues about the levels at which natural selection customarily operates (see Calow 1987, 60; DeLaplante and Picasso 2011, 184). As we shall see, a linkage of the notion of ecological function to community and ecosystem selection assumes an elucidation of this notion along the lines of the *selection effect* theory of function advocated by many philosophers of biology (e.g. Wright 1973; Millikan 1989; Neander 1991; Godfrey-Smith 1994).² According to this theory, which some refer to as “The Standard Line” on functions given its many adherents (Allen and Bekoff 1995, 13–14), the function of a part or trait of a biological entity is the effect for which this part or trait was preserved by natural selection operating on the ancestors of that entity. A selected effect elucidation of the concept of ecological function would therefore entail that ascribing a function to an organism within an ecosystem amounts to saying that at least some of the traits of this organism have been shaped by ecosystem-level selection. Relatedly, a selected effect elucidation of the ecological function concept, as we shall also see, would in some way revive the old idea of communities and ecosystems as tightly integrated *superorganisms* shaped by natural selection (Allee et al. 1949; D. S. Wilson and Sober 1989).

In this chapter, I will argue that the common association between function ascriptions in functional ecology and issues about levels of selection is ill-founded. As just mentioned, this association assumes an understanding of ecological functions along the lines of the *selection effect* theory of function, and I will maintain that the understanding of the function concept at play in functional ecology does not in fact align with this theory. I will do so through identifying important ways in which functional ecology’s use of the ecological function concept diverges from the understanding conveyed by the selected effect theory. This will highlight that, when they ascribe functions to organisms within ecosystems, functional ecologists are not committed to views of ecosystems as units of selection. Their understanding of ecological functions and ecosystem functional organization, as I will emphasize, attributes to ecosystems a lower degree of part-whole integration than what would be entailed by the selected effect theory. The discussion of the ecological function concept presented in this chapter will therefore reinforce the near consensus that has recently emerged among philosophers of biology and ecology, according to which the ecological

²For overviews of philosophical theories of function, see McLaughlin (2001), Wouters (2005), Walsh (2008), Saborido (2014), and Garson (2016).

function concept should be elucidated along the lines of non-selectionist alternatives to the selected effect theory of function (Maclaurin and Sterelny 2008, sec. 6.2; Odenbaugh 2010; Gayon 2013; Nunes-Neto et al. 2014).

My discussion will be organized as follows. In Sect. 14.2, I will discuss the common contention that the use of the function concept in ecology raises issues about levels of selection. I will explore the implications of Wilson and Sober's defence of multilevel selection for the prospects of defending a selected effect account of ecological functions. In Sect. 14.3, I will dispute the claim that the ecological function concept raises issues about levels of natural selection. I will do so by highlighting three important ways in which functional ecology's understanding of the ecological function concept diverges from the selected effect theory. Finally, in Sect. 14.4, I will briefly discuss two non-selectionist accounts of ecological functions that have recently been proposed by philosophers of biology and ecology; namely, the *causal role* account (Maclaurin and Sterelny 2008, sec. 6.2; Odenbaugh 2010; Gayon 2013), and the *organizational* account (Nunes-Neto et al. 2014). I will maintain that neither of these two accounts fully accords with how ecological functions are understood in functional ecology.

14.2 Ecological Functions and Levels of Selection

As mentioned in the introduction, the ascription of ecological functions to organisms in functional ecology is often taken to raise issues about levels of natural selection. As DeLaplante and Picasso (2011, 184) recall:

[A]ttitudes toward function language in ecology have been influenced by the group selection debate that took place in the 1960s (Wynne-Edwards 1962; Williams 1966). The critique of group selection was based on the affirmation that within orthodox evolutionary theory, natural selection acts primarily at the level of individual organisms (or, indeed, the level of individual genes), and rarely if ever at the level of groups. [...] Evolutionary ecologists tend to associate the language of functions with organism-environment relationships relevant to selection and adaptation (e.g., "functional traits"). But if natural selection only acts at the level of individuals within species populations, then the language of functions should only apply at this level [...]. Consequently, evolutionary ecologists are inclined to be skeptical of function attributions at the community and ecosystem level.³

Along similar lines, in the inaugural issue of the journal *Functional Ecology*, Calow (1987, 60) maintains that a focus on the functions fulfilled by organisms within communities "implies that the way they contribute to the balanced economy of the community is an important criterion of selection".

Such a linkage of the notion of ecological function to community or ecosystem selection assumes an understanding of this notion along the lines of the *selected effect* theory of function developed in the philosophy of biology (Wright 1973;

³For a more detailed discussion of the issues raised by the group selection debate for functional approaches to ecology, see Hagen (1992, chap. 8).

Millikan 1989; Neander 1991). Some support for this assumption can be found in the fact that the selected effect theory has, to some extent, established itself as “The Standard Line” on functions in the philosophy of biology (Allen and Bekoff 1995, 13–14). Since its initial introduction, it has been adopted by many prominent philosophers of biology (e.g. Griffiths 1993; Mitchell 1993; Godfrey-Smith 1994). According to the selected effect theory, the function of a part or trait of a biological entity is the effect for which this part or trait was preserved by natural selection operating on ancestors of this entity. Thus, ascribing a function to an organism within an ecosystem would amount to saying that at least some of the traits of this organism have been shaped by ecosystem-level selection. In other words, ascribing a function to an organism within an ecosystem would amount to saying that organisms from its lineage have the traits on account of which they are classified in a particular *functional effect group* partly because their having those traits conferred a selective advantage to the ecosystem they are part of. Thus, functional ecologists’ ascribing ecological functions to organisms within ecosystems would commit them to the idea that communities and ecosystems are units of natural selection. The view of ecosystem functional organization implicitly adopted in functional ecology would therefore be similar to that espoused by mid-Twentieth century ecologists who believed that communities and ecosystems were tightly integrated *superorganisms* subject to community or ecosystem-level selection (e.g. Allee et al. 1949).

Although, as remarked by DeLaplante and Picasso (see quote above), many biologists and ecologists are sceptical about the idea that natural selection customarily operates at the level of communities and ecosystems, some support for this idea can be found (as they also remark) in Wilson and Sober’s defence of multilevel selection (see e.g. Wilson and Sober 1989; Sober and Wilson 1994). Wilson and Sober’s main focus is population-level selection, but they also apply their multilevel selectionist approach to communities and ecosystems. Wilson and Sober’s defence of multilevel selection improves upon previous defences in part by identifying an unrealistic assumption underlying classical arguments against it. This assumption is that individual organisms within populations interact randomly with each other and therefore have equal chances of mating with any other member of their population. Contrary to this assumption, Wilson and Sober emphasize, the heterogeneity of many environments entails that, in practice, populations in the ecological world tend to be structured in ways that make their individual members more likely to interact with only a small subset of their whole population. This, as Wilson and Sober explain, creates conditions favourable to the operation of natural selection on single-species groups of organisms and even communities and ecosystems (Wilson and Sober 1989, 341–4).

They illustrate the possibility of community-level selection with the example of *phoretic associations*. Phoretic associations are communities formed by a winged insect associated with many wingless organisms (e.g. mites, nematodes, fungi and microbes) that rely on the winged insect for transportation from one resource patch to another. When the winged insect reaches a new resource patch (e.g. carrion, dung, or stressed timber), it brings along a whole community of “phoretic associates”

which then colonize the patch. Wilson and Sober explain how natural selection might operate on phoretic associations as a whole:

Consider a large number of resource patches, each of which develops into a community composed of the insects, their phoretic associates, plus other species that arrive independently. The community of phoretic associates may be expected to vary from patch to patch in species composition and in the genetic composition of the component species. Some of these variant communities may have the effect of killing the carrier insect. Others may have the effect of promoting insect survival and reproduction, and these will be differentially dispersed to future resource patches. Thus, between-community selection favors phoretic communities that do not harm and perhaps even benefit the insect carrier. At the extreme, we might expect the community to become organized into an elaborate mutualistic network that protects the insect from its natural enemies, gathers its food, and so on. (Wilson and Sober 1989, pp. 348–9)

Such a scenario, they emphasize, is not only a theoretical possibility. Empirical data from studied phoretic communities show no negative effects on the carrier insect in most cases and positive effects in many cases. In a subsequent paper, Wilson (1997), 2020–22) discusses other likely cases of community selection that conform to his and Sober’s approach, as well as a likely case of ecosystem selection involving micro-ecosystems forming at the surface of lakes and oceans.⁴

Wilson and Sober’s defence of community and ecosystem selection thus seems to provide grounds for interpreting at least some of the functions fulfilled by organisms within communities and ecosystems along the lines of the selected effect theory of function. For instance, the selected effect theory entails that some phoretic associates in Wilson and Sober’s phoretic association case have functions within the phoretic association. This is the case of phoretic associates that are part of the association partly because some of their traits conferred a selective advantage to the phoretic association as a whole. Similar function ascriptions would be implied by the selected effect theory in relation to organisms involved in the other cases of community and ecosystem selection described by Wilson (1997). In line with those observations, Wilson and Sober themselves conceive their defence of multilevel selection as legitimizing the view that some communities and ecosystems are *functionally organized* entities (Wilson and Sober 1989, 337–344; see also Wilson 1997). They even claim that communities and ecosystems that are units of selection according to their approach can genuinely be regarded as *superorganisms* (Wilson and Sober 1989, 349).⁵

However, it should be emphasized that Wilson and Sober’s defence of multilevel selection lends at best very limited support to the application of the selected effect theory in ecology. Wilson and Sober are careful to emphasize that their defence of community and ecosystem selection is professedly modest. They see it as an important strength of their approach that it does not consist in an “overly grandiose” superorganism theory that attributes “functional design [...] to ecosystems in general”

⁴For related discussions of artificial ecosystem selection experiments, see Swenson et al. (2000a), Swenson et al. (2000b) and Blouin et al. (2015).

⁵For a discussion of Wilson and Sober’s defence of multilevel selection in relation to the selected effect theory of function, see Basl (2017, sec. 4.2).

(Wilson and Sober 1989, 352). As they insist, their approach entails that “[n]ot all groups and communities are superorganisms, but only those that meet the specified (and often stringent) conditions” (Wilson and Sober 1989, 343). Functional ecologists, in contrast, envision their approach as a framework for the study of ecosystems in general. Such a broad scope is not legitimized by Wilson and Sober’s approach. Therefore the support lent by Wilson and Sober’s defence of multilevel selection to the application of the selected effect theory of function in ecology seems too limited for the purposes of functional ecology.

In the next section, I will argue that significant aspects of the use of the function concept in functional ecology point to an understanding of function that diverges from the selected effect theory. This will show that, contrary to what is sometimes suggested (see above), the ascription of ecological functions to organisms in functional ecology does not hinge on claims that ecosystems are units of natural selection.

14.3 Ecological Functions in Functional Ecology

14.3.1 *Ecological Context vs. Selective History*

Historically and conceptually, contemporary functional ecology’s construal of the function concept derives from the renowned community ecologist Charles Elton’s (1927, 1933) understanding of the *ecological niche*. Elton’s understanding of the niche was tied to a functionalist view of ecological communities, which drew an analogy between feeding interactions within ecological communities and economic exchanges in human societies.⁶ In Elton’s coinage, the term “niche” referred to “what [an animal] is *doing* in its community”, and emphasized an animal’s “*relations to food and enemies*” in contrast to “appearance, names, affinities, and past history.” (Elton 1927, 63–64, emphasis in the original) The niche concept was “used in ecology in the sense that we speak of trades or *professions* or *jobs* in a human community” (Elton 1933, 28, emphasis added). Thus, Elton’s understanding of the niche was tied to a picture of ecological communities in analogy with human societies (with an economic focus), rather than with individual organisms. The niches of organisms, as he conceived them, were analogous to the economic roles fulfilled by individuals within human societies, rather than with the functions of organs within organisms. This communitarian-economic analogy attributed to ecological

⁶Elton’s understanding of the niche contrasted with the one previously adopted by Joseph Grinnell (1917), the other originator of the niche concept, who used the niche concept to denote a species’ particular *environmental requirements* (see Leibold 1995, 1372–1373). The contrast between Grinnell’s and Elton’s niches parallels the contrast presented in the introduction between on the one hand, *guilds* and *functional response group* and on the other hand, *functional effect groups* (see Hooper et al. 2002, 196). For discussions of the contrast between Grinnell’s and Elton’s niche concepts, see also Schoener (1989), Griesemer (1992), and Pocheville (2015).

communities of a lower degree of part-whole integration than the one characteristically found in individual organisms. Notably, Elton (1930) emphasized that individual organisms retain a significant degree of autonomy with respect to the communities in which they are involved, and he rejected the view (held by some later Twentieth-century ecologists) that natural selection customarily operates on ecological communities as a whole (McIntosh 1985, 167; Haak 2000, 32).

Contemporary functional ecology's understanding of ecological functions is in many respects similar to Elton's functional understanding of the niche. A first important aspect of this understanding that does not align with the selected effect theory concerns the basis on which ecological functions are ascribed to organisms in functional ecology. In functional ecology, the ecological functions of organisms within ecosystems are conceived as *context-based* properties of those organisms, which they bear on account of their actual and potential interactions with other organisms. This context-based understanding contrasts with that conveyed by the selected effect theory, according to which the functions of biological items are *history-based* properties of those items (i.e. properties borne by those items on account of their selective history). The conceptual dissociation of the ecological function concept from evolutionary considerations is made explicit by some functional ecologists. Petchey and Gaston (2006, 742), for instance, state that “[f]unctional diversity [in ecology] generally involves understanding communities and ecosystems based on what organisms do, rather than on their evolutionary history”.

Functional ecology's context-based understanding of ecological functions is aptly portrayed by Jax (2010, 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.

On this context-based understanding, the ascription of ecological functions to organisms within ecosystems does not entail claims about selective history. For instance, an ecologist's depiction of a rabbit as fulfilling the role of a prey (or primary consumer) within an ecosystem does not entail the claim that rabbits and their traits were selected for serving as food for predators. Rabbits eat grass and grow muscles for their own survival and, as a by-product, acquire traits that make them nutritious and palatable for those predators. Likewise, an ecologist's reference to foxes as fulfilling the role of regulator of herbivore populations within an ecosystem does not entail the claim that foxes and their traits were selected for regulating herbivore populations. Foxes chase and eat preys to feed themselves and, as a by-product, exert a form of control over their preys' populations.

It should be noted, however, that contemporary functional ecology expands upon Elton's approach to the study of ecological communities in two important ways.

First, it expands upon Elton's approach by integrating ecosystem ecology's thermodynamic and biogeochemical outlook on the ecological world (see Hagen 1992, chaps. 4–5). Thus, whereas Elton used the niche primarily to study how interspecific interactions within communities explain the regulation of populations within them and the maintenance of their structural features (Hagen 1992, 52; Pocheville 2015, 549), the ascription of ecological functions to organisms in contemporary functional ecology is more primarily tied to the aim of studying how the traits of organisms determine their potential contributions to ecosystem processes (see K. W. Cummins 1974; Naeem 2002). Thus, in contemporary functional ecology, the ecological functions of organisms are their particular contributions to ecosystem processes (e.g. nutrient cycling, primary productivity, energy flows). Contemporary functional ecologists ascribe functions to organisms in order to delineate their particular contribution to the realization and maintenance of those processes.

Second, contemporary functional ecology expands upon Elton's focus on feeding (or trophic) interactions between organisms, by also considering ecological functions acquired by organisms through *non-trophic* interactions with other organisms. Those non-trophic interactions are ones in which organisms affect each other's lives through other means than the direct provision of food (in the form of living or dead tissues). Important non-trophic ecological functions include those fulfilled by *ecosystem engineers*, i.e. organisms that create, modify and maintain habitats in ways that affect the lives of other organisms (e.g. beavers build dams and in so doing create habitats and make many resources available for numerous other organisms) (Jones et al. 1994, 1997; Berke 2010). Non-trophic ecological functions also include those of *pollinators* and *seed dispersers* (see Blondel 2003, 227–228).

Those two significant expansions notwithstanding, it remains the case that ecological function ascriptions as conceived in functional ecology do not involve claims about selective history. For instance, an ecologist's saying that, by building a dam, a beaver fulfils the role of a pond provider with respect to the numerous organisms for which the pond is a favourable habitat does not entail the claim that beavers were selected for providing habitats to those organisms. Beavers build dams and create ponds for their own benefit and, as a by-product, provide habitats to numerous organisms.

An important research aim associated with functional ecology's context-based understanding of function is that of studying the *functional equivalence* between phylogenetically-divergent organisms. Elton (1927, 65), for instance, remarked that the arctic fox, which subsists on guillemot eggs and seal remains left by polar bears, occupies essentially the same niche as the spotted hyæna in tropical Africa, which feeds upon ostrich eggs and zebra remains left by lions. Although they have evolved their traits in distinct selective contexts, arctic foxes and spotted hyæna occupy similar niches. Along similar lines, contemporary functional ecologists have identified functional equivalences, for instance, between ants, birds and rodents, which similarly contribute to seed dispersal in some desert ecosystems, and between hummingbirds, bats and moths, which similarly contribute to the pollination of Lauraceae (a family of plants from the group of angiosperm that usually have the form of trees or shrubs) (see Blondel 2003, 226). The acknowledgement of functional equivalences

between phylogenetically-divergent organisms conflicts with the understanding of function conveyed by the selected effect theory, in that this theory would entail that two organisms can have similar ecological functions only to the extent that their traits have evolved in similar selective contexts.

14.3.2 *The Explanatory Aim of Ecological Functions*

A second important aspect of functional ecology's understanding of functions that diverges from the selected effect theory concerns the *explanatory aim* attributed to the function concept. In functional ecology, as seen in the preceding section, the *explanandum* of ecological function ascriptions is ecosystem processes. The ecological functions of organisms are their particular contributions to the ability of ecosystems to realize and maintain those processes. This contrasts with the *explanandum* of function ascriptions according to the selected effect theory. According to the selected effect theory, the *explanandum* of ecological function ascriptions is the *presence* of the biological items to which functions are ascribed within a system (typically an organism). For instance, according to the selected effect theory, saying that pumping blood is the function of the heart entails not only saying that pumping blood is the way in which hearts contribute to blood circulation in animals with circulatory systems. It also entails saying that animals with circulatory systems have hearts because hearts pump blood (i.e. that hearts *are present* within those organisms because they pump blood). The selected effect functions of biological items explain the presence of those items because, by definition, those functions are the effects for which those items were preserved by natural selection.

To make plain that the *explanandum* of ecological function ascriptions in functional ecology is not the *presence* of organisms within ecosystems, we must recall functional ecology's three main modes of functional classification identified in the introduction. As seen in the introduction, functional ecologists use three main modes of functional classification: (1) *guilds* (groupings based on similar resource use), (2) *functional response groups* (groupings based on similar response to environmental factors), and (3) *functional effect groups* (grouping based on similar roles in ecosystem functioning). As also seen in the introduction, the mode of functional classification that is concerned with functions of organisms within ecosystems is the third one (i.e. *functional effect groups*). However, the modes of functional classification that are primarily involved in the theoretical frameworks used by functional ecologists to explain the presence of organisms within ecosystems are the two other ones (*guilds* and *functional response groups*). Those functional classifications are the ones primarily involved in theories developed for explaining the *assembly* of ecological communities and how communities respond to changes in environmental conditions (through changes in species composition). According to those theories (see Keddy 1992; Díaz et al. 1999), the ability of some particular organisms to establish and maintain themselves in a given community depends, first, on their ability to tolerate the local environmental conditions, and, second, on their ability to

exploit the resources available in this community (which requires them to be able to successfully compete with other organisms also using those resources or to share those resources with them). The former ability depends upon the *functional response group* to which organisms belong, and the latter one depends upon their *guild*. The *functional effect groups* to which organisms belong play no significant role in explaining the assembly of ecological communities and their responses to environmental changes.

To be sure, if some regular coincidence could be found between, on the one hand, *guilds* and *functional response groups*, and on the other hand, *functional effects groups*, then one could argue that an explanatory connection nevertheless exists between the ecological functions of organisms and their presence within ecosystems. Functional ecologists, however, emphasize the frequent non-coincidence of those groupings (see e.g. Lavorel and Garnier 2002; Blondel 2003). For instance, birds can disperse some plants' seeds in three different ways: (1) through catching seeds in their plumage and then accidentally dropping them elsewhere (epizoochory), (2) through swallowing fruits and then regurgitating or defecating them elsewhere (endozoochory), or (3) through caching dry fruit seeds for future use and then "forgetting" them (synzoochory). Birds that disperse some plants' seeds in those three ways all belong to the same *functional effect group*. However, insofar as only the birds that disperse seeds in the two latter ways (endozoochory and synzoochory) use the seeds as resources, those birds and those that disperse seeds in the former way (epizoochory) do not belong to the same *guild* (see Blondel 2003, 227–228). Likewise, some varieties of dung beetles feed upon the non-digestive part of large herbivores' green food. Those dung beetles do so in three different ways: (1) through dwelling inside the dung, (2) through burying pieces of the faeces from 0.5 to 1 meter under the dung, and (3) through making a ball of dung, laying eggs within it and rolling it to a place where they can bury it. All dung beetles use the dung as a resource and therefore belong to the same *guild*. However, insofar as the different ways of using the resource lead to different decomposition processes, the three types of dung beetles do not belong to the same *functional effect group* (see Blondel 2003, 228).

It may be objected that the *functional effect groups* to which organisms belong must at least partly explain their presence within ecosystems, given that organisms depend upon the achievement of ecosystem processes for their own existence, and, for this reason, depend, at least indirectly, upon the reliable fulfilment of their own functional contributions to those processes. By fulfilling their ecological functions, in other words, organisms must indirectly contribute to the realization and maintenance of their own conditions for existence, such that they are indirect causes of their continued presence within the ecosystem (or at least of the continued presence of organisms of their *functional effect group*).

I think, however, that this kind of causal link between the fulfilment of their ecological functions by organisms and their presence within ecosystems can, at best, be very weak. Strictly speaking, what organisms contribute to realizing, by fulfilling their ecological functions, is not the conditions necessary for their own presence within an ecosystem, or even for the presence of organisms from their *functional*

effect group. What they contribute to realizing is, more accurately, the conditions necessary for the presence of organisms from the *guild* or *functional response group* to which they belong. Abilities to exploit the conditions organisms contribute to realizing by fulfilling their ecological function are determined by membership in *guilds* and *functional response groups*, not by membership in *functional effect groups*. This is well illustrated by a phenomenon studied by ecologists as the “negative selection effect” (Jiang et al. 2008). The “negative selection effect” occurs when some ecological function stops being fulfilled as a result of the displacement of a species that fulfils this function (i.e. that belongs to a particular *functional effect group*) by another species that does not fulfil it (i.e. that does not belong to the same *functional effect group*). The reason why the latter species displaces the former one is that both species use the same resource (i.e. belong to the same *guild*) and the latter species is better at competing for this resource. Thus, suppose, that a species S fulfils the ecological function F within the ecosystem E , and that, by doing so, S contributes to the realization of environmental condition C and to the availability of resource R within E . S therefore belongs to the *functional effect group* f (which encompasses organisms that are able to fulfil F), and also belongs to the *guild* r and the *functional response group* c (which encompass, respectively, organisms that use resource R and that require environmental conditions C). Now, we can see more clearly that, by contributing to the realization of C and the availability of R , organisms from S only weakly promote their own presence (or the presence of other species from f) in E . What organisms from S promote by contributing to the realization of C and the availability of R is, in fact, the presence of any species from *guild* r and *functional response group* c . By doing so, therefore, organisms from S promote their own presence within E only provided that there is no other species S_i that also belongs to c and r and that is more efficient than S in exploiting R . If such a species comes around, then the fulfilment of their ecological function by organisms from S will instead promote the presence of S_i within the ecosystem, and consequently S 's own displacement by S_i . And if S_i does not belong to f and S was the only species that fulfilled F within E , then F will stop being fulfilled in E . Likewise, by contributing to the realization of C and the availability of R , organisms from S may promote the presence of other species from *functional effect group* f only to the extent that those other species belonging to f also belong to r and c . There, however, is no reason to assume that, on a general basis, species that belong to f will also belong to r and c . The possibility of such a “negative selection effect,” I think, makes clear that the *functional effect groups* to which organisms belong have only limited relevance to the aim of explaining why they are present within ecosystems.

14.3.3 *By-Products and the Notion of “Functioning as”*

As indicated in Sect. 14.3.1, in functional ecology, ecological functions may be ascribed to organisms on the basis of traits that are evolutionary by-products rather than selected effects (on this point, see also Maclaurin and Sterelny 2008, 115; and

Odenbaugh 2010, 251). This observation points to a third important aspect of functional ecology's understanding of functions that does not align with the selected effect theory. This aspect can be highlighted by drawing the connection between functional ecology's understanding of the function concept and Achinstein's (1977, 350–6) delineation of three distinct meanings of “function” in ordinary language: *design*, *use* and *service* functions. An entity's *design* function consists 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* function consists in what it is *used for* (e.g. this table is used for sitting), and an entity's *service* function consists in what it *serves as* (e.g. a watch's second hand serves as a dust sweeper). A table's functioning as a seat or the second hand of a watch's functioning as a dust sweeper do not entail that tables and second hands have been (intentionally) designed for those functions. This distinction between design functions on the one hand, and use and service functions on the other hand, is sometimes also expressed in terms of a contrast between the notion of *being the function of* (e.g. breathing is the function of the nose) and that of *functioning as* (e.g. the nose functions as an eyeglass support) (e.g. Boorse 1976, 76; Bedau 1992, 787–789).

In light of this distinction, the selected effect theory of functions can be interpreted as concerned with *design* functions, that is, as concerned with specifying *the function of* some biological item (as is reflected in selected effect theorists' typical association of function with *design*, see e.g. Wright 1973, 164–65; Millikan 1984, 17). In contrast, functional ecology's context-based functions can be conceived as concerned with *use* and *service* functions, that is, as concerned with specifying what an ecological item can *function as* in relevant ecological contexts. For instance, rabbits that are preyed upon by foxes in an ecosystem *function as* primary consumers within that ecosystem. In turn, foxes that prey upon those rabbits and exert some control on their population *function as* regulators of the rabbit population within that ecosystem. And likewise, beavers that build dams within an ecosystem and by doing so create habitats and make many resources available for numerous other organisms *function as* pond providers within that ecosystem. Similar to the cases of a table's functioning as a seat and the watch's second hand's functioning as a dust sweeper, rabbits' functioning as primary consumers, foxes' functioning as regulators of rabbit populations and beavers' functioning as pond providers within an ecosystem do not entail claims that rabbits, foxes and beavers were (evolutionarily) designed for fulfilling those functions. Functional ecology thus seems to make use of an ordinary notion of function that is conceptually distinct from the one that the selected effect theory is meant to elucidate. It is not concerned with functions that organisms are (evolutionarily) *designed* to fulfil within ecosystems, but, with functions that they (more fortuitously) fulfil as a result of being (context-dependently) involved in use and service interactions with other organisms.

Above, I maintained that functional ecology attributes to ecological communities a lower degree of part-whole integration than the one characteristically found in individual organisms (in line with Elton's analogy between ecological communities and human societies). Interpreting ecological functions as use and service functions provides some illumination of this idea. A notable feature of individual organisms

seems to be their characteristic *teleological integration* (see Queller and Strassmann 2009, 3144). The parts of organisms seem, in some biologically relevant sense, to be *designed* for fulfilling their functions within those organisms. In Achinstein's terminology, the parts of organisms have *design* functions. For instance, hearts do not merely fulfil the role of pumping blood within organisms with circulatory systems, they are (evolutionarily) *designed* for doing so.

Insofar as functional ecology conceives the functions fulfilled by organisms within ecosystems as *use* and *service* functions (in contrast to *design* functions), then functional ecology does not attribute to ecosystems the kind of teleological integration commonly attributed to individual organisms. From the theoretical perspective of functional ecology, ecosystems are functionally organized in a much weaker way than paradigm individual organisms. They are functionally organized not in virtue of being superorganisms shaped by ecosystem-level selective processes, but, more weakly, in virtue of being more or less self-maintaining networks of organisms involved in use and service interactions with each-other. Those use and service interactions collectively generate the ecosystem processes in relation to which functional ecologists ascribe functions to organisms. This view of ecosystem functional organization contrasts with that espoused by mid-Twentieth century ecologists who depicted ecosystems as tightly unified *superorganisms* shaped by community or ecosystem-level natural selection.

14.4 What Is an Ecological Function, Then?

In the previous section, I identified three aspects of functional ecology's understanding of ecological functions that do not align with the selected effect theory of function:

1. Functional ecology conceives ecological functions as *context-based* rather than *history-based* properties of organisms
2. Functional ecology attributes to the ecological function concept the aim of explaining ecosystem processes rather than that of explaining the presence of organisms within ecosystems
3. Functional ecology conceives the ecological functions of organisms as *use* and *service* functions rather than *design* functions

Those three aspects, I think, indicate that, contrary to what is often assumed (see Sect. 14.2), the ascription of ecological functions to organisms in functional ecology does not hinge on claims that natural selection customarily operates at the level of ecosystems. Functional ecology's understanding of the function concept diverges from "The Standard Line" on function according to which functions in biology must be understood as naturally selected effects.

Through highlighting the three aspects just mentioned, the above discussion reinforces the near consensus that has recently emerged among philosophers of biology and ecology, according to which the ecological function concept should be eluci-

dated along the lines of non-selectionist alternatives to the selected effect theory of function (see Nunes-Neto et al. 2013).⁷ Philosophers who share this consensus have proposed accounts of ecological functions along the lines of Cummins's (1975) *causal role* theory (Maclaurin and Sterelny 2008, 114–115; Odenbaugh 2010, 251–252; Gayon 2013, 76–77), or along those of Mossio et al. (2009) *organizational* theory of function (Nunes-Neto et al. 2014). How do these accounts stand with respect to functional ecology's use of the function concept?

In some significant respects, the *causal role* theory of function accords with functional ecology's use of the function concept as characterized above. The causal role theory ascribes functions to the parts of biological entities in a way that is entirely independent of their selective history. Function ascriptions, in the causal role theory, serve to identify the particular contributions of the parts of a system to the activities or capacities of that system. This use of the function concept concords with functional ecology's understanding of ecological functions as contributions of organisms to ecosystem processes (see Cooper et al. 2016, sec. 4). Moreover, in line with the above linkage of functional ecology's understanding of functions with Achinstein's notions of *use* and *service* functions (see Sect. 14.3.3), the causal role theory does not confer a privileged epistemic status to the notion of *being the function of* over that of *functioning as* (see Cummins 1975, 762; Craver 2001, 55). Thus, the causal role theory seems to better accord with functional ecology's use of the function concept.

However, a significant limitation of the causal role theory in relation to functional ecology, I think, is its ultimate relativization of functions to the epistemic interests of researchers. According to the causal role theory, parts of a system can be ascribed functions in relation to any capacity or activity of this system that researchers are interested in explaining, provided that the relation between this capacity or activity and the individual contributions of the system's parts is complex enough.⁸ As many critics of the causal role theory point out, one problem with this liberal take on functions is that it implausibly entails that functions can be ascribed to the parts of a system on account of their contributions to capacities that amount to deteriorations of those systems (e.g. that a function can be ascribed to a tumour on account of its contribution to the capacity of an organism to die from cancer, see Neander 1991, 181). Thus, on a causal role account, ecological functions could, for instance, be ascribed to organisms from an invasive species on account of their contribution to the ecosystem's capacity to collapse (the fragilization of ecosystems and their possible collapse resulting from the establishment of invasive species is indeed something that ecologists are interested in explaining). Such a degree of inclusive-

⁷Dissenters from this consensus are Bouchard (2013) and Dussault and Bouchard (2017), who argue that ecological functions should be understood as contributions to ecosystem fitness (conceived as ecosystem resilience). It should nonetheless be noted that Dussault and Bouchard do not advocate a selected effect account of ecological functions, but rather a forward-looking evolutionary account derived from Bigelow and Pargetter's (1987) dispositional theory of function.

⁸For more details on how causal role theorists substantiate this complexity requirement, see Cummins (1975, 764), Davies (2001, chap. 4), and Craver (2001, sec. 3.2).

ness, I think, does not appropriately reflect the fact that functional ecologists tend to ascribe functions to organisms mainly in relation to capacities or activities of ecosystems that contribute to those ecosystems' ability to maintain themselves. Those processes include primary productivity, nutrient cycling, water uptake, storage of resources, etc. (see, enumerations of ecosystem processes in Walker 1992, 20; and Blondel 2003, 226). Thus, the common objection that the causal role theory is overly liberal also seems to apply in the case of ecological functions.

An organizational account of ecological functions would avoid this problem. The organizational theory defines the functions of the parts of a system as their contribution to the ability of the system to maintain its organization (see Mossio et al. 2009). Such a linkage between functions and the self-maintenance of systems excludes function ascriptions in relation to capacities that amount to deteriorations of systems (see Nunes-Neto et al. 2014, 137–138). In this respect, the organizational theory of function seems to restrict function ascriptions in a way that is consistent with the use of the concept in functional ecology.

However, an important limitation of the organizational theory in relation to functional ecology, I think, is that it shares with the selected effect theory the idea that function ascriptions in part explain the presence of function bearers within systems. According to the organizational theory, a biological item has a function within a system if, on the one hand, it contributes to the maintenance of the organization of this system, and if, on the other hand, it is in turn maintained by the organization of the system (Mossio et al. 2009, 16–20). Thus, according to the organizational theory, the function bearing parts of a system indirectly contribute to (and therefore explain) their own presence within this system through contributing to that system's maintenance. In this regard, the organizational theory is similar to the selected effect theory (though, in contrast to the selected effect theory, the organizational theory does not make it a requirement that natural selection be the process through which the function bearing parts of systems promote their own presence). The organizational theory therefore attributes to function ascriptions an explanatory aim that is foreign to functional ecology's understanding of the concept. As seen in Sect. 14.3.2, ecological functions as understood in functional ecology are not conceived as explanatory of the presence of organisms within ecosystems. The presence of organisms within ecosystems is explained by their belonging to some *guilds* and *functional response groups*, not by their belonging to some *functional effect groups*. Ecological function ascriptions and the grouping of organisms in *functional effect groups* serve to explain the realization and maintenance of ecosystem processes through delineating the particular contribution of organisms to those processes.

Hence, neither the *causal role* nor the *organizational* account of ecological functions fully accord with functional ecology's use of the function concept. The observations made in this section, however, suggest that functional ecology requires an account of functions that combines aspects of those two accounts while eschewing some of their other aspects. An elaboration of such an account must be deferred to future work.

14.5 Conclusion

In the preceding sections, I criticised the common supposition that the ascription of ecological functions to organisms in functional ecology hinges on claims that natural selection customarily operates at the level of ecosystems. This supposition, I maintained, rests on the incorrect assumption that the function concept as understood in functional ecology aligns with the selected effect theory of function advocated by many philosophers of biology (sometimes deemed “The Standard Line” on functions). After exploring the implications of Wilson and Sober’s defence of multilevel selection for the prospects of defending a selected effect account of ecological functions, I identified three main ways in which functional ecology’s understanding of the function concept diverges from the selected effect theory. Specifically, I argued (1) that functional ecology conceives ecological functions as *context-based* rather than *history-based* properties of organisms; (2) that it attributes to the ecological function concept the aim of explaining ecosystem processes rather than with that of explaining the presence of organisms within ecosystems; and (3) that it conceives the ecological functions of organisms as *use* and *service* functions rather than *design* functions. I then briefly discussed the recently proposed accounts of ecological functions along the lines of the causal role and organizational theories of function, and concluded that functional ecology requires an account of functions that selectively draws on those two accounts.

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