Two Notions of Ecological Function

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Abstract

This paper discusses Millstein's (2020) criticism of the consensus view formed against selected-effects ecological functions. I argue that Millstein's defense of coevolution-based selected-effects ecological functions applies to a notion of function as an *activity*, whereas proponents of the consensus view are concerned with a notion of ecological function as the contribution of an organism, population, species, or abiotic item to the maintenance of its community and/or the functioning of its ecosystem. Millstein's arguments hence do not invalidate the consensus view, but draw attention to a notion of function that has been neglected in philosophical discussions and that deserves more attention.

1. Introduction

Philosophers of biology have recently become interested in ecologists' descriptions of organisms, species, and even abiotic items as fulfilling functions or roles within ecological communities and ecosystems (see, e.g., Maclaurin and Sterelny 2008, sec. 6.2; Odenbaugh

2010, sec. 3; Nunes-Neto, Moreno, and El-Hani 2014; Dussault and Bouchard 2017; Dussault 2018; Lean 2020). Despite the novelty of the topic, philosophers who have contributed to it seem to have reached an "implicit consensus" (see Nunes-Neto, Moreno, and El-Hani 2014, 124; Dussault 2018, 2–3). The consensus view is that ecologists' ascriptions of functions cannot be accounted for through the prism of the *selected-effects* theory of function advocated by many philosophers of biology (e.g., Millikan 1989; Neander 1991; Garson 2017; see also Wright 1973). A selected-effects account of ecological functions would require the general occurrence of community- or ecosystem-level selection, while contemporary biologists and ecologists tend to conceive natural selection as primarily operating at the level of individual organisms (or their genes). This consensus view is significant, since the selected-effects theory is often regarded as the most influential philosophical theory of function (e.g., Lewens 2007, 530).

In a recent issue of this journal, Roberta Millstein (2020) challenges this consensus view and defends the possibility of selected-effects ecological functions based in *coevolution* between species, rather than in community- or ecosystem-level selection. Since coevolution is more prevalent in communities and ecosystems than community- or ecosystem-level selection, Millstein's arguments entail that more of the ecological functions recognized by ecologists can be interpreted as selected-effects than proponents of the consensus view assume, thereby making a selected-effects account of functions more relevant for ecology.

This paper proposes a clarification of the implications of Millstein's arguments regarding the consensus view.[1] I will maintain that Millstein's arguments apply to a notion of function or role that is distinct from the one with which proponents of the consensus view have been concerned, such that Millstein's arguments and those of proponents of the consensus view do not contradict each other. I will also contend that the main import of Millstein's discussion is that it makes plain the need to distinguish two complementary notions of ecological function, each tied to distinct epistemic aims pursued in ecology, and one of which has been neglected in philosophical discussions of ecological functions. This contention stands in line with Millstein's pluralistic stance on functions (Millstein 2020, 1107), while clarifying the nature of this pluralism in the context of ecology.

In section 2, I will give more details about the consensus view, and summarize Millstein's challenge to it. In section 3, I will spell out the above-mentioned distinction between two notions of ecological function or role, and situate Millstein's arguments with respect to them. In section 4, I will link the distinction presented in section 3 with with two corresponding modes of functional classification that ecologists apply to organisms: *guilds* and *functional-*

[1] Here, I will be concerned exclusively with Millstein's defense of selected-effects ecological functions, not with her attribution of a selected-effects understanding of functions to Aldo Leopold.

effect groups. In section 5, I will summarize my account of the implications of Millstein's arguments.

2. The consensus view and Millstein's challenge

The consensus view referred to above supports a negative thesis: ecological functions cannot generally be interpreted as selected-effects functions. Its proponents differ as to the positive theses that they defend. Some advocate an account along the lines of Cummins's (1975) *causal role* theory of function (Maclaurin and Sterelny 2008; Odenbaugh 2010); others promote an account derived from Mossio et al.'s (2009) *organizational* theory (Nunes-Neto, Moreno, and El-Hani 2014); still others support an account that extends Bigelow and Pargetter's (1987) *contribution to fitness* theory to ecosystems (reinterpreting Darwinian fitness as a propensity to persist) (Dussault and Bouchard 2017); and Lean (2020) adopts a pluralistic view. This variety of accounts implies divergences on key issues. One important divergence is whether ecological functions should or should not be conceptually dissociated from evolutionary considerations (the *causal role* and *organizational* accounts advocate such dissociation, while the *contribution to fitness* account preserves a connection between functions and Darwinian fitness—reinterpreted as persistence). Related issues are whether communities and ecosystems may legitimately be regarded as functionally organized entities or systems, and the extent to which our understanding of their functional organization should be based in evolution. Proponents of the consensus view also differ over whether their accounts are focused on communities (Maclaurin and Sterelny 2008; Lean 2020), or on

ecosystems (Odenbaugh 2010; Nunes-Neto, Moreno, and El-Hani 2014; Dussault and Bouchard 2017; Dussault 2018).

Nevertheless, these versions of the consensus view share two key ideas:

A conceptual claim: An ecological item (organism, population, abiotic item) can have a selected-effects ecological function only if some of its traits have been shaped by natural selection operating on its community or ecosystem as a whole; and

An empirical claim: Since community- and ecosystem-level selection occur rarely, only few of the ecological functions recognized by ecologists can be interpreted as selected-effects functions, and a general selected-effects account of ecological functions is therefore implausible.

Millstein challenges the conceptual claim.[2] She starts by considering two commonsensical broadly defined ecological functions (or roles): *predation* and *parasitism*. Drawing on John Thompson's (1994; 2005) account of coevolution, she argues that such broadly defined ecological functions or roles do not accurately reflect how specialized ecological interactions that occur within ecological communities tend to be. As Thompson highlights, although generalist species exist, "most species are specialized to interact with only a few other

[2] For a discussion of the empirical claim and an alternative argument against selected-effects ecological functions, see Dussault (2018).

species" (Thompson 1994, 121; quoted in Millstein 2020, 1111). Through coevolutionary interactions with other species, most species have acquired traits that constrain them to feed upon, compete against, and seek to avoid a very restricted number of species. Similar specialization also commonly occurs among different populations of the same species.

According to Millstein, the fact that most species are specialists entails that broadly defined ecological functions or roles like *predator* and *parasite* are misguiding. Instead of focusing on such broad roles, we should focus on more specialized ones such as "predator of type of organism *X*" or "parasite of population *Y*." These are the roles organisms actually perform; for instance, what qualifies the blister beetle in general as a parasite is the fact that the Oregon blister beetle is a dune silver bee parasite and the Mojave Desert blister beetle is a white-faced bee parasite.

Millstein contends that when ecological functions are defined with this higher degree of specificity, their selected-effects character and their rootedness in past coevolution become obvious:

> What makes the functional role claim, "The blister beetle is a parasite" true is that there was coevolution between the Mojave Desert blister beetle and the white-faced bee as well as coevolution between the Oregon blister beetle and the dune silver bee. In other words, both populations of blister beetle underwent reciprocal natural selection to

> become parasites to their respective hosts, underwriting the functional role claim(s), from specific to general. (Millstein 2020, 1113)

Hence, a particular species S_1 or population P_1's being the predator or parasite of another species S_2 or population P_2 is a *selected effect*. It is an effect of selection on members of S_1 or P_1, favoring traits that enable them to (more efficiently) prey on or parasitize S_2 or P_2.[3]

3. Two notions of ecological function or role

In the ecological literature, the terms "function" and "role" are often used ambiguously. Jax (2005, 641–42) identifies four function-related concepts used by ecologists: (1) function as an interaction between two species; (2) the functioning of a complex system; (3) function as the role of an organism, species, or abiotic item in a community or ecosystem; and (4) ecosystem services.

Jax's third notion, however, remains ambiguous, and, I submit, can mean at least two different things: either (3a) a type of *activity* that occurs across communities or ecosystems

[3] I should note that the degree to which Millstein's account can be generalized partly hinges on how prevalently species interactions within communities are shaped by local coevolution, as opposed to "ecological fitting," the association of organisms based on traits that have evolved elsewhere and in response to different environmental conditions (e.g., Agosta and Klemens 2008). I leave this issue aside here.

(e.g., predation, parasitism); or (3b) the *contribution* of such an activity to the maintenance and/or functioning of the community or ecosystem within which it occurs.[4] With respect to general uses of the term "function," 3a is an ecological version of the notion of function involved in the structure/function or form/function distinction (on this notion, see Wouters 2003, sec. 2.1; Gayon 2010, 127–29). Roughly, "function" in this sense distinguishes what an item does or is capable of doing from what it is made of, what it looks like, or where it originates from. Equating "function" in this sense with "role" involves a notion of role as a position that something may occupy in an abstract model, and which might (at least in principle) be occupied by more than one type of thing. "Ecological role" is sometimes used in this sense by biologists and philosophers of biology in discussing ecological niches as "places" that can (in principle) be occupied by different species or populations in an abstract model of communities, similar to "roles" in a play, which can be taken on by different actors in different circumstances (e.g., Hull 1987, 179; Colwell 1992, 242–43; Sterelny 2001, 153–54).[5] Importantly, this notion of ecological role does not imply any idea of contribution to the activities or capacities of a higher-level system. What it characterizes is simply how a type of

[4] Millstein (2020, 1109n1) recognizes the ambiguity of Jax's third notion, but interprets 3b in a different way than I do. The below discussion will motivate my interpretation.

[5] The ecological roles, though, need not be static or predefined as the "roles in a play" analogy may suggest.

organism is disposed to interact with other types of organisms, and, as a result of this, what place it occupies within the interactive network that constitutes its community.

In contrast, 3b is an ecological version of the notion of function involved in characterizations of how the traits and parts of a biological system (typically an organism) contribute, or are supposed to contribute, to the capacities or activities of this system. This notion is the one that has been the focus of philosophical discussions of function (for reviews, see Wouters 2005; Lewens 2007; Garson 2016). The various theories offered by philosophers of biology differ mainly over what they take to be the relevant systemic activities or capacities in relation to which functions should be defined, and over whether they take functions to be *actual* contributions of traits and parts to those systemic activities or capacities, or rather contributions they are *supposed* to achieve. For instance, the *causal-role* theory sees *any* systemic activity or capacity as potentially relevant, and focuses on the *actual contributions* of traits and parts (Cummins 1975), whereas the *selected-effects* theory restricts relevant activities and capacities to *those that are products of selection*, and focuses on contributions that traits and parts are *supposed to* achieve (e.g., Millikan 1989; Neander 1991; Garson 2017; see also Wright 1973). Equating "function" in this sense with "role" involves a notion of role that is bound up with biologists' thinking about the part-whole organization of living entities. A role, in this sense, is something that a system's part does (or is supposed to do) in the context of that system, and which, collectively with other roles fulfilled by other parts, realizes overall capacities or activities of this system. "Ecological role" is used in this sense by

ecologists and philosophers of ecology when they discuss roles fulfilled by organisms, species, or abiotic items within communities and/or ecosystems conceived as functionally organized systems (analogously, though only weakly so, to individual organisms) (e.g., Odum 1971; Schulze and Mooney 1993; Naeem 2002). The "ecological roles" of organisms, species, or abiotic items here consist (roughly) in their contributions to the maintenance of their communities and/or the functioning of their ecosystem (i.e., ecosystem-level processes such as nutrient cycling and energy flow, Jax's concept (2) identified above).

I submit that proponents of the consensus view against selected-effects ecological functions have been concerned with ecological functions or roles in the 3b sense. What they deny is the general possibility of a selected-effects account of the notion of ecological function that denotes organisms', species', and abiotic items' contributions to the capacities or activities of communities and/or ecosystems. This is the notion that they are concerned with when they claim that a selected-effect account of ecological functions would implausibly require the general occurrence of community- or ecosystem-level selection. To use Sober's (1984) well-known distinction, without community- or ecosystem-level selection, there could be *selection of* traits that lead organisms or populations to contribute the maintenance of their community or the functioning of their ecosystem, and therefore to fulfill ecological functions in the 3b sense, but these traits could not be *selected for* their 3b ecological functions. The reason for this is that only selection at community or ecosystem levels seems capable of selecting organismal traits for how they contribute to community maintenance or ecosystem

functioning (as opposed to selecting them for effects that are beneficial to the organisms themselves). Hence, ecological functions as contributions to community maintenance or ecosystem functioning seem better construed as non-selected-effects functions, functions that organisms, populations and abiotic items fulfill without necessarily having been shaped by natural selection to fulfill them. They are functions along the lines of alternatives to the selected-effects theory, such as the causal role, the organizational, or the contribution to fitness theory (see Maclaurin and Sterelny 2008; Odenbaugh 2010; Nunes-Neto, Moreno, and El-Hani 2014; Dussault and Bouchard 2017; Lean 2020).

That what proponents of the consensus view deny is the general possibility of selected-effects ecological functions in the 3b sense, as opposed to 3a, is apparent in their discussions. This is particularly so in Odenbaugh's (2010, 250–51) discussions of the ecological functions of fungi and *Rhizobium.* What Odenbaugh denies is not that the *activities* by which fungi and *Rhizobium* achieve their ecological functions—namely, the decomposition of woody product and the fixation of nitrogen—are selected effects, but that those activities have been selected for their contributions to the ecosystem level processes (respectively, the carbon and nitrogen cycles). It is also apparent in MacLaurin and Sterelny's (2008, 114–15) discussions of the ecological functions of eucalypts in Australian woodlands and of keystone predators like starfish. They are not concerned with whether eucalypts' flammability and starfish's predation on mussels are selected effects, but with whether those effects have been selected for their contributions to the overall behavior of the eucalypts' ecosystem and the maintenance of

diversity, respectively. Nunes-Neto et al. (2014), Dussault and Bouchard (2017), and Dussault's (2018) general focus on the use of the function concept to denote the contributions of biodiversity items (e.g., traits, populations, functional groups) to ecosystem-level processes, also makes clear that their rejection of selected-effects ecological functions concerns functions as contributions to the capacities or activities of a higher-level system (i.e., 3b).

Millstein's discussion, in contrast, as she herself highlights (Millstein 2020, 1109n1), is concerned with functions as *activities*, and hence with ecological functions in the 3a sense. Strictly speaking, *predation* and *parasitism* and their more specialized subdivisions (Millstein's paradigmatic examples of coevolution-based selected-effects ecological functions), are not ecological roles in the sense of contributions to capacities or activities of communities or ecosystems (3b). They are types of feeding activities that are realized by many types of organisms, and which determine the types of ecological interactions they will be involved in and the "place" that they will tend to occupy in communities (3a). Those feeding activities will indeed have community- and/or ecosystem-level effects, and will therefore engage the organisms that realize them in the fulfillment of ecological functions in the 3b sense. Typically, predators and parasites will contribute to the circulation of nutrients and energy through their ecosystems and to the regulation of the populations that they consume. However, contributions to nutrient and energy circulation and to population regulation are not *equivalent* to predation and parasitism; these contributions are the community- and ecosystem-level *consequences* of these activities and they are not themselves selected for under predator-

prey or parasite-host coevolution.[6] Hence, predation and parasitism, Millstein's paradigmatic examples of coevolution-based selected-effects ecological roles, illustrate the notion of function as an *activity,* and the notion of ecological role as a position that a species or a population occupies in a model of a community (i.e., 3a).

Millstein and proponents of the consensus view are thus concerned with two distinct notions of ecological function, and their arguments therefore do not contradict each other. Hence, Millstein's defense of the possibility of coevolution-based selected-effects ecological functions in the 3a sense does not invalidate the consensus view. Selected-effects ecological functions in the 3b sense still (implausibly) require the general occurrence of community- or ecosystem-level selection, because only selection at those levels can favor some organisms' traits on the basis of their contribution to their community or ecosystem.

4. Guilds versus functional-effect groups

The two notions of ecological function distinguished in the previous section essentially correspond to two concepts that underlie functional classifications used by ecologists, in relation to which they use the term "functional role": *guilds* and *functional-effect groups*

[6] Lean (2020, 5n1) makes a similar point when he notes that, "without 'selection of' ecosystems," it is hard to see "how to connect [Millstein's] co-evolutionary roles with the larger ecological community they sit within."

(Blondel 2003; Stroud et al. 2015, 4762).[7] *Guilds* are groups of organisms that use similar resources in similar ways—for instance, predators, grazers, seed eaters, and their more fine-grained subgroups (Root 1967; Simberloff and Dayan 1991; Blondel 2003; de Satgé, Teichman, and Cristescu 2017). The classification of organisms into guilds is primarily tied to the aim of studying competition and coexistence among species using similar resources, as well as the coevolutionary specialization that typically results from competition among guild members. *Functional-effect groups*, in contrast, are groups of organisms that contribute similarly to some important ecosystem process or community property—for example, producers, primary and secondary consumers, seed dispersers, and their more fine-grained subgroups (Naeem 2002; Blondel 2003; Thornhill et al. 2018). The classification of organisms into functional-effect groups is tied to the epistemic aim of explaining and predicting the effects of changes in the species composition of communities on ecosystem processes and on their ability to maintain themselves. The guild concept thus essentially corresponds to 3a ecological functions, whereas the functional-effect group concept essentially corresponds to 3b.

[7] Blondel uses the simpler term "functional group" for what I introduce here as "functional-effect group." The latter expression, however, is more commonly used by ecologists (e.g., Lavorel and Garnier 2002; Hooper et al. 2002).

The contrast between guilds and functional-effect groups has proven important for ecological research, because organisms that belong to the same guild need not belong to the same functional-effect group, and vice-versa (see Blondel 2003, 228; Stroud et al. 2015, 4762). For instance, birds that consume fruits and seeds, and thus belong to frugivore and granivore *guilds*, need not all belong to seed-dispersers *functional-effect groups*. Only those that do not fully digest the seeds (and defecate or regurgitate them elsewhere) disperse them. Conversely, seed dispersers need not be *consumers* of fruits and seeds. Some birds passively disperse seeds by catching them in their plumage and dropping them elsewhere. A model that mixes up guilds and functional-effect groups can therefore have limited explanatory and predictive power.

The contrast between guilds and functional-effect groups indicates that the above distinction between 3a and 3b ecological functions is important for ecological research, and that the 3a notion on which Millstein focuses is one that ecologists actually use. Hence, a significant import of Millstein's discussion is that it draws attention to a notion of ecological function or role that has been neglected in philosophical discussions, but is central to some ecological research programs.

5. Conclusion

To the extent that species interactions within communities are shaped by coevolution among the species constituting them, Millstein seems to be correct that the notion of ecological function she focuses on is suitable to a selected-effects interpretation. Guilds,

insofar as they are shaped by coevolutionary interactions among species, seem plausibly envisioned as selected-effects functions in the 3a sense. However, this result concerns a notion of function that is distinct from the one that the consensus view and philosophical theories of function in general are focused on. Proponents of the consensus view, in line with general theories of function developed in the philosophy of biology, have been concerned with ecological functions or roles as contributions of ecological items to community- or ecosystem-level capacities—i.e., with function in the 3b sense. Those ecological functions, even if Millstein's arguments are correct, remains unsuitable to a general selected-effects account, because such an account would require the general occurrence of community- or ecosystem-level selection. Millstein nevertheless draws attention to a notion of ecological function that seems suitable to a selected-effects account and that is central to some ecological research programs.

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