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RESEARCH ARTICLE

Generalized Selected Effects Functions and Ecology

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Expanding upon the "classical" selected effects (SE) theory of function, Justin Garson's generalized selected effects (GSE) theory states that functions may derive not just from natural selection, but from a broader range of selection processes involving differential retention as well as reproduction. In this paper, we consider whether the GSE theory's broadened range of selection processes makes it more promisingly applicable to ecology than the classical SE theory. We argue that, although a GSE account of ecological role functions would evade some of the reasons that the SE theory of function has been considered poorly applicable to ecology, alternative theories of function, and notably the persistence enhancing propensity (PEP) account of ecological role functions, remain more appropriate partly given the purpose for which the concept of role function is used in ecology. The GSE theory's backward-looking character meshes poorly with the fact that, in ecology, the concept of role function is used mainly to explain how ecosystems are able to achieve their processes reliably rather than to explain the presence of certain ecological items (e.g., organisms, populations, species) within them. We argue this in part by comparing the implications of a GSE account of ecological role functions with those of the PEP account with respect to three types of cases: dormant species, sink populations, and abiotic items. We draw out implications of our discussion for Garson's take on function pluralism and his overall defense of the GSE theory.

Keywords

selected effects theory • ecological role functions • ecosystem selection • biodiversity and ecosystem function • contribution-to-fitness theory of function • function pluralism

1. Introduction

In a series of publications, Justin Garson has developed and defended a *generalized selected effects* (GSE) theory of function, which, as its name suggests, consists in an expansion of the "classical" selected effects (SE) theory (e.g., Garson 2016, sec. 3.4; 2017, 2019, 2024). The SE theory

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states that a biological item's function is an effect of that item that led it to be favored by natural selection (e.g., Millikan 1989; Neander 1991; Godfrey-Smith 1994; see also Wright 1973). The GSE theory broadens this picture, and states that functions may derive from *any* selection process operating on a population of the appropriate type, rather than from natural selection exclusively. Relevant selection processes may involve differential reproduction (just like in standard natural selection), but also differential retention or persistence. The GSE theory is among the most important recent contributions to the function literature in the philosophy of biology. Garson's case for its superiority over the classical SE theory is strong, and, as he remarks, the theory addresses an issue of excessive restrictiveness that the classical SE theory has commonly been thought to raise. Its broadened picture of the selection processes from which biological items may acquire functions makes the GSE theory more easily applicable to biological domains that have seemed to fall outside the scope of function theories of the SE family (henceforth SE theories). In particular, it more straightforwardly applies to neurons and neural elements by means of neural selection, and to behavioral dispositions by means of trial-and-error learning (Garson 2016, 56–58, 92–94; 2017, secs. 3–4; 2018, sec. 5; 2019, chaps. 4–5).

In this paper, our focus will be on one particular domain that has been thought to fall outside the scope of SE theories: *ecology*. We will consider whether and to what extent an account of ecosystem natural selection in terms of differential persistence like the one advocated by Frédéric Bouchard and others provides vindication for a GSE account of ecological role functions (Bouchard 2008, 2013a, 2013b, 2014; Bourrat 2014, 2023; Doolittle 2014, 2017, 2019; Inkpen and Doolittle 2021; Papale and Doolittle 2024; Lenton et al. 2018, 2021; Boyle and Lenton 2022). In ecology, ecological role functions are often ascribed to organisms, populations, species, or their traits, in relation to the communities or ecosystems in which they are involved (for discussions, see Jax 2005; 2010, sec. 4.1; Nunes-Neto, Do Carmo, and El-Hani 2016). These role functions link the traits of organisms to their contributions to community- and ecosystem-level processes, such as nutrient cycling, energy flow, pollination, seed dispersal, etc. Philosophers who have discussed these functions have usually considered them incompatible with the SE theory, because interpreting them along its lines would commit one to the at best controversial view that communities and ecosystems are, on a general basis, units of natural selection (Maclaurin and Sterelny 2008, 114; Odenbaugh 2010, 250–51; 2019, 172; Nunes-Neto, Moreno, and El-Hani 2014, 124; Lean 2020, 9320). Given that skepticism with regard to community- and ecosystem-level natural selection is partly based on the observation that communities and ecosystems do not reproduce, the GSE theory's recognition of functions based on differential retention (besides reproduction) makes it look more easily applicable to ecology.[1]

Garson does not discuss ecology in detail, but he points to the hope for an application of the GSE theory to ecology that seemingly resides in Bouchard's account of natural selection in terms of differential persistence (Garson 2019, 150). Bouchard (2008, 2013a, 2013b, 2014) argues that ecosystem evolution by natural selection can take place through the *differential persistence* of ecosystems and hence does not require ecosystem reproduction (see also Bourrat 2014, 2023; Doolittle 2014, 2017, 2019; Inkpen and Doolittle 2021; Papale and Doolittle 2024; Lenton et al. 2018, 2021; Boyle and Lenton 2022).[2] This suggests the possibility of grounding GSE ecological role functions in *ecosystem differential persistence*. Bouchard (2013a) himself defends an account of ecological role functions based on ecosystem differential persistence, though one

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[1] For another attempt at relaxing the SE theory so that it more easily applies to ecology, see Millstein (2020), and see Dussault (2022) for a discussion.

[2] This broader understanding, he claims, is also better suited to account for the evolution of other biological entities, such as clonal organisms and symbioses.

aligning with Bigelow and Pargetter's (1987) evolutionary forward-looking theory of function rather than an SE theory. Dussault and Bouchard (2017) further develop this account and label it the *persistence-enhancing propensity* (PEP) account of ecological role functions. One might ask, however, why could ecosystem differential persistence not also serve as a basis for a GSE account of these functions?[3]

This paper tackles this question. We will consider whether the GSE theory's admission of functions based on differential retention (or persistence) makes it more applicable to ecology than the classical SE theory. Being able to encompass ecology would be a significant achievement for the GSE theory. It would reinforce its ability to evade the above-mentioned issue of excessive restrictiveness allegedly raised by the classical SE theory. We will argue, however, that there is little prospect for a GSE account of ecological role functions, even when ecosystems are conceded to undergo natural selection through differential persistence, and that for two reasons. First, it is unclear whether the kind of natural selection that can be shown to operate on ecosystems meets Garson's conditions for GSE functions. Second, the explanatory purpose for which the concept of role function is used in ecology better aligns with theories of function under which functions explain the higher-level capacities of some systems their bearers contribute to, than with theories under which, like for SE theories, functions explain the presence of their bearers in these systems. The former theories mainly include the *causal role* (or systemic) theory (e.g., Cummins 1975), the *goal-contribution* theory (e.g., Boorse 1976), and the *evolutionary forward-looking* (or contribution-to-fitness) theory (e.g., Bigelow and Pargetter 1987), from which Bouchard and Dussault's PEP account is derived. We will hence argue that an account that links ecological role function to ecosystem-level selection processes would more promisingly be a PEP than a GSE account.

Our goal is thus to use ecology as a test case for the GSE theory, and to assess whether its inclusion of differential retention (or persistence) among selection processes from which functions may arise enables it to bring ecology back within the scope of SE theories (as Garson argues it does for other biological domains that these theories have been thought to exclude). In this regard, the point of our focus on the GSE and PEP accounts' comparative advantages and drawbacks is to untangle two key aspects that distinguish SE theories (including the GSE theory) from most other theories of function—(1) their linkage of function to selection, and (2) the explanatory purpose they assign to the concept of function—in order to show that the latter, not the former, is what ultimately restricts SE theories' applicability to ecology. Since the PEP account shares the former aspect with SE theories, but differs from them precisely regarding the latter aspect, it is especially helpful for untangling those aspects. Hence, although the PEP account will occupy a central place in our discussion, our chief aim in this paper is not to argue for this account (though we indeed hope our discussion will provide some indirect support for it). We will assume, for the sake of the discussion, that there is sufficient provision for linking ecological role functions to ecosystem persistence, and focus on what this implies with regard

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[3] We should note that, although Bouchard and Garson both consider how selection processes involving differential persistence (or retention) may usefully expand standard pictures of naturally occurring selection processes centered on differential reproduction, they pursue different philosophical projects. Bouchard's project is to expand Darwinian *natural* selection and encompass selection through differential persistence within it (see Bouchard 2008, 2009, 2010, 2011). Garson takes no stand in this debate about *natural* selection. Rather, he is concerned with showing that selection through differential persistence generates functions, irrespective of whether it should count as bona fide natural selection (Garson 2017, 526; 2018, 4n5; 2019, 69, 95–96). We intend our argument to hold regardless of which of these two projects is pursued. The main difference is that within a project like Bouchard's, GSE ecological role functions based on ecosystem differential persistence would be functions based in *natural* selection, whereas within Garson's project, they would not necessarily be.

to the prospects for a GSE account of ecological function.[4]

In section 2, we will examine the GSE theory, Garson's reasons for supporting it, and its scope of application. In section 3, we will rehearse some key aspects of the use of "function" in ecology and make a first exploration of the applicability of the GSE theory to ecology. In section 4, we will discuss the applicability of GSE functions to ecology in more detail. We will argue that the PEP account is better applicable to ecology than the GSE account, first, because it is unclear whether ecosystem differential persistence as it can plausibly be thought to generally occur meets Garson's conditions for GSE functions, and second, because the PEP account is more appropriate given the explanatory purpose for which the concept of role function is used in ecology. In section 5, we will link this conclusion to Garson's (2016, sec. 5.3; 2018; 2019, chap. 9) remarks on function pluralism, and suggest some implications for his overall defense of the GSE theory.

2. The Generalized Selected Effects Theory

The GSE theory broadens the classical SE theory and considers that functions may derive from *any* selection process operating on a population. It states that a biological item's function is an effect of that item that has led to its differential reproduction or differential retention in a population of the appropriate type (see Garson 2016, 58; 2017, 534; 2019, 93).[5] As we remarked earlier, an advantage of the GSE theory over the classical SE theory is its ability to encompass uses of function unaccounted for by SE theories, thus dealing with an issue of excessive restrictiveness allegedly raised by the classical SE theory. Garson shows, for instance, that since relevant selection processes occur in the biological domains studied by behavioral sciences, neurosciences, and immunology, the GSE theory is more straightforwardly applicable than the classical SE theory to uses of function that occur in these disciplines (Garson 2016, 56–58, 92–94; 2017, secs. 3–4; 2018, sec. 5; 2019, chaps. 4–5).

Although this is a significant advantage, its comprehensiveness is not, according to Garson, the prime reason for accepting the GSE theory. The prime reason is *parity of reasoning* (Garson 2016, 59; 2017, 530–31; 2019, 73, 93–94). In Garson's view, the classical SE theory's main appeal lies in its ability to make sense of what are often considered as cardinal features of functions, and the GSE theory also makes sense of these features, but with fewer arbitrary restrictions. These cardinal features are: *difference from accident*, i.e., functions differ from lucky beneficial effects (e.g., filtering, warming and moistening the air that enters the body, not holding glasses, are the nose's functions); e*xplanatoriness*, i.e., functions explain the presence of their bearers (e.g., pumping blood is not just an effect that hearts happen to produce, but an effect that explains why many types of animals have hearts); and *normativity*, i.e., function-bearing

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[4] Importantly, the PEP account's linkage of function to ecosystem persistence has faced challenges, to which we will not respond here (see Odenbaugh 2019, 174; Morrow 2023, 447, 449–50). Addressing these challenges would require an extensive discussion which would take us away from the main purpose of this paper. We should note, however, that our linkage of ecological role function to ecosystem persistence is not entirely out of favor among discussants of ecological function. In particular, it is an aspect that the PEP account shares with the organizational account, though the latter account speaks more in terms of ecosystem self-maintenance than of persistence (Nunes-Neto, Moreno, and El-Hani 2014; El-Hani, de Lima, and Nunes-Neto 2024). Moreover, the challenges come mainly from proponents of causal role accounts of ecological functions, whose more liberal take admitting functions detrimental to persistence has been argued to come with costs (see Nunes-Neto, Moreno, and El-Hani 2014, 137–38; Dussault and Bouchard 2017, 1120; though see Morrow 2023 for an innovative approach to the liberality problem developed within the scope of the causal role theory).

[5] Garson's own formulation of the theory speaks of *activities* being functions of *traits*, instead of *effects* being functions of *items*. We focus on *effects* of *items* because this will make comparisons with other theories of function and their ecological applications easier.

items may sometimes be unable to perform their function and/or function inadequately (e.g., a stomach that cannot digest food in the appropriate context is dysfunctional) (Garson 2016, 4–6, 35–36; 2017, 526–27; 2019, sec. 1.1, 2.1). The classical SE theory easily makes sense of these three features: filtering, warming and moistening the air, not holding glasses, are the nose's functions because noses have been selected for the former, pumping blood explains the heart's presence via natural selection for hearts that pump blood, and a non-digesting stomach is dysfunctional because it cannot produce the effect stomachs were selected for. The GSE theory, Garson points out, also makes sense of these features, but does so with fewer arbitrary restrictions. It recognizes as function-bestowing not just natural selection (narrowly construed), but *any* selection processes capable of generating functions that have these three features. Hence, according to Garson, the GSE theory should be adopted because it makes sense of the three (alleged) cardinal features of function in a more principled manner than the other influential theory capable of making sense of these features, namely the classical SE theory.[6]

In order to be precise about the scope of application of the GSE theory, Garson places important restrictions on the type of selection processes that can be considered to generate functions. As mentioned above, according to the GSE theory, functions may derive from any selection process operating *on a population of the appropriate type*. The issue of what *a population of the appropriate type* is has turned out to be a crucial one for the GSE theory. The restriction of relevant selection processes to ones that occur among members of populations is meant to prevent the theory from being overly inclusive (see Garson 2016, 52–54, 60–61; 2017, 535–39; 2019, 102–8; 2024). It intends to exclude seemingly trivial function ascriptions, such as ones applied to rocks differentially eroding on a beach. Since items like rocks on a beach might be regarded as members of populations if one were to adopt a broad enough notion of population, Garson needs to tie the GSE theory to a sufficiently restrictive notion of population.[7] Garson has refined his characterization of populations in the course of developing the theory and responding to criticism (Garson 2016, 54–55; 2017, sec. 5; 2019, sec. 6.3), and his most recent take is that a population is "a collection of individuals, of the same type, that impact one another's persistence, survival, or reproduction prospects by virtue of the fact that, by using some common resources, they impact each other's ability to use those same resources" (Garson 2024, 964).[8] Competition, cooperation, and parasitism are examples of interactions by which individuals may impact one another's access to resources. According to Garson, this characterization of populations differentiates between selection processes that are GSE-function-bestowing and those that are not (e.g., ones that occur between rocks differentially eroding on a beach). These conditions for function-bestowing selection processes will be an important reference point in our below discussion of whether GSE ecological functions can be grounded in ecosystem differential persistence as characterized by Bouchard and others.

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[6] Another theory that claims to make sense of these features is the organizational theory (e.g., Mossio, Saborido, and Moreno 2009). For Garson's criticism of that theory (and hence his reasons for preferring the GSE theory over it), see Garson (2016, 102–5; 2019, 48–57).

[7] Of course, not everyone would hold back from ascribing functions to items like rocks and/or from considering them as capable of undergoing selection processes. Van Valen (1989, 2), for instance, considers that grains of minerals that compose granite (mainly feldspars and quartz) undergo a form of natural selection. Relatedly, Bourrat (2021, 66) argues that a proponent of the GSE theory should simply accept the result that rocks differentially persisting bear functions.

[8] Some of the criticism came from Conley (2020), Schulte (2021), and Bourrat (2021). For Garson's response, see Garson (2024, sec. 4), and for further criticism, see Dussault (2023, sec. 10.2).

3. GSE Ecological Role Functions, a First Exploration

The term "function" is used in various ways in the ecological literature. Jax (2005, 641–42; 2010, 62–65) identifies four uses of the term: (1) function as an ecological interaction; (2) the overall functioning of an ecological system; (3) the functional role of an organism, species, or abiotic item in a community or ecosystem; and (4) ecosystem services. Philosophers discussing ecological function have focused on the third concept. We also take this concept as our focus here—and have referred to it with the phrase "ecological role function." As Jax (2010, 65) remarks, this concept most closely corresponds to the concept of function on which philosophical theories of function have generally tended to focus, though, of course, these theories were developed in reference to the parts and traits of individual organisms rather than to organisms, species and abiotic items as functional components of ecosystems (for reviews, see Wouters 2005; Lewens 2007; Garson 2016). Using this concept, ecologists describe organisms and species, for instance, as primary producers, others as nitrogen fixers, still others as pollinators, and so on. When they do so, they are somewhat linking Jax's third concept with his second concept, defining the functional roles that organisms fulfill in ecosystems with respect to ecosystem-level processes constitutive of their overall functioning, e.g., productivity, nutrient cycling, pollination, and so on. The aim is to explain how these processes are reliably achieved, and to predict whether and when changes in the species composition of ecosystems will affect the performance of these processes.

The concept of ecological role function occupies a central position in a research domain called *biodiversity and ecosystem* (BEF) research (Naeem 2002; Loreau 2010), a domain in which ecologists seek to establish explanatory relations between the amount and type of biodiversity present in ecosystems and their carrying out of ecological processes such as those just mentioned. In this research, ecological role functions underlie a particular type of functional classification of organisms and species: *functional effect groups,* which gather organisms according to how their traits dispose them to achieve similar contributions to such processes (Jax 2010, 54; see Lavorel and Garnier 2002; Hooper et al. 2002). The idea is that organisms whose traits dispose them to achieve different contributions to ecological processes are *complementary* to each other, whereas organisms whose traits dispose them to achieve similar contributions may, under some conditions, be *substitutable* (see Jax 2010, 53). Hence, ecologists use ecological role functions to delineate the contributions that components of ecosystems make to ecological processes and, in so doing, to formulate explanations and predictions that link changes in the species composition of ecosystems to eventual changes in their functioning.

Our discussion here will thus be centered on this concept of ecological role function. Our question will be: does Bouchard and others' account of ecosystem selection in terms of differential ecosystem persistence provide vindication for a GSE account of the concept of ecological role function? That is, could an account linking ecological role functions to ecosystem persistence be a GSE account instead of (or as well as) a PEP account?

To approach this question, it will be useful to flesh out what PEP and GSE accounts of ecological role function might look like. Dussault and Bouchard's (2017) PEP account, which, as we mentioned, is derived from Bigelow and Pargetter's (1987) evolutionary forward-looking theory of function, can be formulated as follows:

> [PEP-ECO-F] The ecological item I has the ecological role function F in ecosystem E_1 if and only if I's presence in E_1 enhances E_1's propensity to differentially persist over alternative ecosystems E_2, E_3, E_4, etc., which are also suited to maintain themselves for some time under the environmental conditions that prevail in

> the area in which E_1 is located.[9]

Drawing on Garson's discussions, a GSE account of ecological role function can be formulated as follows:

> [GSE-ECO-F] The ecological item I has the ecological role function F in ecosystem E_1 if and only if I is present in E_1 in part because its past presence in it contributed to E_1's differential persistence over alternative ecosystems E_2, E_3, E_4, etc., which were also suited to maintain themselves for some time under the environmental conditions that prevail in the area in which E_1 is located.

At first glance, a GSE account would seem to share some of the advantages that Bouchard and Dussault claim for their PEP account over an account derived from the classical SE theory. The GSE account would seem to share the advantage that the PEP account gains from giving up the importance assigned to reproduction by the classical SE theory (Bouchard 2013a, 88–90; Dussault and Bouchard 2017, 1123, 1125). Since both accounts consider differential persistence as sufficient for the generation of functions, both theories seem prima facie equally able to ascribe functions to components of ecosystems even though they do not reproduce.

Another advantage that the GSE account would seem to share with the PEP account concerns the possibility of ascribing functions to components of transient ecosystems. As Bouchard (2013a, 93–94) notes, many ecosystems are like Donald Davidson's (1987) "Swampmen," that is, they appear and disappear much more transiently than other biological systems. This, he argues, implies that a nonhistorical account of function (like the PEP account) is more useful with respect to transient cases than a historical account (like one derived from the SE theory). For instance, a (happenstance) landslide initiates new ecosystems that will be subject to selective pressures and may eventually evolve, and likewise, a (one-off) hurricane rearranges marshes and establishes new relationships between their component species (Bouchard 2013a, 93). Along similar lines, Dussault and Bouchard (2017, sec. 3.2) maintain that the PEP account has the advantage of being applicable to "Gleasonian ecosystems" formed through the contingent assemblage of populations whose previous evolutionary trajectories are independent.

A GSE account would, it seems, be equally applicable to such transient ecosystems. Although, like the classical SE theory, the GSE theory is historical, it is not so in a way that excludes short-lived systems. However transient they might be, the ecosystems portrayed by Bouchard and Dussault presumably persist at least for some time—indeed, they otherwise could not achieve *differential* persistence. Hence, these ecosystems *do* eventually come to have histories, albeit possibly short ones. Moreover, if their differential persistence partly results from the presence of some types of organisms within them, and if the persisting ecosystems provide these organisms with favorable conditions, then the organisms will be in a position to acquire GSE ecological role functions in the ecosystems. They will acquire such functions whenever their presence in the ecosystems comes to partly result from their contributions the ecosystems' differential persistence. In other words, provided that some ecosystems, although transient, have propensities to persist long enough for their differential persistence to be relevantly explained through the ascription of PEP functions to their components, then it may seem that, quite likely, they will persist long enough for their persistence-enhancing components to acquire GSE role functions within them.

So it seems, at first glance, that a GSE account of ecological role functions based on ecosystem differential persistence would share some important advantages claimed by Bouchard and Dussault for the PEP account over an account based on the classical SE theory. However, we will see in the next section that the issue is more complicated than it may seem at first glance.

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[9] For another formulation, see Dussault and Bouchard (2017, 1122).

4. Ecosystem Persistence and GSE vs. PEP Ecological Functions

4.1. Ecosystem Persistence and GSE-Function-Bestowing Processes

A first complication arises from Garson's conditions for GSE-function-bestowing selection processes (see sec. 2). As we may recall, according to Garson, a selection process is GSE-function-bestowing if it occurs among "a collection of individuals, of the same type, that impact one another's persistence, survival, or reproduction prospects by virtue of the fact that, by using some common resources, they impact each other's ability to use those same resources" (Garson 2024, 964). Bouchard and others' account of ecosystem evolution by differential persistence truly vindicates a GSE account of ecological function only if differential persistence as it can plausibly be thought to occur among ecosystems meets those conditions.

Does ecosystem differential persistence as construed by Bouchard and others meet those conditions? The conditions seem to require that differential persistence occur among a collection of reasonably discrete ecosystems that synchronically exist and contend for similar resources.[10] Ecosystems, however, have at best porous boundaries, so delineating ecosystems that can be envisioned as contending with each other for the same resources is far from straightforward. Garson (2017, 535) himself notes that ecosystems do not seem to form populations. The "discrete ecosystems" requirement might be relaxed, however, by adopting Bouchard's (2014) suggestion that, in the case of ecosystems, differential persistence is more fruitfully understood as occurring among the *parts of a more encompassing entity* than among *individuals belonging to populations* (in a way similar to how intraorganismal selection may be thought to occur in some plants and fungi; see Bouchard 2008, 2011; Clarke 2011, 2012; Booth 2014). The picture would then be of a larger ecosystem with sections that—although not discretely separate from each other or from the larger ecosystem—differ from each other in ways that bequeath them different propensities to persist. Some sections of the ecosystem, say, are dominated by a tree species that provides advantageous conditions to a given set of other species, while other sections are dominated by another tree species that attracts another set of species, and these differences make the assemblages formed in each section differently able to persist given the environmental conditions that prevail where the overall ecosystem finds itself. In such a picture, we would have two sub-ecosystem configurations that synchronically exist and contend cohesively for the same resource, i.e., space in the region.

Such a picture may seem plausible enough as a representation of how things might occur in some ecosystems, and it might come sufficiently close to meeting Garson's conditions for function-bestowing selection processes. However, Bouchard and other proponents of ecosystem selection by differential persistence have yet to provide concrete examples of such a differential persistence scenario actually occurring among synchronically existing parts of ecosystems (or sub-ecosystems).[11] Coming up with such examples would require empirical investigations that

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[10] 10. We set aside potential issues arising from Garson's requirement that differential persistence occurs among "individuals, *of the same type*." Although Garson does not fully specify what he means by this, he says that membership in the same species is the *paradigm* of it (Garson 2022, 11–12). Obviously, differential persistence, in the case of ecosystems, will be among systems with heterogeneous species compositions, such that it will not match this paradigm. However, since the notion that species membership is the *paradigm* for being "of the same type" does not entail that it is a *criterion* for it, we will assume that nothing precludes ecosystems from being *of the same type* in the sense that is relevant here. We will take two ecosystems (or ecosystem configurations) as being of the same type in the relevant sense if their features and circumstances place them in a situation where they compete for the same resource (for simplicity, we will focus on space). This construal of similarity-of-type seems consistent with the spirit of Garson's characterization of GSE-function-bestowing selection processes.

[11] 11. For an innovative approach to ecosystem selection, which sidesteps the issue of ecosystem individuation by focusing on the evolution of ecosystem properties, see Ibanez (2020).

philosophers of biology are not themselves equipped to perform, but which, however, indicate possibly interesting lines of research for ecologists.

In any case, what proponents of ecosystem selection by differential persistence tend to provide are examples in which differential persistence applies to ecosystems that *diachronically* succeed one another: a formerly existing ecosystem is replaced by a newer one with a better propensity to persist. Lenton et al. (2021, 336) remark, for instance, that in the gradual colonization of the land over geological time, ecosystems dominated by vascular plants have displaced ones dominated by non-vascular plants, microbial mats and lichens, and that, likewise, ecosystems dominated by angiosperms with their plant-fungus association have displaced ones dominated by gymnosperm. It is at best an open question whether, when such ecosystem replacement episodes took place, there were circumstances of the kind described above, in which the older and the newer ecosystem configurations coexisted and contended cohesively for space. An alternative scenario is that the older ecosystem configuration shifted to the newer one through a more hodge-podge Gleasonian-individualistic process, in which the previously dominating species were replaced one-by-one by newer ones, each species independently responding to newly arising environmental opportunities. The ecosystem shift would then have occurred through a ship-of-Theseus-like replacement process rather than a process of differential persistence among synchronically existing ecosystem configurations. In this scenario, the persistence of the two ecosystems may be thought of as *differential* only in the sense that the newer ecosystem configuration has features that make it better able to thrive where the previous configuration (eventually) failed to do so.

Nothing in what Bouchard and Dussault have said so far about the PEP account precludes its application to cases where the hodge-podge Gleasonian-individualistic replacement scenario is the actual one. With regard to the explanation of ecosystem selection, the PEP account's main asset pertains to how it helps make fitness comparisons among ecosystems despite their species-compositional heterogeneity. Identifying what contributions some ecological items make to an ecosystem's ability to persist given the environmental conditions that prevail where it finds itself helps one to estimate its fitness and compare it to that of other ecosystems (actually or potentially) subject to those conditions. Moreover, as Dussault and Bouchard (2017, 1121, 1136) make clear, although they consider this asset for understanding ecosystem evolution to be a significant payoff of their account, they do not consider the link it establishes between ecological function and ecosystem selection as *necessary*. Functions, according to the PEP account, are contributions to ecosystem persistence, and the validity of this claim is independent of that of other claims it may help to formulate about ecosystem evolution. Hence, should the hodge-podge Gleasonian-individualistic ecosystem replacement scenario described above look too deviant from the typical picture of natural selection to count as among its genuine variants, the PEP account would remain applicable to ecosystems forming through such a scenario.

This, therefore, is a first aspect with respect to which the PEP and GSE accounts differ in a way that makes the former more easily applicable to ecology than the latter. The hodge-podge Gleasonian-individualistic replacement scenario seems quite clearly incompatible with Garson's conditions for a function-bestowing selection process. It seems implicit that Garson's "individuals, of the same type, that impact one another's persistence, survival, or reproduction prospects" must synchronically exist. The substitution of *parts of more encompassing entities* for *individuals belonging to populations* introduced above was arguably a reasonably minor amendment to Garson's conditions. However, including the hodge-podge Gleasonian-individualistic replacement scenario among such processes seems to go against the spirit of the GSE theory.

Hence, although its inclusion of differential persistence in addition to differential reproduction among selection processes from which functions may derive makes the GSE theory less stringent than the classical SE theory in a way that makes it seem prima facie better applicable to ecology, it turns out to (likely) remain too stringent for such an application. The possibility of applying the GSE theory to ecology, it seems, hinges on the possibility of showing that the above-described scenario of differential persistence among synchronically existing sub-ecosystems (or ecosystem configurations) corresponds to how ecosystem replacement generally (or at least commonly) occurs in nature.

Yet we think that this might not be the most fundamental reason why the GSE theory is of limited applicability to ecology. In the next subsection we will argue that, even when issues about how one should construe *differential* persistence in the case of ecosystems are set aside, functions defined in relation to differential ecosystem persistence are still preferably PEP rather than GSE functions, given the explanatory purposes for which the concept of function is used in ecology.

4.2. *Ecological Role Functions Are Forward-Looking*

Besides those identified in the previous subsection, a central difference between the PEP and the GSE accounts is that, according to the former, an ecosystem component acquires a function *as soon as* it starts contributing to the differential persistence of an ecosystem, whereas, according to the latter, it acquires a function *only after* it has contributed to that differential persistence for some time. In this respect, the PEP account can be regarded as *forward*-looking—it ascribes functions based on foreseeable future effects of items—whereas the GSE account can be regarded as *backward*-looking—it ascribes functions based on past effects (in both cases, effects on differential persistence).

As seen above (sec. 3), ecologists use the concept of ecological role functions to delineate contributions of ecosystem components to ecological processes and, in so doing, to formulate explanations and predictions that link changes in the species composition of ecosystems to eventual changes in their functioning. We will now contend that, given this explanatory purpose, its forward-looking character makes the PEP account preferable to the GSE account for ecological explanations. This follows from how each account delineates between functions and non-functions. If the aim is to explain community and ecosystem processes, then one had better use a concept that ascribes functions to items *as soon as* they contribute to these processes rather than *only after* they have contributed to them long enough for their presence in the ecosystem to partly result from their contributions. We will illustrate this by comparing the implications of the PEP and GSE accounts with respect to three types of cases: dormant species, sink populations, and abiotic items.

4.2.1. Dormant Species

The first type of case concerns the phenomenon of *functional dormancy* and the related concept of *dormant species*. "Dormant species" are species that fall in neither of the common categories of "drivers" and "passengers" in which species present in an ecosystem are often located (see Walker 1995; Elmqvist et al. 2003; Mori, Furukawa, and Sasaki 2013). While "drivers" are defined as species that exert influence on their ecosystem's functioning, and "passengers" as species that are present but exert little such influence, some ecologists argue that the latter category should be further subdivided. Among current passengers, we should distinguish "true passengers," species that are unlikely ever to exert any influence on ecosystem processes, and "functionally dormant species," species that *currently* exert little such influence, but could come to do so (and become drivers) if the local environmental conditions changed.

This notion of functional dormancy underlies an important explanation of the relationship often observed between biodiversity and the stability or resilience of ecosystem processes, according to which this relationship in part results from an *asynchrony of responses* among functionally similar species (see Loreau and de Mazancourt 2013; Loreau 2022). Two or more species disposed to contribute similarly to an ecosystem process differ in their responses to environmental conditions. Under the current environmental conditions, some of the species thrive and are mainly responsible for carrying out the ecosystem process, but when the environment changes in a way that is detrimental to those species, some other species (which were previously functionally dormant) take over. Asynchrony of responses among the "functionally similar" species thus explains why the ecological process keeps being carried out despite the change in environmental conditions.

Elmqvist et al. (2003, 490) give the following example of such a scenario. In Samoa, an island in Western Polynesia, a large proportion of trees depend on vertebrate frugivores for their dispersal. The trees produce fruits that are consumed by two species of flying foxes (*Pteropus tonganus* and *Pteropus samoensis*), as well as three species of fruit pigeons and doves (*Columba vitiensis*, *Ducula pacifica*, and *Ptilinopus porphyraceus*). In the early 1990s, cyclones and fires caused damage to the island's forests, whose regeneration was limited by seed dispersal. The frugivorous species showed different responses to the cyclones, either in terms of behavior or of mortality (e.g., the *P. tonganus*'s population dropped by 90% while the *P. samoensis*'s dropped by less than 10%). Hence, when the cyclones caused the species formerly responsible for seed dispersal to drop, seed dispersal was maintained because other, formerly subdominant, species took over. Asynchrony of response among the frugivores explains why this process was maintained, and why the forest's previous composition was able to regenerate (as opposed to being replaced by a forest composed of wind-dispersed and other passively dispersed plants).[12] According to many ecologists, such asynchrony of response among functionally similar species is an important mechanism underlying the relationship between biodiversity and the reliability of ecosystem processes. Because more biodiverse ecosystems are more likely to contain response-diverse species capable of achieving each ecological role function required for the carrying out of their processes, they are more likely to maintain these processes under environmental changes.

Let us compare the implications of the PEP and GSE accounts with respect to functionally dormant species. According to the PEP account, a functionally dormant species has a function as soon as it contributes to the ecosystem's propensity to persist. Hence, it bears an ecological role function even when it is dormant, and it does so even if it has so far *always* been dormant. That, by its presence, it makes the ecosystem better able to withstand some eventual environmental changes is sufficient for the functionally dormant species to bear a function within it. Both drivers and functionally dormant species thus bear functions in the ecosystem, and the species that do not bear functions are the true passengers, that is, those that are unlikely to exert influence on ecosystem processes under any environmental conditions that might foreseeably come to prevail. According to the GSE account, in contrast, a functionally dormant species acquires a function only after it has contributed to the ecosystem's propensity to persist for long enough for its presence to partly result from its contribution (hence only after it becomes a driver and is thus no longer dormant). At the very least, a species that once was a driver and then ceased to be one for a time might have a function (to the extent that its presence still partly results from its former status of driver), but a species that has *always* been dormant would have no function. In other words, only current or past drivers may bear functions, and many species whose presence enhances the ability of the ecosystem to keep carrying out its processes turn out not to bear functions.

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[12] For other illustrations of this asynchrony pattern, see Elmqvist et al. (2003, 490–91).

We contend that the PEP account's way of delineating between functions and non-functions in relation to such cases is more appropriate given the explanatory purpose ecologists assign to the concept of function. If the aim is to explain how ecosystems are able to achieve their processes reliably, then an account that ascribes functions to ecosystem components according to whether they contribute to this ability or not is more appropriate than one that ascribes functions according to whether they are present in the ecosystem because they have contributed to this ability. The line between functions and non-functions is drawn precisely where doing so is useful given the explanatory purpose for which the concept of function is used in ecology. In contrast, the GSE account draws the line between functions and non-functions at a point that has no direct relevance to that purpose. At best, the fact that some ecosystem component is present in an ecosystem because it has contributed to its ability to achieve its processes (i.e., that it has a GSE ecological role function) may be indirectly relevant as an indicator that, should no significant environmental change occur, the ecosystem will retain its ability to achieve its processes. However, a significant environmental change is precisely the kind of situation in relation to which a functional understanding of the relationship between biodiversity and ecosystem functioning seems the most useful. In the current context of drastic anthropogenic environmental changes, such a functional understanding is relevant not just for explaining how ecosystems have so far been able to maintain their processes, but also, and more acutely, for helping scientists and society to anticipate whether and how they might remain able to do so when subject to change. Hence, with regard to cases of functional dormancy, the PEP account is more in tune than the GSE account with the purpose for which the concept of function is used in ecology.

4.2.2. Sink Populations and Abiotic Items

Sink populations and abiotic items are cases brought out by Dussault and Bouchard (2017, 1134–36) as challenges to the organizational account of ecological role functions advocated by Nunes-Neto et al. (2014).[13] These cases raise similar challenges for the GSE account.

"Sink" populations are populations that are unable to independently maintain themselves in the environments in which they are located, and which would run extinct if not constantly replenished through dispersal from a "source" population located in a nearby environment (Amarasekare and Nisbet 2001; Loreau, Mouquet, and Holt 2003). The dispersal process that occurs between source and sink populations is often called *source-sink dynamics*. Importantly, sink populations can, as much as populations capable of maintaining themselves without replenishment, achieve important contributions to ecosystem processes. For instance, adult insects moving from lakes and streams to neighbouring terrestrial ecosystems can contribute to secondary productivity in these ecosystems by being fed upon by predatory insects, amphibians, birds, etc.

How do the PEP and GSE accounts deal with sink populations that contribute to some important ecosystem process? The PEP account straightforwardly ascribes functions to these populations. By contributing to some ecosystem process, a sink population contributes to the ecosystem's ability to persist, and this is all that is required for the PEP account to ascribe a function to it. In contrast, the GSE account does not ascribe functions to such sink populations. Since, by definition, a sink population is not maintained by the ecosystem whose processes it contributes to, its presence in this ecosystem does not result from this contribution. However a sink population contributes to an ecosystem's ability to persist, this will never be the reason why it is present within it.

Just as for dormant species, the PEP account's way of delineating between functions and

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[13] Though see El-Hani et al. (2024) for a recent attempt by proponents of the organizational account to downplay the issues raised by sink populations and abiotic items for that account.

non-functions seems, with respect to sink populations, more consonant with the purpose for which the concept of role function is used in ecology. If the aim is to explain how ecosystems are able to achieve their processes reliably, then an account that ascribes functions to a population according to whether it contributes to this ability, and does so irrespective of whether its presence results from this contribution, is more appropriate than one that ascribes functions only under the latter condition.

A similar verdict seems in order with regard to abiotic items. Although ecologists more typically ascribe functions to biotic than to abiotic items, the latter often contribute to ecosystem processes in ways similar to the former. Hence, it is often argued that a satisfactory account of ecological role functions should make the concept applicable to abiotic items (e.g. Odenbaugh 2010, 251; 2019, 172; Dussault and Bouchard 2017, 1134–35). Like sink populations, abiotic items are often not maintained by the ecosystem whose processes they contribute to. For instance, nitrogen fixation is an important ecological role function that is part of the nitrogen cycle. As Odenbaugh (2010, 251; 2019, 172) notes, although nitrogen fixation is mainly achieved by organisms (e.g., *Rhizobium*), some of it (around 5–8%) is achieved by lightning. Lightning does not occur because it contributes to nitrogen fixation and/or to ecosystem persistence; in this respect, it is like many other abiotic phenomena that seem functionally important for ecosystems (e.g., winds, which contribute to seed dispersal; see McClure 1990). The PEP account ascribes functions to abiotic items more liberally than the GSE account. According to the PEP account, an abiotic item that contributes to an ecosystem process, and hence to the ecosystem's ability to persist, bears an ecological role function within it. In contrast, the GSE account would ascribe ecological role functions to abiotic items only if they are under biotic control and are present in the ecosystem as a result of contributions to its processes. The GSE account could, for instance, ascribe a function to a soil's increased pH if this pH is in part produced by some biotic components of the ecosystem (e.g., microorganisms) and if these components are present because their effect on pH has contributed to the ecosystem's differential persistence in the past (Bouchard 2013a, 91–92).

Hence, with regard to abiotic items, just as for dormant species and sink populations, the PEP account delineates the boundary between functions and non-functions in a way that is more consonant with the purpose for which the concept of role function is used in ecology. If the aim is to explain how ecosystems are able to achieve their processes reliably, then ascriptions of functions to abiotic items based on how they contribute to these processes, irrespective of whether their contributions explain their presence, are more relevant. Hence, the PEP account provides sounder criteria than the GSE account for the application of the concept of ecological role function to abiotic items.

It is not surprising that the GSE account has the same limitations as the organizational account with respect to sink populations and abiotic items. A key aspect that the GSE account shares with the organizational account is its *backward-looking* approach to functions.[14] Both accounts consider that what an item did in the past has some bearing on whether it *now* has a function. The cases of dormant species, sink populations and abiotic items discussed in this section, we contend, highlight the unsuitableness of such a backward-looking approach for ecology.[15]

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[14] As Charbel El-Hani reminded us, though, the organizational theory, unlike SE theories, is not exclusively backward-looking, but rather both backward-looking and forward-looking, in that it would not ascribe a function F to an item whose presence is explained by its doing F, but that is no longer capable of doing F. Our claim here is that an account of function that is appropriate for ecology should include no backward-looking dimension.

[15] A proponent of the GSE account, however, might retort that its backward-looking character makes the GSE account superior to the PEP account given how it helps make sense of the *normativity* of functions (one of Garson's

5. Ecology, GSE Functions, and Pluralism

The considerations brought up in the previous section indicate that there are few prospects for a GSE account of ecological functions even when ecosystems are seen as subject to some kind of selection through differential persistence. What is the upshot of this for Garson's overall defense of the GSE theory? We suggested above that encompassing ecology would be a significant achievement for the GSE theory, because it would reinforce its ability to evade the issue of excessive restrictiveness allegedly raised by the classical SE theory. Should the GSE theory's inability to encompass ecology be a converse cause for worry for its proponents?

In a sense, no. As we highlighted above (sec. 2), Garson's main rationale for the GSE theory is that it is as able as the classical SE theory to make sense of what are often considered as cardinal features of functions—difference from accident, explanatoriness, and normativity—and that it does so with fewer arbitrary restrictions. Garson, however, is well aware that this rationale for the GSE theory rests on the premise that functions do in fact have these three cardinal features, and that not all discussants of function accept this. He thus surveys examples showing that the concept of function is frequently used in biology in a way that attributes those features to it (Garson 2016, 37–38; 2019, sec. 1.1). He also acknowledges, however, that not *all* uses of "function" that occur in biology necessarily involve a concept that has these features. For this reason he, like previous proponents of selected effects theories (e.g., Millikan 1989; Neander 1991; Godfrey-Smith 1993), adopts a *pluralist stance* on function (Garson 2016, 11, 94; 2017, 528; 2018; 2019, 142).[16] His intent when advocating for the GSE theory is thus not to defend it as *the* exclusive theory of function that will capture *all* biological uses of the concept. Rather, he advocates it as the theory that best makes sense of "function" when the concept is used in a way that involves the three above cardinal features. Garson thus recognizes that "function" is sometimes used by biologists in ways that do not involve these three features, and that these uses are to be accounted for by alternative theories, presumably ones that are more in line with alternatives to SE theories for which functions explain the higher-level capacities of systems rather than the presence of their bearers (he focuses on the *causal role* theory, but the *evolutionary forward-looking* theory, from which the PEP account is derived, also fits the bill here; see Garson 2016, 33–34, 90; 2017, 528; 2018, 11, 17).[17]

Hence, our above discussion should, in a sense, not be a cause for worry for proponents of the GSE theory, since this theory purports to account for uses of *function* in which an item's function

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alleged cardinal features of function, see sec. 2). The backward-looking character entails that an item may have a function that it is unable to perform, and hence be *dysfunctional*, whereas it is less clear how (forward-looking) PEP functions might be similarly normative (on this point, see Lean 2020, 9322–24). Although we cannot fully address the issue of functional normativity here, three remarks seem in order. First, proponents of alternatives to SE theories of function have proposed alternative ways of making sense of functional normativity, and these (or other possible alternatives) might (with relevant modifications) usefully be integrated into the PEP account (e.g., Walsh 1996, 568–69; Christensen and Bickhard 2002, 12–15). Second, as Morrow (2023, 435–36, 444) remarks, SE theories' take on functional normativity may in fact speak against their applicability to ecology, since ecologists' use of the concept of function does not usually involve the possibility of function-bearing ecosystem components (e.g., organisms, species, populations) themselves being dysfunctional (normative notions like ecosystem degradation and ecosystem health usually apply to whole ecosystems rather than to their components). Third, as we shall see in the next section, Garson himself acknowledges that not all functions have his three (alleged) cardinal features (including normativity), and that those that do not may more properly be accounted for through alternatives to his GSE theory, hence possibly an alternative along the PEP account's lines. We thank an anonymous referee for prompting us to comment on the issue of normativity.

[16] Pluralism has also been popular among discussants of ecological functions (e.g., Bouchard 2013a; Millstein 2020; Lean 2020).

[17] Garson has however more recently become skeptical that the causal role theory really captures the non-SE uses of function (see Garson 2019, 141–42, 147–48, 151).

is explanatory of its presence, whereas what we showed above is that ecology tends to use *function* in a way that is *not* explanatory in this way. Ecology just happens to use function in precisely the way that the GSE theory does not purport to capture, and Garson readily recognizes that such uses are to be accounted for by alternative theories.

In another sense, however, we contend that the GSE theory's omission of ecology should be at least a minor cause for concern for its proponents, especially if the theory is advocated in a function-pluralistic context. The concern ensues from a *marginalization issue* that, as Garson rightly notes, arises within pluralism (Garson 2016, 90; 2019, 143). As we have seen, Garson's defense of the GSE theory is grounded in its ability to make sense of the three (alleged) cardinal features of function in a more principled manner than the classical SE theory. This ability, to be sure, demonstrates the superiority of the former over the latter. What it does not show, however, is that SE theories, overall, better capture the use of function in biology than alternative theories for which functions explain the higher-level capacities of systems. The GSE theory could be superior to the classical SE theory and still capture a use of function that remains very localized and marginal within biology. It would then be true, but unimportant. This, we contend, is in essence what critics of SE theories have been arguing when pointing out the excessive restrictiveness of the classical SE theory. The latter theory at best captures an interesting use of function, but one that remains overall marginal within biology. The GSE theory's ability to bring purportedly non-SE disciplines back within the scope of SE theories tackles this threat of marginalization.

In his discussions of function pluralism, Garson argues that the GSE theory's inclusion of purportedly non-SE disciplines invalidates a particular form of function pluralism: *between-discipline pluralism*. He defines between-discipline pluralism as the view that "different theories of function are appropriate to different branches of biology" (Garson 2018, 3, 5; see also 2016, 90; 2019, 142), and contrasts it with *within-discipline pluralism*, a standpoint that "seeks out and emphasizes the plurality of function concepts within any branch of biology" (Garson 2018, 4; see also 2016, 94; 2019, 151). As he recognizes, between-discipline pluralism need not be "a strict stand" or "hard-and-fast rule," stating that researchers in a discipline *always* use function in line with one type of theory or the other. What it implies is that different disciplines "place overwhelming emphasis" on one theory of function or the other, and that there is a "strong correlation" between the use that prevails in a discipline and a particular theory of function (Garson 2018, 5; 2019, 149). According to what we have shown above, ecology appears to be a good candidate for a discipline with respect to which between-discipline pluralism still holds. Ecology *places overwhelming emphasis* on a use of function that diverges from SE theories, and this remains so even given a shift on the part of proponents of SE theories from the classical SE to the GSE theory. Ecology's prevailing use seems prone to *strongly correlate* with a theory of function according to which functions explain the higher-level capacities of systems rather than the presence of their bearers. In our view, it correlates more particularly with the PEP account of function, but our current point about pluralism would still hold if another theory that assigns a similar explanatory purpose to functions, such as the causal role theory (e.g., Morrow 2023), turned out to be the more appropriate one.

Is this in itself sufficient to marginalize the GSE theory? Probably not. However, it indicates a possible cause for concern for the theory's proponents. If more disciplines, or more biological uses within disciplines, turned out to line up with ecology and its non-SE use of *function*, then a more serious risk of marginalization of the GSE theory would start to emerge.

And Garson's line of argumentation for the GSE theory's applicability to purported non-SE biological domains leaves room for this risk to be more than just hypothetical. Certainly, his demonstration of the existence of relevant selection processes in biological domains with respect to which SE functions have been thought implausible compellingly demonstrates the *possibility* of applying the GSE theory to these domains. However, this in itself does not show that biologists' most common use of *function* with respect to these domains aligns with this theory. It is at best a demonstration that, among biologists' uses of function with respect to these domains, those that involve the three above-mentioned cardinal features of function (difference from accident, explanatoriness, normativity), accord with that theory. This is compatible with the possibility that some, many, or even most of these uses concur with theories that do not assign those features to function, and that overall, the use of *function* in biology more consistently aligns with these theories.

6. Conclusion

We argued that there are few prospects for a GSE account of ecological functions, because ecosystem differential persistence as it can plausibly be thought to generally occur among ecosystems is unlikely to meet Garson's conditions for GSE-function-bestowing processes, and because such an account would be in tension with the explanatory purpose for which the concept of role function is used in ecology. Ecosystem differential persistence may more plausibly be thought of with respect to ecosystems diachronically succeeding one another than with respect to ecosystems synchronically contending for similar resources. Moreover, ecologists use the concept of function to explain ecosystem processes, whereas a GSE account would be more appropriate to the aim of explaining the presence of function-bearing items within ecosystems—as we illustrated with the cases of dormant species, sink populations, and abiotic items. Linking this verdict to Garson's remarks on function pluralism, we suggested that, although the GSE theory's omission of ecology is not in itself a cause for concern, it may become one should more biological uses of function turn out to line up with ecology's non-SE use of the concept.

With regard to the question of which philosophical theory of function is most appropriate for ecology, and, in particular, that of the applicability of SE theories to this field, the above discussion yields an important observation. It indicates that this applicability hinges less on the presence or absence of relevant selection processes at work in ecosystems, than on the suitability or unsuitability of SE theories to the explanatory purpose for which the concept of role function is used in ecology.

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