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A Causal-Role Account of Ecological Role Functions

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Abstract

I develop an account of ecological role functions—the functions of species within ecosystems—that is informed by alternative regime phenomena in ecology. My account is a causal-role theory that includes a counterfactual sensitivity condition. The account tracks and explains a distinction ecologists make between functions and various activities that are not functions. My counterfactual sensitivity condition resolves the liberality problem often attributed to causal-role theories of function while also illuminating the explanatory centrality of role functions within ecology.

1. Introduction

Role functions in ecology—the roles of species or other ecosystem components that help explain ecosystem behavior—have recently gained attention among philosophers of biology (Odenbaugh 2010; Nunes-Neto and El-Hani 2011; Saborido et al. 2011; Nunes-Neto et al. 2014; Nunes-Neto, Freitas, Saborido, et al. 2016; Dussault and Bouchard 2017; Dussault 2018; Odenbaugh 2019; Lean 2021; Millstein 2020). In this article, I develop a new account of ecological role functions. Ecosystems can undergo sudden major organizational changes, or regime shifts, in response to disturbance. My account of role functions is informed by explanations having to do with alternative regime phenomena. The account thus captures the fact that species are parts of dynamical and changing ecosystems. This context has not been fully captured in prior accounts of ecological role functions, which have focused on how species' activities[1] contribute to the maintenance of ecosystem organization (Nunes-Neto et al. 2014) or to the tendency of ecosystem states to persist (Dussault and Bouchard 2017). Prior accounts have not considered regime changes or ecosystem degradation as central explanatory targets.

This article also illustrates how considering functional explanations in the context of ecology can generate new solutions to existing philosophical problems. I will show

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[1] Throughout this article, I use the term *activity* to refer to what organisms do in ecosystems, such as metabolizing, decomposing, or invading. In some cases, *behavior* might be a more natural term to use; however, to avoid any ambiguity, I will reserve the term *behavior* to refer to ecosystem-level phenomena only.

how, in this context, we can solve the liberality problem for causal-role theories of functions, that is, the problem of discriminating between functions and nonfunctions. In the present account, I solve the liberality problem by including a counterfactual sensitivity condition, which states that role functions are less counterfactually sensitive to changes in ecosystem organization than are activities that do not count as functions.

In the next section, I introduce role functions and explain why Robert Cummins's theory of functions provides a promising partial account of role functions. Cummins's theory is partial because it does not, by itself, explain why ecologists distinguish functions from certain explanatorily important activities that are not functions. The distinction between functions and nonfunctional activities may arise uniquely within ecology and goes beyond the conventional distinction between function versus mere effect, for reasons that will be explained. I then present my account and argue that it accurately captures and explains the distinction between functions and nonfunctional activities. Later sections of the article compare my account with alternative views of role functions, including a consideration of the relationship between causal-role and normative accounts of functions.

2. Role functions

Role functions are the roles played by species and other relevant units in an ecosystem, including familiar activities such as pollination and browsing. Role functions are distinct from the functions or functioning of whole ecosystems.[2]

Some main goals of my account of role functions will be to (a) correctly identify role functions while excluding activities that ecologists do not consider functions and (b) illuminate some of the implicit criteria by which ecologists identify role functions. Philosophical theories of functions can be more faithful or revisionary in intent. I have opted for a mostly faithful-to-practice approach here for a few reasons. First, a clear understanding of how ecologists understand functions is needed before useful criticism is possible. Second, alternative theories of role functions seem to intend to be descriptively accurate, making accuracy a useful point of comparison. However, this does not mean that the account presented here cannot be applied prescriptively to cases where there is disagreement or unclarity about a possible function. I will leave consideration of such cases to future work.

Later in the article, I will argue that my account more accurately captures ecological practice than some of the existing theories, at least for the types of examples I consider. My focus here is on functions in community and ecosystem ecology at medium scales, for example, the ecology of lakes, forests, and prairies. Of course, accuracy is not the only potential virtue of a theory of functions. Some degree of inaccuracy could be intended by other theories if they are meant to provide a basis for revising the usage of the term *function* in ecology. In my view, though, there ought to be some specific practical reason for wanting to revise term usage. I am working at

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[2] Overviews of the several distinct functional concepts in ecology include Jax (2005, 2010) and Nunes-Neto, de Freitas, Santos do Carmo, et al. (2016). On occasion, the same process can be considered both a role function and an ecosystem function; for example, denitrification can be considered a function of bacteria or of a wetland ecosystem (e.g., Peralta et al. 2010). In contrast, browsing is exclusively a role function, whereas nitrogen cycling is exclusively an ecosystem function. The distinction is especially important for reading ecological research on how role functions affect ecosystem functioning (e.g., Gagic et al. 2015).

primarily a descriptive level in this article because I am not aware of an obvious reason to think that there is a flaw with the conception of role functions in ecology. But I do believe that further consideration of the appropriate or inappropriate uses of functional concepts in ecology will prove fruitful.

Having explained my approach, I will now present an overview of examples of role functions in ecology. Then I will consider the suggestion that Robert Cummins's theory of functions can provide the best account of role functions.

There are multiple areas of ecology that study role functions. What follows is an illustrative but not exhaustive list. One way ecologists study the functional composition of communities is by characterizing food webs (Elton 1927), which help to explain associated phenomena such as trophic cascades and regime shifts (e.g., Wolf et al. 2007). Trophic activities, including predation, grazing, parasitism, decomposing, and filter feeding, are core examples of role functions. Additional examples of role functions have to do with reproductive strategies and roles pertaining to the reproduction and dispersal of other species. Examples include being a pollinator or being insect-pollinated (Ollerton 2017). A third class of examples includes activities that contribute to the cycling of elements through ecosystems, such as denitrification (Peralta et al. 2010) and nitrogen fixation. Additionally, species considered "ecosystem engineers" are species whose functional activities have major transformative effects on resource availability within their ecosystems (Jones et al. 1994; Coggan et al. 2018). A notable example of an engineering function is dam building by beavers.

Ecologists who study the functional composition of plant communities or the effects of functional diversity on ecosystem properties often study *functional types.* Functional types are groups of species that exhibit relevantly similar role functions within their community for some explanatory purposes. Examples of functional types from various studies include C3 and C4 grasses,[3] legumes, forbs,[4] warm-season forbs, trees, and early-succession plants (Díaz and Cabido 2001). Examples of the role functions of members of these functional groups include supporting primary production during drought (C4 grasses), introducing nitrogen into the soil via nitrogen fixation (legumes), and producing vertical structure and shade (trees). The diversity of functional types in a community or the existence of a particular functional type may help to explain ecosystem properties and processes, including biomass, nitrogen cycling, decomposition rates, or invasibility. To sum up, role functions include various activities of species that help to explain many ecological phenomena.

An additional point is that role functions do not permit malfunctions. Although species' activities can sometimes be undesirable[5]—for example, they can contribute to the degradation of ecosystems—it would be inappropriate to say that species have malfunctioned in these contexts. Ecologists do not ordinarily speak of species as having malfunctioned, and there are good reasons not to think this way. One reason is that species can act in exactly the same way in two different ecosystems, but the activity can be desirable in one ecosystem and undesirable in another. Thus, the

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[3] That is, grasses that undergo C3 or C4 photosynthesis—different photosynthetic pathways.

[4] Forbs are herbaceous flowering plants, excluding grasses and grass relatives. Most common garden vegetables and annual flowers are forbs.

[5] Judgments about desirability could come either from a human perspective or from the ecosystem's perspective. I've left this open because it does not affect my account of role functions.

undesirability of an activity is often due to the context in which it is performed. For example, nitrogen-fixing plants are desirable within many ecosystems but are undesirable in Hawaiʻi, where invasive nitrogen fixers have altered forest structure as a result of its historically low level of nitrogen fixation.

Second, undesirable effects often result from changes in population size rather than changes in the functions of individual organisms. Individual deer that contribute to overbrowsing in a forest ecosystem have not malfunctioned but have simply gone on performing their role of browsing. The problem is that the ecosystem contains too many deer—perhaps because there are too few predators. Thus, it is more appropriate to speak of dysfunction at the level of ecosystem structure than at the level of individual species.

Due to considerations like these, I hold that the concept of role functions is relatively nonnormative, in that it does not permit talk of malfunction or dysfunction. In contrast, I do hold that ecosystem-level concepts like *ecosystem functioning* and *ecosystem health* are normative. One might wonder how this normative conception of ecosystem health is consistent with a causal-role view of role functions. Briefly, degraded ecosystems are often characterized by altered trophic structures and nutrient cycling, as well as runaway processes such as erosion. These are major organizational changes to the ecosystem that do not arise from individual components having malfunctioned. Rather, they may arise from disturbances such as increased nutrient input, climate change, a major reduction in the size of a key population, and so forth. When we speak of some such ecosystems as being degraded (i.e., unhealthy), the normative judgment pertains to undesirable properties of the whole ecosystem state rather than to its individual components. My view is that these judgments are supplied partly by human preferences, but one could also hold that facts about the ecosystem itself determine its state of health. My account of functions is not affected by this issue.

So, I begin with the observation that role functions are a type of causal-role function; that is, they are explanatory activities that do not permit malfunction. A few philosophers have previously suggested that ecological role functions can be understood roughly as Cummins functions (Maclaurin and Sterelny 2008, chap. 6; Odenbaugh 2010, 2019). Robert Cummins's theory of functions states:

> **(C)** *x* functions as a φ in *s* (or: the function of *x* in *s* is to φ) relative to an analytical account *A* of *s*'s capacity to ψ just in case x is capable of φ-ing in *s* and *A* appropriately and adequately accounts for *s*'s capacity to ψ by, in part, appealing to the capacity of *x* to φ in *s*. (Cummins 1975, 762)

In plainer language, the theory states that a component of a system has a function φ just when the component's capacity to φ helps to explain a capacity of the system. Thus, for example, the capacity of plants for primary production helps to explain an ecosystem's ability to sequester carbon or generate biomass. Similarly, the capacity of sea otters to eat urchins—to engage in predation[6]—helps explain how kelp forests have been eliminated from some parts of the West Coast of North America. In a classic trophic cascade, reduced predation as a result of reductions in otter populations caused an increase in urchin populations, which in turn eliminated the kelp forests

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[6] Or *depredation*, if you're a stickler.

through their browsing activity. This is an example of a regime shift, a phenomenon that plays a key role in my account of role functions (Holling 1973; Beisner et al. 2003; Suding et al. 2004; Wolf et al. 2007). A regime shift is a sudden, discrete, qualitative change in the physical and trophic properties of an ecosystem. The potential of marine kelp forests to undergo a regime shift is explained by the trophic structure of the ecosystem, which includes the trophic role functions of otters and urchins.

This would be a short article if Cummins's theory as stated provided a complete account of ecological role functions. However, Cummins's theory does not fully explain why ecologists consider only certain activities to be functions among those appealed to in explanations. There are many examples of activities of species that help to explain ecological outcomes and yet are not considered to be functions. Cummins's theory ties functions to explanatory aims, a program I am amenable to. The question we are left with is what explanatory aims or considerations help to delineate functions from nonfunctions in ecology. In the following, I develop a criterion that tracks this distinction.

Some examples of activities that are explanatorily important but not functions include the following:

- Overbrowsing. As noted, overbrowsing is not a malfunction, and it is also not considered a function, in contrast with browsing.
- In eutrophic lakes, algae can form mats on top of the water, covering plants and blocking sunlight. In the wake of algae blooms, the actions of decomposers can then deplete the water of oxygen, with resulting effects including fish kills. These activities (mat formation, oxygen depletion) are not considered functions, although they are explanatorily important.
- Bleaching is not a function of corals.
- Invading North America is not a function of dandelions.
- Eliminating urchins is not a function of otters, although eating urchins is.

Cummins's theory might seem to count all of these activities as functions because they are capacities of organisms that can help to explain ecological outcomes.

An initial issue is that Cummins's theory is stated in terms of explaining system-level capacities. In the algae case, a relevant capacity would be the capacity of water bodies to kill their fish; in the otter and urchin case, a relevant capacity would be the potential to undergo a regime shift. Calling these "capacities" may sound like an odd way of talking, but I see nothing illegitimate in doing so, assuming "capacity" means roughly the potential to do something.

If you do not think these outcomes are appropriately characterized as capacities, then Cummins's theory simply will not apply to the cases. It will follow, however, that Cummins's theory has a seriously restricted scope within ecology. Ecologists frequently appeal to role functions when explaining various kinds of ecological outcomes or processes that we would not ordinarily describe as a capacity—including single past events. Cummins's theory will not apply to these cases if we cannot treat diverse types of ecological outcomes as capacities. In view of this, when I present my own account in the following discussion, I will swap the term *behavior* for *capacity* to indicate that role functions explain various types of ecosystem processes, properties, outcomes, or potentials.

However, let us assume that we can redescribe all relevant ecosystem outcomes in terms of capacities. Then, in addition to capturing more examples of functional explanation, Cummins's theory will potentially regard various nonfunctional activities as functions, such as the examples described previously. This creates another instance of the well-known liberality objection to Cummins's theory. A defender of Cummins's theory might urge that it is not meant to be prescriptive but is only meant to capture the form of functional explanations, given scientists' actual explanatory practices. Although this move sidesteps the liberality objection, it leaves us wanting an explanation of why ecologists regard only certain activities as functions. As stated, my account is meant to be a useful addition to Cummins's because it supplies this explanation.

At this point, I can address another question about the framing of my project. I am contrasting functions with *nonfunctional activities* rather than contrasting functions with *mere effects*, the latter distinction being more common in the functions literature.[7] The reason for doing this is supplied by the previous examples. In ecology, I argue, one can identify many activities of organisms that help to explain some system outcomes but that are not functions. So, a descriptively accurate theory should track the distinction between functions and nonfunctional activities. This distinction may well be unique to ecology because it does not arise in the received literature on physiological functions.

A distinction between functions and mere effects can also be made in ecology, but this distinction is less interesting. For example, felling trees is a function of beavers, and producing gnawing sounds while doing so is a mere effect. Cummins's theory already explains why making gnawing sounds is not a function: felling trees helps to explain ecosystem capacities, whereas gnawing sounds do not contribute to relevant explanations.

An initial suggestion is that value judgments may have something to do with my distinction between functions and nonfunctional activities. All of the example activities might be considered undesirable (as noted previously, one could read this from the perspective of either humans or the ecosystem). So, you might think that an account of role functions could be given by Cummins's theory plus the stipulation that role functions must be desirable activities, however you want to cash out the desirability. This is not a good solution to the liberality problem because some functions have undesirable consequences. For example, some trees, including eucalyptus, produce compounds that stimulate fire. Promoting fire is a functional role of these trees. However, increasingly severe forest fires resulting in part from past mismanagement can compromise forest regeneration and also damage human property. Even if it is undesirable for trees to contribute to severe forest fires, promoting fire is still a role function. Another example comes from invasion biology. Organisms that are successful invaders are sometimes thought to be invasive by virtue of their role functions. As noted previously, a nitrogen-fixing plant that invades Hawaiʻi, a place with low levels of native nitrogen fixation (Vitousek and Walker 1989), still has the role function of nitrogen fixing, even though performing this function may have destructive consequences for native Hawaiian forests.

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[7] Thanks to the anonymous reviewers for asking about this.

So, stipulating that role functions must be desirable activities would throw out too many actual functions in addition to the examples of nonfunctions. Still, I do not want to claim that values are irrelevant to thinking about role functions, even though I have characterized them as largely nonnormative because they do not permit malfunction. One avenue for values to indirectly influence role-function assignments will be discussed later in the article.

Finally, notice that there is a level-of-description issue with some of the nonfunctions. For example, decomposition is a role function, but eliminating oxygen from lakes is not a function of decomposers, even though oxygen depletion results from rapid decomposition. Similarly, deer function as browsers when they are overbrowsing—where overbrowsing is intuitively the wrong level of description to count as a function. These distinctions might seem unprincipled or arbitrary, but they are a feature of how ecologists think about functions, so a descriptively accurate account should explain them. I will argue later on that there actually is a surprisingly principled way to make these level-of-description distinctions.

3. The account

I will argue that the main difference between functional roles and capacities that are not functions is that functional roles exhibit less counterfactual sensitivity. Being a decomposer, pollinator, canopy-producing tree, or grazer is fairly consistent across changes to ecosystem structure or the environment. Mostly, primary producers do not change into predators when there is a change in ecosystem organization. In contrast, overbrowsing, mat formation by algae, and elimination of urchins only occur under particular ecological regimes. For instance, algae only form mats in eutrophic systems or systems that permit a rapid bloom. Algae cannot form mats in oligotrophic (nutrient-poor, clearwater) lakes. In contrast, algae are always primary producers, regardless of their abundance or the overall ecological organization of the lake. Thus, mat formation is more counterfactually sensitive than primary production, in the sense that it is more likely to fail to occur under a range of potential changes to surrounding ecological conditions. Similarly, overbrowsing only occurs under conditions of high population density of deer or other browsers. Because the population density of browsers can be altered by manipulating ecosystem structure (e.g., by reintroducing more predators), overbrowsing is more counterfactually sensitive than browsing. This difference in counterfactual sensitivity provides the principled basis for the level-of-description distinctions discussed previously.

Notice that judgments about counterfactual sensitivity do not rely on any evaluative judgments about the desirability of the activity, but they do rely on assumptions about what range of possible ecological and environmental conditions is relevant. When (implicitly) recognizing counterfactual sensitivity, ecologists do not consider all metaphysically or even physically possible environmental conditions. They instead consider how organisms behave under a range of salient ecological conditions— meaning conditions that are (a) considered relevant targets of study in their area of ecology and (b) considered likely or plausible, if not actual, ecological conditions under recent past or projected future changes. Thus, for instance, forest ecologists typically ignore how organisms would behave if the forest were to convert into a shopping mall because shopping mall ecosystems are outside the explanatory

purview of most forest ecologists. Forest ecologists also typically ignore how organisms would behave if Earth's orbit were substantially different because this circumstance is not likely to occur. In contrast, they might consider what would happen if the region were to become hotter, wetter or drier, or more invaded. These judgments about salience will be sensitive to nonepistemic values. In this way, my account recognizes a route for value judgments to influence ecological role-function assignments.

One might wonder what happens, according to my view, as climate change results in changes to the range of "normal" ecological states on Earth. My prediction is that role-function attributions will change to reflect new judgments about what ecosystem states are typical. My view is that role-function attributions are not fixed but that they are relative to the proposed explanatory and counterfactual conditions, both of which can change over time as a result of alterations in ecological circumstances and ecologists' interests and values. Thus, an activity that is at one point considered novel or atypical may come to be described as a function at a later time.

Cummins emphasizes the explanation relativity of functions, so what I have just discussed may be consistent with Cummins's theory. As a pluralist about theories of functions, my goal is not to defeat Cummins's theory but to provide a targeted account for the context of ecology. In particular, by developing an explicit counterfactual sensitivity condition that tracks the distinction between functions and nonfunctions, my account avoids the liberality that is often attributed to Cummins functions. If you are of the view that Cummins can successfully respond to liberality concerns by appealing to explanatory aims, then my account can be read as an explication of the relevant explanatory circumstances in ecology.

I will call my account *Cummins plus counterfactual insensitivity* (CCI) because the structure is borrowed from Cummins's theory.

> **(CCI)** x functions as a φ in ecosystem e (or: the function of x in e is to φ) just in case there are various explanatory accounts $A_1, A_2, \ldots, A_n$ of e's behaviors[8] $\psi_1,$ $\psi_2, \ldots, \psi_n$ across possible alternative regimes of e and x is capable of φ-ing in all alternative regimes in which it is present and some of $A_1, A_2, \ldots, A_n$ account for e's behaviors by, in part, appealing to the capacity of x to φ in e.

The account states, in summary: role functions are the activities of ecosystem components that are consistent across possible alternative regimes and that may be appealed to in explanations of ecosystem behaviors across those regimes. Put differently, role functions are those explanatory activities that would be counterfactually constant across ecosystem reorganizations. Other kinds of activities can be explanatorily important in some contexts but are not functions. A presupposition of the account is that although role functions always explain ecosystem behaviors, ecosystem behaviors are not always explained in terms of role functions.

Here are two examples to show how this works. Consider beavers, which have the function of constructing dams. Beavers can always construct dams under appropriate environmental conditions, regardless of the surrounding regime of the ecosystem.

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[8] I am using the term *behavior* as a catchall for ecosystem phenomena that may be targets of explanation. These can include regime stability, changes in regime, processes such as the nitrogen cycle, population dynamics, historical events, and so forth.

Table 1. STRUCTURAL COMPARISON OF C AND CCI

	C (Cummins 1975, 762)	CCI (ecological role functions)
1	x functions as a φ in s (or: the function of x in s is to φ)	x functions as a φ in ecosystem e (or: the function of x in e is to φ)
2	relative to an analytical account A of s's capacity to ψ	just in case there are various explanatory accounts $A_1, A_2, \ldots, A_n$ of e's behaviors $\psi_1, \psi_2, \ldots, \psi_n$ across possible alternative regimes of e and
3	just in case x is capable of φ-ing in s and	x is capable of φ-ing in all alternative regimes in which it is present and
4	A appropriately and adequately accounts for s's capacity to ψ by, in part, appealing to the capacity of x to φ in s.	some of $A_1, A_2, \ldots, A_n$ account for e's behaviors by, in part, appealing to the capacity of x to φ in e.

And the fact that they construct dams helps to explain various ecosystem properties. For example, beavers can modify hydrology by slowing water flow and creating flood-plains, which then support the regeneration of water-loving trees (Wolf et al. 2007). So, dam building counts as a function because it is explanatory and counterfactually consistent. Deer overbrowsing does not count as a function because it cannot occur in some relevant forest regimes (i.e., those with lower deer populations), although it does help explain ecosystem properties, including changes in the tree community, when it occurs. Note that high deer populations and low beaver populations both can trigger a regime shift. The relevant difference is that beavers can go on building dams in a new regime, whereas overbrowsing is only possible within some regimes. This difference tracks the convention of considering dam building, but not over-browsing, a function.

The reader may wonder if *some* possible regime exists that would disrupt the capacity of beavers to build dams. I grant that this is possible, but if the regime is a very distant possibility, this will not affect the function assignment. Recall that in my view, assessments of counterfactual stability focus on regimes that are considered salient for reasons of likelihood or explanatory interest. This does add some human subjectivity to the account of role functions. I believe this is warranted in the interest of capturing actual explanatory practices.

My account differs from Cummins's theory in several ways to reflect the unique explanatory circumstances in ecology (Table 1). First, Cummins specifies that functions are relative to "analytical accounts," by which he means something roughly like a mechanistic explanation. In my account of ecological role functions, I change *analytical account* to *explanatory account* in order to remain more clearly neutral about the form of the explanations. There has been discussion about whether and under what circumstances explanations in ecology are mechanistic (e.g., Pâslaru 2009; Raerinne 2011). My sense is that ecologists sometimes give mechanistic and often give non-mechanistic explanations, but the CCI account is phrased to remain neutral about this.

The second main difference between the accounts is that in CCI, functions feature in multiple explanations of multiple behaviors of the ecosystem across different regimes. When applied to the examples I have discussed, Cummins's original theory cannot fully illuminate how ecologists differentiate between functions and activities

that are nonfunctions. In contrast, CCI explains this by appealing to the counterfactual stability of certain activities. Activities that will usually count as functions under CCI include trophic activities, engineering activities, growth forms, and salient metabolic properties because these processes are relatively counterfactually stable. This is consistent with the kinds of activities that are regarded as functions in ordinary ecological thought.

Much of this article argues that my account accurately captures the way role functions are assigned. However, there is an independent reason to think counterfactual stability is an important property within ecological explanations. Because ecosystems are quite organizationally flexible, creating stable representations of ecosystems relies on identifying features of their structure that are relatively insensitive to surrounding changes. One of the early developments in community ecology was the description of food webs (Elton 1927). Food webs are useful because their general structure can remain relatively constant within a token ecosystem, even when the ecosystem's other features change substantially. The reason for this is that the trophic roles of organisms are less sensitive to surrounding changes than are other ecosystem properties (e.g., nutrient levels or population sizes). So, it is unsurprising that these comparatively insensitive properties have explanatory centrality in many parts of ecology. A property or activity that changes rapidly as the environment changes can still be explanatorily important, but only under a particular circumstance; these types of activities do not have the distinction of being regarded as functions.

Although I have emphasized the relative counterfactual stability of role functions, it is not my claim that role functions are rigid. In fact, there are many types of role functions that are sensitive to the environment. In the next section, I explain how environmental sensitivity is compatible with counterfactual stability. After that, I discuss how the account compares with existing theories of role functions.

4. Aren't role functions sensitive to the environment?

Ecological role functions have often been characterized as highly context dependent and sensitive to environmental conditions (Jax, 2005; Jax 2010, 79). The reader may wonder how CCI handles examples of functions that are flexible or environmentally variable. In this section, I will further clarify what sense of counterfactual stability is intended by the account. CCI is consistent with role functions being sensitive to spatial and temporal environmental fluctuations, as well as to changes in ecosystem structure that do not constitute a regime shift. Explaining how this works should resolve concerns about the handling of plasticity.

Environmentally sensitive role functions include functions that occur during certain times of the day or year (e.g., photosynthesis), functions that occur in response to environmental conditions (e.g., feeding only during high tide), functions whose expression can be altered by environmental conditions (e.g., growth form in some plants), and functions that are responsive to changes in population size (e.g., prey switching). Other functions may occur only during certain life-history stages (e.g., feeding on different sources in different insect life stages) or certain stages of succession (e.g., some trees can only occur later in forest succession).

A key point is that an ecosystem regime is an abstract concept pertaining to the overall organizational state of the ecosystem. Ecosystems within a certain

regime—for example, an oligotrophic lake or an overbrowsed forest—will exhibit both spatial variation and temporal changes, such as succession and seasonal cycles. Therefore, the requirement that role functions be counterfactually insensitive to regime changes does not require that they be insensitive to spatial and temporal variations within an ecosystem.

Prey switching—preferentially hunting different prey depending on prey population densities—is one interesting example of a flexible role function. Suppose that coyotes preferentially hunt rabbits only in certain seasons or during times when rabbits are especially abundant. Suppose also that coyotes' behavioral hunting strategies are sensitive to the local abundance of other predators, such as wolves. These are not problems for CCI because the concept of an ecosystem regime accommodates both spatial and temporal fluctuations in population densities. For *rabbit predation* to count as a role function, the requirement is that coyotes must be able to exhibit rabbit-hunting activity in any salient ecosystem regime, not that they must actually hunt rabbits constantly. Put differently, hunting may occur in a spatially or temporally patchy manner within a given ecosystem regime. The activity still counts as a role function as long as its occurrence would not be disrupted by a counterfactual regime change (e.g., changing the system from a forest to a prairie).

Similar points can be made about organisms that are only periodically active, such as adult cicadas, organisms that experience dormancy, or organisms that only occur in certain stages of succession. CCI requires that their functional capacities must not be disrupted by a regime shift, but it does not require that the organism must be constantly active over time. Thus, deciduous trees need not photosynthesize in all seasons in order to have the function of primary production.

Another point of clarification is that CCI is primarily meant to assess functions at the level of individual token ecosystems. Species with large geographic ranges or species that migrate seasonally might play different functional roles in different parts of their ranges, in response to environmental gradients or differences in local community composition. For example, various species that are trees under some conditions will grow only into small shrubs at a high latitude or elevation. Animals of the same species may exhibit physiological and behavioral differences in milder versus more hot and arid climates. Predators with large ranges may hunt different species in different regions. These species may then have different role functions in different token ecosystems. This accords with commonsense ways of describing role functions. For instance, you would not say that the wolves in Minnesota are (function as) predators of ptarmigan or bighorn sheep because neither ptarmigan nor bighorn sheep are present in Minnesota, although wolves do hunt these species in more northern and western parts of their current North American range. Thus, functions are commonly described such that they are indexed to token ecosystems, which is consistent with the intended application of CCI.

In summary, CCI allows that species' functions are exhibited in spatially or temporally patchy ways within ecosystems and that species' role functions can differ across ecosystems. What CCI does assert is that to count as function, a capacity must be maintained across salient potential regime changes to a token ecosystem, assuming that the species is still present. This condition is met by many activities that are variable, seasonal, or context dependent, so CCI does count such activities as functions.

5. Comparison with other theories

5.1. Selected-effect accounts

So far, I have considered whether ecological role functions might be Cummins functions. I have argued that my account, which adds a counterfactual insensitivity condition, performs better than the original Cummins theory in terms of both accuracy and explanatory value (i.e., illuminating what considerations are relevant to role-function assignments).

Having laid out my account, the rest of the article will consider how it compares to other views about role functions. A preliminary comment is that I endorse pluralism about functions in biology. I take pluralism here to mean that there are multiple distinct conceptions of *function* in biology and that these distinct uses warrant separate philosophical accounts (see Allen and Neal 2020). For instance, biologists utilize both causal-role and etiological functional explanations in different contexts (Amundson and Lauder 1994). So, causal-role and etiological accounts of functions should not be seen as inherently in conflict but rather as illuminating different features of functional explanation.

The account I give in this article is a broadly causal-role account of role functions; that is, it identifies functions with some actual activities of system components that do not permit malfunction. We can now consider whether it is possible to give an etiological account of role functions. Etiological theories of functions in biology are derived from the work of Larry Wright (1973). The general idea of etiological accounts is that a trait or component's function is the activity that explains why it is present in the system. In a biological context, this is usually interpreted to mean that the function is the activity or consequence for which the component was selected in recent evolutionary history. This etiological theory—also known as a *selected-effect account*—has provided a successful account of functional explanations in several areas of biology, particularly physiological functions considered from an evolutionary perspective (Millikan 1989; Neander 1991; Godfrey-Smith 1994; Mitchell 1995).

The standard etiological theory describes proper functions—that is, functions that permit malfunction. For example, my heart has the proper function of circulating my blood, a function that it could fail to perform. However, I have already argued that role functions do not permit malfunction. Although it is common to speak of whole ecosystems as being degraded or dysfunctional, ecologists do not talk about individual organisms, species, or functional types as having malfunctioned—even when they act in ways that are considered detrimental to the ecosystem.

An additional problem for the selected-effect account in this context is that there is not a consistent explanatory connection between what traits are adaptive and what traits are considered role functions. Because role functions are actual activities of species in ecosystems, ecologists often do not make presumptions about the evolutionary history of the traits underlying those activities. A role function can explain ecosystem behaviors regardless of its evolutionary origins, and not all adaptive traits have explanatory relevance in ecosystem ecology. So, it is clear that the standard selected-effect theory of functions is not relevant to ecological role functions. This has been a matter of general agreement among philosophers of ecology (Nunes-Neto et al. 2014; Dussault and Bouchard 2017; Dussault 2018; Odenbaugh 2019).

Recently, Roberta Millstein has developed an evolutionary account of role functions that takes a slightly different approach. She argues that role functions can be understood as products of coevolution because

> 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). (Millstein 2020, 1113)

Millstein's account of role functions is structured slightly differently from the standard selected-effect account. In her view, organisms have role functions when the organism's traits are products of the species coevolving with other species. Although ascribing a selected function to a whole organism rather than to the trait is nonstandard, I agree with Millstein that nothing clearly prevents thinking in this way, particularly because ecologists do assign role functions to whole organisms based on organisms' traits.

This coevolutionary account is more plausible than the standard selected-effect account for the ecological context because it explains why evolutionary history is relevant. The claim is that evolutionary history is relevant when role functions are products of coevolution because coevolution pertains directly to the ecological interactions between species. The history of tight ecological interactions between two species creates the selective pressure that helps to explain why certain activities are role functions. This is especially plausible for species with mutualistic relationships, such as figs pollinated by wasps or legumes and rhizobial bacteria; for highly specialized organisms like the parasites discussed by Millstein; and for organisms that rely on a specific food source, like monarch caterpillars and milkweed.

I think the coevolutionary account can illuminate some features of role-functional explanations, especially for the ecology of specialist organisms and cases of coevolved mutualism. As I said previously, I do not think that causal-role and evolutionary accounts of functions are in conflict with each other, to the extent that they capture different explanatory contexts. However, in the event that not all role functions are products of coevolution, my CCI account may capture a broader range of functions than does the coevolutionary account. Further work might consider why evolutionary history is relevant to some ecological explanatory contexts and not others.[9]

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[9] Malaterre et al. (2019) make the interesting suggestion that *functional response traits* can be captured by some type of evolutionary account of functions, whereas *functional effect traits* should be captured by a causal-role account. Functional response traits are traits pertaining to an organism's responses to the environment (e.g., drought tolerance), whereas functional effect traits pertain to an organism's effects on ecosystem processes (e.g., nitrogen fixing). Prima facie, both drought tolerance and nitrogen fixing may be selected for, *and* they both help to explain ecosystem behaviors. So, although the suggestion merits further consideration, I am doubtful that traits should be given different functional accounts just by virtue of their classification as response or effect traits.

5.2. The propensity theory

The classic source for the propensity theory of functions is Bigelow and Pargetter (1987). This propensity theory is a forward-looking evolutionary theory of functions. In this view, a component has a function when it increases the fitness of the individual of which it is part. This theory has recently been applied to ecology by Antoine Dussault and Frédéric Bouchard. In order to apply this to ecology, Dussault and Bouchard have argued that ecosystems are evolutionary units.

In their words,

> Under the ecological interpretation of the propensity theory of fitness, a trait increases the fitness of an entity insofar as it contributes to that entity's ability to persist in the face of the challenges posed by its environment. (Dussault and Bouchard 2017, 1131)

Thus, what they mean by the "fitness" of an ecosystem is its tendency to persist. Species have functions within an ecosystem, in their view, when those species support the ecosystem's tendency to persist. They call this the *persistence-enhancing propensity* (PEP) account:

> **(PEP)** The function of x in an ecosystem E is to F if, and only if, x is capable of doing F and x's capacity to F contributes to E's propensity to persist. (Dussault and Bouchard 2017, 1122)

Dussault and Bouchard further explain that in their view, the persistence of an ecosystem has to do with its resilience rather than with stability in the sense of constancy or equilibrium. So, in their view, species have functions in ecosystems if and only if they contribute to the ecosystem's resilience. Part of the reason the authors build resilience into their theory of role functions is to exclude "destructive" activities from counting as functions. For example, they believe that invasive species responsible for ecological degradation do not have a function of causing the degradation.

As noted, Dussault and Bouchard believe that ecosystems can be treated as evolving under this framework. However, it seems this is not a necessary interpretation of their theory of functions. One could accept that species have functions when they contribute to an ecosystem's resilience and ability to persist, even if one disputes that ecosystems thereby count as evolving. So, I will discuss only the theory of functions as stated and set aside the evolutionary interpretation here.

I agree that causing or maintaining degradation per se is not an ecological role function. My CCI theory also provides a natural explanation of this. Degraded states of ecosystems contrast with alternative healthy regimes. The activity "helping to maintain a degraded state" of a given ecosystem, by definition, fails to occur in some alternative regimes of that ecosystem, and therefore, it does not count as a function. However, we should be careful not to assume that invasive or destructive species do not have role functions at all. Explanations of invasion dynamics often do appeal to invasive species' functional traits.

The major shortcoming of PEP is that it links all role functions of ecosystem components to ecosystem resilience. In practice, role functions are relevant to explaining many ecological phenomena that can have little to do with persistence or that involve the breakdown of resilience, including trophic cascades and regime changes. So, PEP does not capture the explanatory scope of role functions within ecology. A similar criticism is made by Jay Odenbaugh, who argues that this theory problematically "takes one type of effect of the constituents of ecosystems [i.e., promoting ecosystem persistence] and assumes all ecosystem [role] functions consist in just this effect" (Odenbaugh 2019, 174).

Another problem is that resilience is a high-level ecosystem property that seems to be driven by other higher-level properties, such as connectivity[10] (Adam et al. 2011; Olds et al. 2012) and functional trait diversity (Mori et al. 2013; Sakschewski et al. 2016). In most cases, activities of individual species are explanatorily distant from ecosystem resilience. Therefore, it would be difficult to assign functions to most species in this theory. This problem has both a factual and an epistemic component. Factually, many species' functions will not be recognized by PEP if they are not explanatorily relevant to ecosystem resilience. Epistemically, even supposing that some species' particular activities do contribute in meaningful ways to ecosystem resilience, it would be difficult to discover many of these functions. This would require infeasibly detailed knowledge of how individual species contribute to high-level ecosystem properties.

A final problem is that some ecosystems are apparently not very resilient in the face of climate change, including especially coral reefs and some high-latitude and high-elevation systems. Many such ecosystems are undergoing a regime shift or may be in imminent danger of collapse. Yet role functions are still assigned to coral reefs and high-latitude species. Because PEP assigns role functions only within persisting, resilient ecosystem states, this feature of the theory is in tension with ecological explanatory practice. Thus, PEP is limited in scope as compared to CCI because it links all role functions to a single ecosystem property, resilience.

5.3. The organizational theory

The organizational theory has been developed by a group of authors in philosophy and biology, including Charbel El-Hani, Alvaro Moreno, Matteo Mossio, Nei Nunes-Neto, and Cristian Saborido. The organizational theory holds that biological functions can be characterized in terms of how parts contribute to the self-maintenance of a larger organization. A statement of the theory is as follows. The statement refers to traits, but the authors' other work clarifies that the term *components* could be substituted for *traits* to reflect the intended generality of the theory.

(OT) [A] trait T has a function if and only if:

C1. T contributes to the maintenance of the organization O of S;

C2. T is produced and maintained under some constraints exerted by O;

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[10] *Connectivity* refers to the rate at which organisms move between ecosystems.

C3. S realizes organizational closure. (Saborido et al. 2011, 594; also Moreno and Mossio 2015, 73)[11]

Further work extends this approach to ecological systems. For example, Nunes-Neto, Freitas, Saborido, et al. (2016) explain that in ecology,

> The producers, consumers, and decomposers play functions that contribute to the self-maintenance of the ecological system and these functions correspond to their constraining action on the flow of matter and energy within the ecosystem closure of constraints. (271)

Nunes-Neto et al. (2014) claim that

> the ascription of function to the biodiversity or to its components (such as the traits, populations, functional groups, etc.) aims at explaining the maintenance of ecosystem properties (nutrient cycling, primary productivity, etc.) (125)

under circumstances in which

> the items of biodiversity harness (constrain) the matter in the ecosystem in a way that the coordinated action of all these items makes ecosystem properties possible. (131)

Thus, the organizational theorists focus on the roles of components in maintaining certain organizational properties of the system, where the systemic properties are also conditions for the maintenance of the components.

So, OT as applied to ecology can be summarized as follows. Organisms constrain the movement of matter and energy through ecosystems via their metabolic activities. These activities of organisms make possible the properties and processes of ecosystems, including their nutrient cycles. These properties in turn allow for the continued existence of the component organisms, which depend on the presence of, for example, certain nutrient sources. Thus, the organisms' activities help explain the ecological organization, which in turn helps explain the existence of the organisms. In this view, role functions are those activities that are involved in constraining matter and energy flow in certain ways, as in the case of organisms' trophic activities.

The organizational framework may be helpful for understanding the self-maintenance of biological entities like cells and organisms. However, there are some questions about how the framework applies to ecology and to the assignment of role functions.

First, this framework assumes that ecosystems can be treated as self-maintaining units along the same lines as organisms (although it need not assume that these

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[11] *Organizational closure* refers to a certain type of mutual dependence among constraints, where constraints are certain entities that influence matter/energy flow within a larger organization. I do not have space for a detailed discussion of the authors' sense of "organizational closure" or "closure of constraints," so the reader is referred to the cited works. Mossio et al. (2009) contains a prior version of the cited theory.

entities realize the same degree of complexity or stability). It has been a matter of controversy whether ecological units can be treated as relatively unified, self-maintaining entities or whether they should be treated as more accidental aggregations of populations (e.g., Lean 2018). Interestingly, the organizational framework may have the resources to address some of these debates:

> Constraints subject to closure *constitute* the biological organisation and, accordingly, make an essential contribution to determining the identity of the system . . . . [O]ne may conjecture that closure in fact defines biological individuality. (Moreno and Mossio 2015, 23, emphasis in original)

Thus, in this framework, ecosystem individuality is a matter of whether component populations and abiotic structures collectively realize closure (roughly, mutual dependence). Functions are assigned within individual ecosystems in such a state. As noted, however, it is bound to be controversial whether ecosystems should be modeled as individuals at all. More work needs to be done to see whether different ecosystems do realize closure in the sense of the organizational theory.

In view of this, a theory of functions that does not make ontological assumptions about ecosystems may be desirable. CCI provides an account of role functions that is ontologically lightweight by comparison. Although functions are indexed to token ecosystems, CCI leaves open that ecosystem boundaries could be purely stipulative or conventional, that ecosystems may not be self-maintaining, and that ecosystems may not even be "real" (meaning, roughly, practice-independent) individuals (see Garcia and Newman 2016). Without intending to endorse all of the preceding ideas, CCI is a useful theory of functions, given that it leaves open the possibility of multiple ontological and empirical views about the nature of the ecosystem. In this respect, it tracks explanatory practice because ecologists disagree among themselves about the nature of ecological units (Jax 2006), yet they tend to agree about the assignment of role functions.

Second, there are plenty of examples of role functions that, speaking loosely, destabilize one regime in an ecosystem and eventually stabilize another regime. Real examples arise from the introduction of nitrogen-fixing plants to an area without native nitrogen fixers (Vitousek and Walker 1989), the introduction of earthworms to an area without native earthworms (Frelich et al. 2019), or the introduction of beavers to an area without native beavers (Jax 2010). In each of these cases, the presence of a new role function in the ecosystem causes major changes to matter and energy cycling within the system, with cascading effects that may lead to a new regime.

The organizational framework may be able to characterize this type of change as a change in ecosystem identity, and it can recognize nitrogen fixing, leaf litter consumption, and tree felling as role functions that contribute to the self-maintenance of the post-invasion ecosystem regimes. However, an issue is what OT says about these functions prior to and during the course of a regime shift. If earthworms have recently been introduced to a part of central North America and are in the process of causing functional changes to the local ecosystem, their litter eating acts against the maintenance of the current organization. The OT framework seems to lack the resources to call this activity a function until after the ecosystem has settled into a new regime. This is counterintuitive because litter eating is a clear example of a role

function, and its status as a function should not depend on whether an ecosystem is temporally before, during, or after a regime shift. One reason for this is epistemic: we knew that litter eating was a function before we knew that introducing this function could cause a regime shift. CCI recognizes these causal roles as functions regardless of whether they disrupt or stabilize the present state of an ecosystem.

Alternatively, suppose that introduced earthworm populations are managed at a low level such that they do not cause a regime shift. Although the earthworm population is too small to disrupt the functional state of the ecosystem, the activities of the earthworms have the tendency or capacity to alter the ecosystem's organizational state. In this circumstance, it appears that OT will also not recognize the earthworms' activities as functions. I have argued that this misrepresents ordinary thinking about ecological role functions. Role functions are maintained across ecosystem regimes, and whether an activity is a function does not depend on whether it tends to stabilize or disrupt the current regime.

Finally, there are some general questions about the consistency of the organizational approach with explanatory aims in ecology. For instance, Moreno and Mossio (2015, chap. 3) write that the organizational approach to functions can be developed to explain various features of functions, including (a) the normativity of functions, (b) the fact that attributing a function to an entity explains its existence, and (c) the nature of malfunction. These features make OT well suited for examining physiological functions within organisms, which are proper functions that permit malfunction. However, these features are in tension with the largely nonnormative understanding of role functions argued for in this article. The cited authors claim that OT can provide a single unified account of biological functions, but for the reasons stated, I am among those who think that we require multiple accounts of functions to accommodate normative and nonnormative functional concepts.

6. Conclusion

I am a pluralist about theories of functions, and I believe that different theories that capture different explanatory uses of functional concepts can peacefully coexist. Nevertheless, I have argued in previous sections that my CCI account performs better than some existing accounts of role functions according to some basic criteria, such as accuracy in identifying functions and consistency with ecological explanatory practices. In addition to achieving a level of accuracy, I have argued that my theory

a. regards the potential for ecological change as central rather than anomalous,
b. resolves the liberality problem facing Cummins-type theories,
c. explains the principled distinction between functions and nonfunctional activities in terms of the explanatory centrality of activities that are relatively counterfactually stable across organizational changes, and
d. does not rely on any ontological assumptions about ecosystems while clarifying how nonepistemic judgments about ecosystem boundaries and relevant ecosystem regimes may influence role-function assignments.

These points are meant to show why my theory is a useful addition to the many existing discussions of role functions.

A defender of one of the other theories can say that their theory is not only meant to achieve some level of accuracy but also is meant to guide or even revise the usage of the term *function* in ecology. Although I would support such a project undertaken for epistemic or ethical reasons, it is not a project I have undertaken in this article. My sense is that the literature needs more reflection on reasons for revising function terminology in ecology. For now, absent a compelling reason to think there is a practical flaw with the role-function concept, I offer an account that is primarily meant to faithfully capture existing usage.

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