

DOI: 10.1017/psa.2025.10101

This is a manuscript accepted for publication in *Philosophy of Science*.

This version may be subject to change during the production process.

Why the Liberality Criterion Is Dysfunctional for Theories of Ecological Function

Colby J. Clark

Department of Philosophy, University of Utah, Salt Lake City, Utah

Email: colby.clark@utah.edu

Abstract

Theories of ecological function often appeal to the liberality criterion to evaluate a theory's adequacy. The liberality criterion requires that a functional description successfully differentiates between functions and nonfunctions. A functional description is considered inadequate if it is excessively liberal or excessively restrictive. I criticize the deference that is shown to the liberality criterion. I present a hypothetical case to illustrate how the application of the liberality criterion needlessly problematizes the four general theories of ecological function. Instead, a theory's functional description should be considered adequate as long as it produces a better understanding of the complex phenomenon under study.

1. Introduction

Debates over functional descriptions in the philosophy of ecology have been popular as of recently (Odenbaugh 2010, 2019; Nunes-Neto et al. 2014; Dussault and Bouchard 2017; Millstein 2020; Lean 2021; Dussault 2022; Krohs and Zimmer 2023; Morrow 2023). Four general theories of ecological function are defended: selected effects, systemic capacity, organizational theory, and persistence enhancing. A theory is often judged as adequate or inadequate based on its ability to include proper functions in and to exclude nonfunctions from its functional descriptions. This evaluative measure is termed the *liberality criterion*.¹ Many claim that one theory is superior when compared to the others given how well it addresses the liberality criterion. In this article I criticize the deference that is shown to the liberality criterion in the evaluation of a theory's adequacy.

The essay is divided into three sections. The first section briefly summarizes the four general theories of ecological function and formally introduces the liberality criterion. The second section presents a hypothetical case. All four theories fail to satisfy the liberality criterion for the hypothetical case. The idea is not to refute the four theories. In fact, each theory yields a meaningful explanation of the hypothetical case that ecologists might find useful. Rather, I aim to refute the liberality criterion's focal role in the evaluation of each theory's adequacy. The third section sketches an alternative strategy. A theory's functional description should be considered adequate as long as it leads to a better understanding of the complex phenomenon under study. I invoke Lean's (2018) account of the indexical community concept as an apt starting point.

2. Theories of ecological function

¹ The liberality criterion is also referred to as the *liberality problem* (see Morrow 2023), but a reviewer suggested that the latter phrasing might cause confusion about the topic of the discussion. I am principally interested in the evaluation of a theory's functional descriptions as either adequate or inadequate.

Several articles review the four general theories of ecological function (Odenbaugh 2019; Lean 2021; Krohs and Zimmer 2023; Morrow 2023), so my presentation here is brief. This section summarizes the theories and introduces the liberality criterion to set the stage for the hypothetical case that is analyzed in the next section.

Jax's (2005, 2010) categorization of ecological functions is the typical springboard for discussions of the subject. He identifies four general meanings of *function* and *functioning* in ecology. The terms are used to reference:

1. A single process that describes a cause-and-effect relationship between two objects.
2. Several processes that operate within the context of the larger system:
 - 2a. What happens? Which processes occur? How do organisms interact?
 - 2b. How does the whole operate or perform? How is the whole sustained?
3. The role attributed to particular objects (i.e., “bearers of function”) within the system.
4. The role attributed to the whole system's practical use (i.e., ecosystem services).

Discussions of the four general theories of ecological function are situated between the second and third interpretations (Dussault and Bouchard 2017; Millstein 2020; Dussault 2022). Both construe a distinct part-whole relationship. The second treats the whole ecosystem as the proper subject of a functional description. The third assigns functions primarily to the parts that comprise the whole ecosystem (Dussault 2022). The notable distinction between these two interpretations is that the former subscribes to a top-down view whereas the latter is bottom up.

The first theory of ecological function is the selected effects (SE) account. Wright (1973) is credited as its originator. Wright's etiological definition assigns SE functions to traits that are naturally selected. A heritable trait possesses an SE function if possession of the trait confers adaptive advantages that increase the organism's overall fitness. A commonly cited example is the human heart (Odenbaugh 2010). The human heart is a heritable trait that increases the fitness of the human species in virtue of its ability to circulate blood. Early accounts of SE functions centered on biological functions, like the function of the human heart (Millikan 1989; Neander 1991), but it is contestable if SE functions scale up

to ecological functions. Many philosophers of ecology reject the SE theory as adaptive traits of organisms are not obviously directed at ecosystem functioning (Maclaurin and Sterelny 2008; Nunes-Neto et al. 2014; Dussault and Bouchard 2017; Odenbaugh 2019; Dussault 2022; Morrow 2023). For instance, a peacock's plumage is an inherited trait selected by peahens that does not cause their ecosystem to adopt any particular functionality. Recently, Millstein (2020) advanced a modified version of the SE theory to account for Leopold's use of *function*. She argues that coevolution between interactive species produces SE functions that operate at the ecological level. Initial reactions to Millstein's account have been mixed (cf. Dussault 2022; Morrow 2023), but her modified SE theory offers explanatory insights that are absent from other theories, like an account of evolution's role and a synthesis of community and ecosystem perspectives.

SE functions are contrasted with Cummins' (1975) causal role (CR) functions (Amundson and Lauder 1994). Odenbaugh (2010, 2019) posits a CR-style account of systemic capacity (SC) functions for ecology. "The systemic capacity function account understands the function of x to F in terms of how the capacity or disposition to F contributes to a system S 's capacity or disposition to C " (Odenbaugh 2010, 252). In other words, a bearer of an SC function is relevant to the causal explanation of an emergent ecosystem behavior. Detritivores that consume litter and generate soils to stabilize the nutrient cycling capacity of the ecosystem possess SC functions (Maclaurin and Sterelny 2008). Similarly, a predator that increases diversity and stabilizes an ecosystem as a result of its predation possesses an SC function. Sterelny (2006) cites Paine's (1966) starfish experiment as one such case. In both examples, neither the detritivores nor the starfish are selected by the ecosystem to perform their SC functions. Rather, SC functions describe how the activities of organisms are causally related to a distinct ecosystem behavior. But SC functions are not restricted to organisms. Odenbaugh (2010, 2019) assigns SC functions to abiotic elements, like lightning and volcanoes that contribute to a natural system's nitrogen fixation capacity. The flexibility to accommodate abiotic elements in functional descriptions is a distinct advantage of the SC theory.

Whereas the first two theories subscribe to a more bottom-up view, the final two are more top down. Nunes-Neto et al. (2014) propose the organizational theory (OT) of ecological function. On this account, an ecosystem component possesses an OT function if, and only if, it cycles the flows of energy and matter that are essential to the structure of the ecosystem's causal loop. The OT theory is informed by two principles from previous accounts of biological functions (Mossio et al. 2009; Mossio and Moreno 2010; Saborido et al. 2011), self-maintenance and closure. Self-maintenance is an ecosystem property. Transfers of energy and matter between the components of an ecosystem are typically asymmetrical. Predators do not return energy and nutrients to the prey species that they consume. But, taken collectively, networks of trophic interactions ensure that the ecosystem sustains its organizational structure over time. At the level of ecosystem components, the bearers of OT functions constrain various flows of energy and matter that regulate and reinforce the ecosystem's boundary conditions. Nunes-Neto et al. (2014) refer to this structural arrangement as a *closure of constraints*. Each constraint governs an interaction so as to close off the causal loop of processes that constitute the ecosystem. Thus, the OT theory differs from the SE and SC theories in that it fixes functional descriptions to a single ecosystem feature (self-maintenance) and a particular type of organizational structure (constrained causal loops).

The fourth theory is the persistence enhancing (PE) account. PE functions are assigned to the parts of an ecosystem that promote the ecosystem's persistence. An ecosystem part is said to possess greater ecological fitness than another if it is better able to solve the design problems that detract from an ecosystem's ability to maintain a distinct state (Bouchard 2008). Dussault and Bouchard (2017) situate the PE theory within the framework of Holling's (1973, 1996) ecological resilience concept. Ecological resilience indicates an ecosystem's ability to endure disturbances to maintain a distinct stability regime (e.g., coral

reef, grassland, pine forest, etc.).² Additionally, the SE theory integrates resilience theory's distinction of functional groups and functional responses (Elmqvist et al. 2003; Folke et al. 2004). A functional group sorts the PE functions performed by species into categories (e.g., nitrogen fixation, grazing, predation, etc.). Multiple species belong to the same functional group but perform PE functions under unique environmental conditions and across spatiotemporal scales to generate a mesh of overlapping functional responses (Jax 2005). The specificity of the functions that the PE theory assigns in relation to a definitive ecosystem property (i.e., ecological resilience) is an advantage that it has over the other theories.

The part-whole dynamic between function bearers and an ecosystem that grounds all four theories invites the liberality criterion. The liberality criterion is simple: a functional description is adequate only if it successfully discriminates between functions and nonfunctions (Morrow 2023). All theories of ecological function construct responses to and develop criticisms on the basis of the liberality criterion (Nunes-Neto et al. 2014; Dussault and Bouchard 2017; Odenbaugh 2019; Morrow 2023). Many retreat to pluralism (Garson 2017; Lean 2018; Odenbaugh 2019; Millstein 2020; Morrow 2023). The retreat to pluralism is sensible since the liberality criterion is a by-product of the idealization of ecosystems as closed systems. In reality, ecosystems are open across multiple scales (Wiens 1989; Holt 2004). Pluralism empowers ecologists to utilize the idealization without a firm commitment to realism about ecosystem discreteness. This is a familiar exercise for philosophers of complexity science (Mitchell 2009; Potochnik 2017) and ecological complexity theorists (Allen and Starr 1982; O'Neill et al. 1986). Yet the philosophy of ecology seems reluctant to abandon the liberality criterion. I argue that this is a mistake because it allows metaphysical inconsistency to obscure the epistemological utility inherent to the theories.

² The detection of distinct stability regimes is an empirical challenge, but resilience theory has made some significant advancements on this front (see Carpenter et al. 2001; Dakos et al. 2011; Sundstrom and Allen 2019).

In the next section I present a hypothetical case to illustrate how deference to the liberality criterion is dysfunctional for all four theories of ecological function. In the final section I suggest that theories of ecological function should be evaluated differently. A theory should be considered adequate as long as its functional descriptions promote a better understanding of the complex phenomenon under study.

3. The hypothetical case

Each theory of ecological function posits its own test case to demonstrate how its definition outperforms others. Millstein (2020) discusses parasitic beetles and their bee hosts in her modified SE account. Odenbaugh (2010, 2019) cites *Rhizobium* and the nitrogen cycle in his defense of the SC account. Nunes-Neto et al. (2014) use a bromeliad and its associated organisms (e.g., spiders and flies) to champion OT functions. And Dussault and Bouchard (2017) can draw on any number of examples from resilience theory (see Folke et al. 2004) to corroborate their PE theory. Rather than follow this model (i.e., offer a definition of ecological function, posit an example to confirm the definition, then explain how the definition is more advantageous than the others), I present a hypothetical case in which all four theories struggle to satisfy the liberality criterion. The objective is not to rank the theories or to propose another definition of ecological function. Instead, I intend to point out how deference to the liberality criterion needlessly problematizes functional descriptions that otherwise provide useful explanatory insights.

Here is the hypothetical case: Imagine a two-island scenario. Both islands possess unique configurations of ecological functions. An ecologist is asked to provide a functional description of the ecosystem found on one of the islands, i_1 . The ecologist satisfies the liberality criterion if, and only if, she successfully differentiates between functions and nonfunctions for the ecosystem on i_1 . Assume that the set of ecological interactions among species A, B, and C satisfies the liberality criterion under normal circumstances regardless of whether the ecological interactions are described with SE, SC, OT, or PE functions. Occasionally, a tramp species, T, on the adjacent island, i_2 , disperses to i_1 (see figure 1).

When T disperses to i_1 , it interacts with A–B–C in an ecologically discernible way. This is the question posed to each of the four theories: how does the functional description of A–B–C on i_1 account for T?

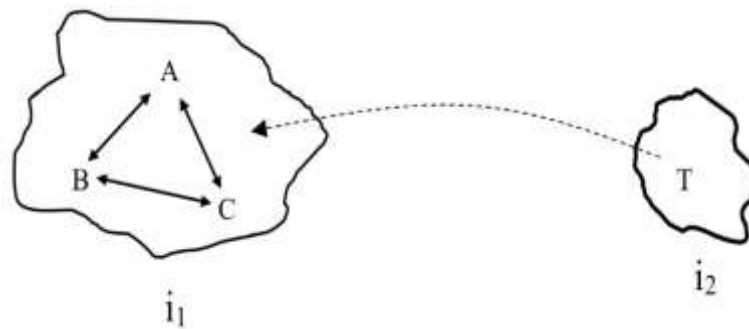


Figure 1. A diagram of ecosystem A–B–C (composed of species A, B, and C) on island i_1 and the tramp species, T, on island i_2 that occasionally disperses to i_1 . The bidirectional arrows between A, B, and C signify ecosystem discreteness rather than any explicit type of causal interactions.

3.1 The SE approach's potential responses

Oceanic islands are often characterized by remarkable coadaptation among resident species due to strong isolation effects on evolutionary histories (Carlquist 1974). So, the SE theory seems well disposed to offer a meaningful functional description of A–B–C, especially Millstein's (2020) modified account since it integrates Thompson's (2005) Geographic Mosaic Theory of Coevolution (GMTC). The GMTC explains the coadaptation that emerges between proximate populations over evolutionary timescales. Populations that happen to coexist in the same geographical area jury-rig their ecological interactions to produce SE functions. But how might the SE theory fit T's arrival into its functional description of A–B–C?

Established island populations sometimes lose their ability to compete against conspecifics if they are highly isolated. Wilson's (1961) taxon cycle concept describes the general replacement procedure. His work on Melanesian ants revealed that established island populations thrived for several generations but were outcompeted as soon as a novel competitor arrived on the island.³ However, it is not necessarily the case that T replaces A, B, or C. Instead, i_1 might be within T's seasonal migratory range when i_1 's productivity supports more populations (MacArthur 1969). If so, T's seasonal arrival could affect the coadaptation dynamics of A–B–C, albeit to a lesser degree.

In a taxon cycle scenario, T probably does not possess an SE function with respect to A–B–C since T lacks a historical connection to the evolutionary process that generated the SE functions possessed by A, B, and C. But the substitutability of T for the replaced population raises a question in regard to the status of the other populations that remain on i_1 . Does the loss of their evolutionary partner affect their SE functions? The question challenges the SE theory's commitment to the idea that coadaptation is a communal process. It seems incorrect to revise the SE functions ascribed to the remaining populations even though one member is lost from the original functional description. The evolutionary processes remain operative as long as the populations continue to interact.

The seasonal migration scenario is a different story. It might be said that T possesses an SE function of increased flight duration (Amundson and Lauder 1994). Specific morphological traits aside, greater vagility is an evolutionary trait that increases T's ecological fitness (Holt 1993). But this interpretation is vulnerable to the liberality criterion. T possesses its SE function irrespective of A–B–C. T's SE function operates over a spatial scale larger than i_1 . Hence, T's SE function is not exclusive to A–B–C. The scalar incompatibility, in turn, exacerbates the problem. If T belongs to the SE theory's functional description of A–B–C, then where is the precise stopping point? Why not include the

³ The taxon cycle is a contestable hypothesis (see Whittaker 1998), but it allows for a specific kind of functional description that is helpful for the general discussion.

populations that T interacts with on other islands, like i_2 ? In most cases the SE theorist makes a thoughtful decision about the appropriate stopping point (in space and time). But such decisions defy the liberality criterion to pursue a better understanding of the complex phenomenon as defined by the SE theorist's research aims.

3.2 The SC approach's potential responses

The SC account requires a designated systemic capacity before it is testable. The hypothetical case was inspired by Diamond's (1975) research on assembly rules for bird guilds located in the South Pacific. Diamond's study discovered evidence for MacArthur's (1972) concept of diffuse competition (i.e., the systematic exclusion of outside competitors by the established members of a community due to their combined niche structure).⁴ So, let A–B–C represent a configuration on i_1 that possesses the systemic capacity of competitive exclusion through diffuse competition. A–B–C's capacity to exclude species is diminished after a disturbance as the alteration to i_1 's environmental conditions (e.g., habitat loss, reduction in resources, etc.) stresses the ecological interactions that hold A–B–C together. T's invasion of i_1 is highly probable at this time, and the configuration on i_1 transforms into A–B–C–T. A–B–C–T possesses the capacity to resist invaders due to its greater niche saturation. Simultaneously, T returns the environmental conditions on i_1 to their pre-disturbance state via subsidy effects, like seed dispersal (Cumming and Norberg 2008). A, B, and C eventually reestablish ecological interactions strong enough to exclude T. All things considered, is it the case that T possesses an SC function with respect to A–B–C's systemic capacity to enact competitive exclusion?

⁴ Even though Diamond (1975) studied guilds (not ecosystems) and diffuse competition depends on suppositions about niche theory that are not universally accepted among ecologists (Hubbell 2005), diffuse competition meets the criteria for an SC account—a configuration of ecological interactions that enables a distinct capacity to emerge at a higher level of organization.

I envision four ways for an SC theorist to respond. The first is to deny that T possesses an SC function given that the systemic capacity of A–B–C tends to exclude T when it is at full strength. Ulanowicz's (1997) ascendancy model posits a similar claim. An ecosystem may support certain species early in its development because the ecological interactions are weak, but all ecosystems tend towards a state of maximum organization. A teleological perspective, like Ulanowicz's (1990), could claim that any species filtered out during an ecosystem's ontogenesis does not belong to the ecosystem proper. In truth, this is an underdeveloped area of the ecological function discussion. It is not clear if some threshold separates functions from nonfunctions. Implementation of an expected threshold is prudent since no functional description fully exhausts the causal complexity of a natural system (Wimsatt 1972). However, such a practice is antithetical to the liberality criterion because elements of the ecosystem that are known to possess an SC function (to some degree) are intentionally omitted from the functional description.

A second way that an SC theorist could respond to the hypothetical case is to emphasize the dispositional nature of SC functions. Perhaps T only possesses an SC function in relation to A–B–C if the interactions between A, B, and C are weakened by an exogenous disturbance. *Prima facie*, this looks like a safe bet since the definition of SC function refers to dispositions. A–B–C is the appropriate functional description under ideal conditions, but explanations require flexibility to safeguard consistency when confronted with nonideal cases. But reference to dispositions becomes pernicious if the boundaries of the ecological unit are not well defined (as in the hypothetical case). Species exist all over the planet that, if introduced, would possess an SC function with respect to A–B–C. Despite the fact that T is more proximate and, as a result, more likely to interact with A–B–C, it would be impossible to establish criteria for dispositional SC functions that do not beg the question, why these conditions? Thus, the introduction of dispositional SC functions engenders more conceptual inconsistencies that contravene the liberality criterion.

Third, an SC theorist could accept that T possesses an SC function. As I previously stated, Odenbaugh (2010, 2019) argues for the SC theory given its ability to incorporate

various abiotic elements, like lightning strikes and volcanic eruptions, into functional descriptions of systemic capacities, like nitrogen fixation. Similarly, moderate disturbances (e.g., hurricanes) are regularly incorporated into island dynamics. Patch dynamics theory (Pickett and White 1985), hierarchy theory (O'Neill et al. 1986), and resilience theory (Scheffer 2009) all support this interpretation. So, it appears reasonable to attribute an SC function to T if the abiotic elements that prompt T's dispersal from i_2 are part of the functional description, too. But this interpretation is also imperfect. Two different systemic capacities are conflated. The original systemic capacity was competitive exclusion via diffuse competition, which belongs solely to the ecological interactions between A, B, and C. If the disturbance is incorporated into the functional description, then the systemic capacity is more akin to adaptive capacity, a property associated with resilience (Sundstrom et al. 2022). Competitive exclusion is strongest during the conservation phase of an ecosystem's adaptive cycle—a period marked by low adaptability and low resilience due to the increased rigidity of the internal interactions—but T arrives during earlier post-disturbance phases when ecological interactions are weak (Holling and Gunderson 2002).⁵ Consequently, it is more accurate to say that T possesses a PE function as opposed to an SC function.

The simplest solution, though, is to ignore the liberality criterion. The flexibility of the SC theory to accommodate diverse research interests is a distinct virtue that Odenbaugh (2010, 2019) rightfully emphasizes. Nothing prevents a qualified functional description of A–B–C where an SC function is attributed to T under specific contexts. However, the practice would certainly defy the liberality criterion. The ecological dynamics are not discrete enough to meet the expectations placed on functional descriptions by the liberality criterion. Ultimately, I argue that a functional description should be evaluated based on its explanatory advantages rather than its adherence to the liberality criterion. And the SC theory clearly provides a number of explanatory advantages.

⁵ Ulanowicz's (1997) ascendancy model describes a similar process in which systems become more rigid as their interactions become more efficient.

3.3 The OT approach's potential responses

The hypothetical case tests the OT theory's logical commitment to system closure. On the OT theory, A, B, and C possess OT functions due to each's ability to circulate structure-inducing resources (e.g., biomass) in an autocatalytic way that promotes A–B–C's self-maintenance as an integrated unit. Ulanowicz's (1986, 1997) ascendancy model is a network analysis approach that is highly compatible with the OT theory on this point. The ascendancy model utilizes information theory to calculate ecosystem connectedness. With the additional quantitative dimension (i.e., information theory), a functional description of A–B–C as a collection of OT functions appears practical, scientifically informative, and reasonable as long as A–B–C forms a closed causal loop. But no perfectly homeostatic systems exist in nature, and Nunes-Neto et al. (2014) admit as much. An ecosystem closed at one scale is open at the one above (Wiens 1989; Holt 2004). So, how does the OT theory accommodate T's arrival on i_1 ?

The solution is for the OT theory to revise its idealization of a causal loop. The movements of energy and matter that increase system connectedness do not form a deterministic pattern. The movements from one compartment (e.g., A, B, and C) to another within the network are probabilistic. Organizational structure emerges when the probabilities of interactions all near 1 (i.e., certain). Plenty of errancy exists throughout a network, though. Errancy, or *overhead*, is essential to organizational integrity because it prevents the overconnectedness that induces system fragility (Ulanowicz 1997). In terms of the hypothetical case, an OT theorist could claim that T possesses an OT function once it establishes probabilistic relations with other compartments that promote the ecosystem's self-maintenance to an appreciable degree (figure 2). What probability value constitutes an appreciable degree is a matter of debate, but the logical consistency of the OT theory is preserved and the liberality criterion is seemingly satisfied.

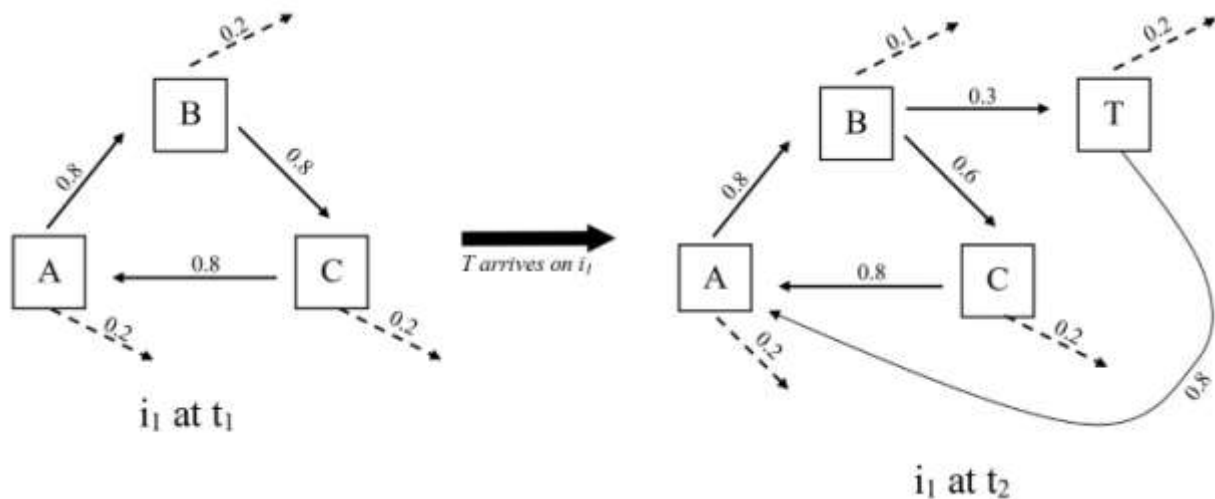


Figure 2. Hypothetical organization diagrams of A–B–C at t_1 (prior to T’s arrival) and A–B–C–T at t_2 (after T’s arrival). From Ulanowicz’s (1997) ascendancy model, arrows represent the flows of information between compartments. Information quantifies flows of structure-inducing energy or matter. Values correspond to probabilities between 0 and 1. Dashed arrows represent errancies (i.e., overhead). Ulanowicz’s (1995, 653) simplest example is the Cone Spring ecosystem, which includes compartments for plants, detritus, bacteria, detritovores, and

Although the proposed solution seems plausible enough, it is inadequate. Two populations of T must first be distinguished to clarify the inadequacy. Let T_1 represent the population of T that immigrates to i_1 , and let T_2 represent the population of T that remains on i_2 . Some vagile species, like T, have a high enough dispersal rate to overcome a high extinction rate. The result is a peculiar situation where a species’ fundamental niche is smaller than its realized niche (Pulliam 1988). In effect, the species contributes to the organization of the ecosystem without reciprocal flows that embed it into the system’s self-maintaining web of interactions (figure 3). In ecological terms, T_2 is a source population that

sustains a sink population, T_1 (Whittaker 1998). Therefore, the conditions that define OT functions are faced with a choice between two unattractive options. Either T_2 does not possess an OT function since it lacks the trademark closure that is central to the OT theory, which appears dubious if the organizational integrity of A–B–C exhibits some dependency on the inputs from T_2 . Or T_2 does possess an OT function, and the notion of system closure needs revision as it is scaled up to the level of ecosystems (Lean 2021).

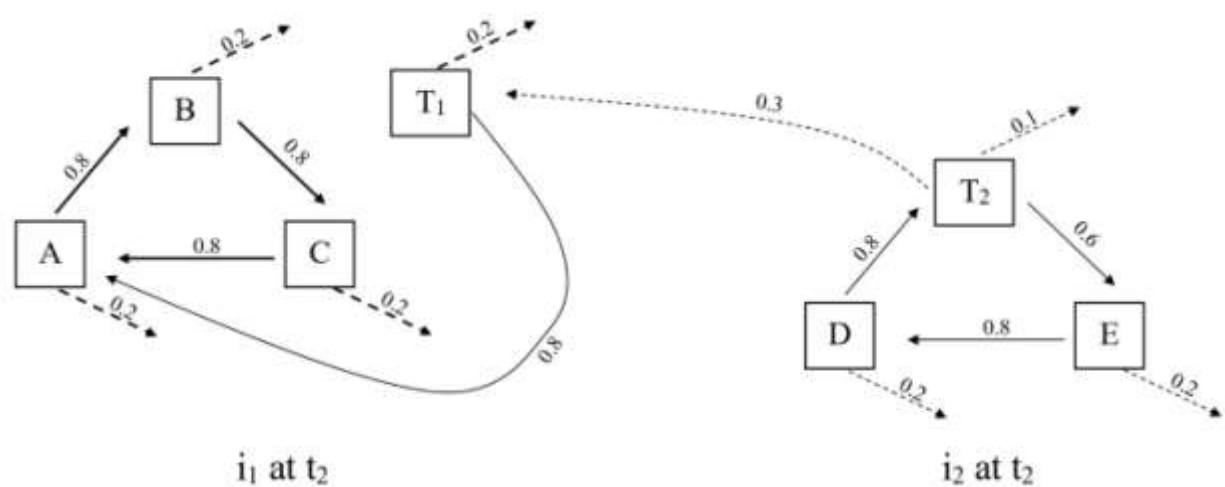


Figure 3. A diagram that represents the organizational structure between the two islands, i_1 and i_2 . D and E are species that belong to the D–T–E ecosystem on i_2 . T_1 and T_2 indicate the populations that are located on i_1 and i_2 respectively. Ulanowicz (1986) suggests a similar approach to handle spatial heterogeneity in an earlier formulation of the ascendancy model.

Nunes-Neto et al. opt for the second of the two options, but their revisions are insufficient to satisfy the liberality criterion. They apply hierarchy theory to refine their conception of a closure of constraints. The logic of their account relies on Simon’s (1962) characterization of systems as nearly decomposable organizational structures. Put simply, the interactions between system parts produce emergent organizational structure (i.e., the whole

is greater than the sum of the parts). But the organizational structure never achieves homeostasis. Instead, a hierarchy of loosely coupled systems regulates the organizational structure of systems through cross-scalar constraints (Simon 1973). Nunes-Neto et al. argue (sensu Pattee 1972) that systems are embedded in a control hierarchy that coordinates flows of energy and matter towards perpetual self-maintenance. Lower-level agents restrict the behaviors of higher-level organizational structures, and vice versa. Therefore, T appears to constitute a constraint that entangles two levels. One level is A–B–C on i_1 , and the other level is the i_1 – i_2 configuration (i.e., the combination of species that belong to both i_1 and i_2 and that form a self-maintaining causal loop). So, neither T_1 nor T_2 technically possess an OT function with respect to A–B–C. Only the metapopulation T properly possesses an OT function in the context of a multi-level hierarchy of constraints.⁶

The hierarchical construal of system closure is vulnerable to at least two criticisms. First, hierarchy theory is fundamentally incompatible with the liberality criterion. The liberality criterion is a matter of metaphysical precision, and hierarchy theory is conceived as an epistemological tool to simplify complexity (Allen and Starr 1982; O'Neill et al. 1986; Allen and Hoekstra 1992; cf. Salthe 1985).⁷ Organizational structure is not neatly differentiated into discrete levels (Potochnik 2021). Second, the hierarchical construal is committed to the unintuitive idea that a member of T_2 possesses an OT function in relation to A–B–C even though it never disperses to i_1 . The idea is equally problematic if the analysis focuses on the members of T_1 . Some members of T_1 will not contribute to the self-maintenance of A–B–C in the same manner or to the same degree. So, do all members of T_1 have to be divided into individual compartments to avert the misattribution of OT functions? If so, that would be an impractical workaround just to satisfy the liberality criterion.

⁶ This is practically a more sophisticated depiction of the SE theory's issue with the hypothetical case.

⁷ Simon (1962), too, cautioned against the confusion of hierarchy theory's epistemological idealizations with claims about the real structure of nature.

3.4. The PE Approach's Potential Responses

Dussault and Bouchard (2017) posit the PE theory as an intermediate account that avoids the excessive liberality of the SC theory and the excessive restrictiveness of the OT theory. As previously shown, one of the SC theory's responses recommends a view that is compatible with the PE theory, and the OT theory fails to include ecological agents that originate from outside an ecosystem's set boundaries. But does the PE theory successfully describe the hypothetical case? I argue that the PE theory is a strong candidate, but it succumbs to the liberality criterion, too.

Since the PE theory's principles are derived from Holling's (1973, 1996) original resilience concept, let A–B–C represent a self-organizing ecosystem with high ecological resilience (i.e., an ability to absorb exogenous disturbances to remain within the same qualitatively distinct stability regime). If A–B–C possesses strong internal feedback dynamics, then T's arrival will likely have a negligible effect on the dominant processes. Walker (1995) refers to species like T as passengers that are entrained by the dominant processes enacted by drivers (i.e., A, B, and C). The passenger–driver designation effectively differentiates T's weaker PE function from the stronger PE functions that hold A, B, and C together. Then, T's functional group and functional response roles can be added as supplemental details to the more definitive functional description of A–B–C.

The PE theory also provides even greater ontogenetic precision in response to the hypothetical case. If T arrives after a stochastic dispersal event, then it probably possesses a minor PE function as a passenger species with respect to A–B–C. T would contribute only slightly to A–B–C's persistence. But if the arrival of T to i_1 coincides with a moderate disturbance, then T's PE function is likely more noteworthy. Vagile species perform PE functions as mobile links to promote ecosystem recovery. Mobile links make ecological contributions as resources linkers (e.g., nutrient transportation), genetic linkers (e.g., seed dispersion), and process linkers (e.g., trophic interaction; Nyström and Folke 2001; Lundberg and Moberg 2003). The significance of mobile links reaches its peak during the reorganization and exploitation phases of the adaptive cycle. As the ecosystem progresses

towards the conservation phase, dominant processes reemerge (Clark 2024). Resilience theorists associate the PE functions that are performed by mobile links with *spatial resilience* rather than the traditional interpretation of ecological resilience that primarily concerns internal self-organizing feedbacks (Cumming 2011). Thus, the PE theory seems to outperform the alternative frameworks in its ability to situate T's PE function within the ontogenetic narrative of A–B–C.

Despite the PE theory's superior ability to differentiate T's PE function, its response to the hypothetical case remains deficient. Dussault and Bouchard's account overlooks two important details about resilience. First, most PE functions are context sensitive. Obviously, a species can perform more than one PE function at a time, but the significance of each PE function will often vary from ecosystem to ecosystem. For example, B's critical PE function in A–B–C might be being prey, whereas its critical PE function in B–D–E (on another island) is being a grazer, especially if the two ecosystems are located in zones with characteristically different stability regimes (e.g., grassland versus montane forest). Does B possess the whole assortment of its PE functions at all locations, or only the ones relevant to the ecosystem under consideration? Even though the species is the same, the functional description fails to satisfy the liberality criterion if it includes more PE functions than actually exist in a given context.

Morrow's (2023) counterfactual account offers a way to respond to this first issue. On this view, B possesses a PE function insofar as it would perform the same PE function regardless of the current stability regime of the ecosystem under consideration. In response to the hypothetical case, T possesses a PE function as long as T performs the same PE function (to some degree) in deserts, forests, tundra, and so on. Morrow's counterfactual account prevents an explosion of PE functions, but, at the same time, it invites a similar T_1 – T_2 problem as before. T_1 's most critical PE function with respect to A–B–C is being a post-disturbance mobile link. But the mobile link PE function does not apply to all members of T_2 . Some members of T_2 never disperse after a disturbance, yet all members of T_1 originate from the T_2 population. Moreover, several generations might pass between moderate disturbance

events (Holling 2001). So, it is unclear if T_2 rightfully belongs to the functional description of A–B–C.

The second neglected detail concerns adaptive capacity. An ecosystem that lacks sufficient adaptive capacity is liable to undergo transformation from one stability regime to another after a moderate disturbance (Allen and Holling 2010). If an ecosystem possesses sufficient adaptive capacity, then it innovates via processes of internal reorganization to remain in the same stability regime (Sundstrom et al. 2022). Innovation complicates the attribution of PE functions because the ecosystem persists but some of its component populations, which possess PE functions, are replaced. Imagine that T develops a PE function to replace B in A–B–C. The PE theory assigns PE functions relative to the persistent ecosystem, so A–B–C and A–T–C are virtually functional equivalents as long as the dominant causal processes have not collapsed and restructured. How does the PE theory explain B's possession of a PE function prior to T's arrival and its lack of a PE function after its replacement if the ecosystem never switches stability regimes? Does B somehow belong to the functional description of A–T–C? Although this line of questioning appears troublesome for the PE theory, it is only troublesome if the liberality criterion serves as the chief measure of the PE theory's adequacy.

4. Understanding complexity

The previous section presented a hypothetical case to assess the four theories of ecological function. The hypothetical case was not meant to refute the four theories but rather to criticize the liberality criterion as a test of adequacy. Each theory of ecological function was shown to offer an insightful interpretation of the hypothetical case that supports real research aims pursued in ecology. But the liberality criterion unravels the explanatory advantages gained from the various theories as it smuggles in a metaphysical commitment about the discreteness of ecological units that is unsatisfied by most accounts. The prevalence of pluralism within ecological function theory suggests that I am not alone in my dissatisfaction with the liberality criterion. Pluralism acts as a means to negotiate between competing views

about the proper boundaries of an ecological unit. The conceptual framework used to delineate the ontological boundaries of an ecological unit determines the appropriate theory of ecological function. The liberality criterion operates as little more than a self-imposed obstacle on the way to that obvious conclusion. This seems needlessly counterproductive. Instead, the functional descriptions detailed by theories of ecological function should be evaluated epistemologically. This section sketches an alternative strategy that abandons the liberality criterion to better understand complex phenomena. The indexical community concept is invoked as an apt starting point.

The liberality criterion fundamentally rests on a conception of ecosystem discreteness. But many realize that no such discreteness exists. Shrader-Frechette and McCoy (1993) argue that no single definition of ecological concepts, like community and ecosystem, exhausts the research aims of ecology. The ecological units are tailored to scientific inquiry: “The exercise of determining, *a posteriori*, the boundaries of a community may have heuristic power for uncovering any structures underlying such communities, if indeed there are any” (Shrader-Frechette and McCoy 1993, 59). Jax (2006, 2010), too, advocates for a heuristic interpretation of ecological unit concepts. Like the hierarchy theorists (Allen and Starr 1982; O’Neill et al. 1986; Allen and Hoekstra 1992), he argues that nature furnishes the data points but the observer decides where to delimit the boundaries of an ecosystem. Odenbaugh (2007, 2010) is more moderate. He asserts that ecosystems are concrete particulars with beginnings and endings. The strength of the causal relationships that constitute the ecosystem ultimately govern the ecosystem’s discreteness. Thus, a continuum exists. Odenbaugh (2007) cites watersheds as examples of where ecosystems possess objective boundaries. Jax (2006) also references watersheds as ecosystems where topographical and functional boundaries coincide, but he cautions that this is rare. At the same time, “[a] watershed ecosystem, or a lake, is far from being uniform” (Kolasa and Zalewski 1995, 1). The boundaries that delimit an ecosystem represent an idealization that assumes uniformity for the sake of understanding (Potochnik 2017).

Lean's (2018) indexical community concept offers a better way forward for the evaluation of functional descriptions. Originally posited by Sterelny (2006), an *indexical community* refers to a population set that is defined relative to a specific research question. Some details are purposefully omitted to better understand others. "Identifying indexical communities enables us to pose some of the traditional problems of community ecology while remaining neutral on the extent to which the relevant phenomenological community is a causal system" (Sterelny 2006, 227). Lean (2018) expands the indexical community concept. Simple indexical communities are useful for analyses of single populations but not for community-level properties. To make community-level properties analyzable, Lean suggests a three-step process that resembles Parker and Pickett's (1998) proposed patch model to account for historically contingent ecosystem dynamics. The first step is to adopt an interventionist account of causation (*sensu* Woodward 2010). Second, a specific set of causal interactions are selected based on the investigation's research aims. Third, the causal interactions are mapped geographically:

Once we identify which causal relations are relevant, we map where these causal actors are distributed geographically, which is the information needed to identify the spatial boundaries of the community. The innovation here is that by using multiple starting points, we can build in robustness and avoid the explanatory fragility of indexical communities built around a single population. (Lean 2018, 514)

Lean admits that interventionist accounts of causation are vulnerable to criticism because actual interventions are usually impossible. Ecological causation is too complex anyway. But his geographical approach is intended to embody Wimsatt's (1972) notion of a *descriptively complex* perspective. When an indexical community is geographically mapped, it reveals how theoretical perspectives align with one another. The appearance of spatially congruent objects that are shared by the theoretical perspectives indicates robustness. The hypothetical case is evidence of this fact. All four theories of ecological function share the same objects of interest (i.e., A, B, C, A–B–C, and T) that are similarly bounded in physical

space. Collectively, the theories fill in each other's explanatory gaps to produce a multicausal interpretation of the hypothetical case.

If the liberality criterion is abandoned, then philosophers of ecology require a new test to evaluate the adequacy of functional descriptions after an indexical community is defined.⁸ I argue that adequacy should be evaluated based on how a given functional description leads to a greater understanding of complexity. Ecosystems emerge from a mix of internal feedbacks, cross-scalar constraints, and stochastic disturbances. Ecosystems are also path dependent insofar as they “preserve the memories of their pasts” (Levin 1999, 158). Despite the widespread complexity and contingency, a robust understanding of complex phenomena is possible (Allen and Starr 1982; Lawton 1999).⁹ Each theory of ecological function effectively idealizes the causal structure of a phenomenon to improve understanding. Importantly, idealizations do not need to be robust to all investigative aims to be adequate. This is Potochnik's (2017) point with respect to complexity science more generally. The same applies here. Functional descriptions are motivated by specific research aims, and their adequacy should be evaluated accordingly.

As a corollary, the savviness afforded by a pluralist approach is essential to success. Each theory supplies a constructive framework to interpret complex phenomena. Whether a

⁸ Another alternative is to reject ecological functions altogether (see Krohs and Zimmer 2023). But this is a mistake. The theories offer explanatory insights that clarify research aims and aid understanding. And the indexical community concept seems like a step in the right direction to retain the positive qualities of the theories without any metaphysical commitments that needlessly complicate functional descriptions.

⁹ Several philosophers of ecology take issue with Lawton's contingency thesis since it suggests that ecological laws are rare or nonexistent (Colyvan and Ginzburg 2003; Mikkelsen 2003; Linquist 2015). To clarify, the approach that I defend is neutral with respect to ecological laws. The notion of contingency at work in my account is epistemological. Different explanations of causal patterns are tied to specific research perspectives. Ultimately, an explanation may appeal to ecological laws if doing so promotes a better understanding of the complex phenomenon under study.

functional description satisfies the liberality criterion for all interpretations is a nonissue as it pertains to the pursuit of understanding. Ecological complexity theorists make a similar claim with respect to scale. The correct scale to interpret data is determined by a study's interests in a particular complex phenomenon (Allen and Starr 1982; O'Neill et al. 1986; Meentemeyer and Box 1987; Kolasa 1989; Levin 1992; Wiens et al. 1993; Cadenasso et al. 2003). To this end, theories of ecological function are invaluable epistemological tools (for philosophers and ecologists alike) to describe complex phenomena. And the liberality criterion is little more than an obstacle on the path to understanding.

5. Conclusion

This article discussed how four general theories of ecological function evaluate a functional description's adequacy for a hypothetical case. Each theory failed to satisfy the liberality criterion. Nevertheless, the theories were used to articulate meaningful interpretations of the hypothetical case. I reasoned that deference to the liberality criterion is a mistake because it needlessly problematizes legitimate scientific inquiry. The various theories facilitate understanding even if they do not satisfy the liberality criterion. I suggested that a theory should be considered adequate if it leads to a better understanding of complexity. This shift in perspective unlocks new investigative avenues for theories of ecological function that respond to the diverse research aims of ecologists (e.g., genetics, populations, communities, landscapes, etc.).

Acknowledgments

I sincerely appreciate the feedback that I received from Melinda Fagan and the participants of the Institute for Practical Ethics at the University of California San Diego's 2025 workshop on environmental philosophy, which included Derek Halm, Roberta Millstein, Jay Odenbaugh, Carlos Santana, Shermin de Silva, Natalie Jacewicz, Annabelle Tao, Joaquin López-Huertas, Drew Dittmer, Ellis Jones, and Andrés Garzón-Oechsle. I am also grateful for the comments and suggestions that I received throughout the review process.

Declarations

None to declare.

Funding Information

None to declare.

References

- Allen, Craig R., and C. S. Holling. 2010. "Novelty, Adaptive Capacity, and Resilience." *Ecology and Society* 15 (3):24. <https://doi.org/10.5751/es-03720-150324>.
- Allen, Timothy F. H., and Thomas B. Starr. 1982. *Hierarchy: Perspectives for Ecological Complexity*. Chicago, IL: The University of Chicago Press.
- Allen, Timothy F. H., and Thomas W. Hoekstra. 1992. *Toward a Unified Ecology*. New York: Columbia University Press.
- Amundson, Ron, and George V. Lauder. 1994. "Function Without Purpose: The Uses of Causal Role Function in Evolutionary Biology." *Biology & Philosophy* 9:443–69. <https://doi.org/10.1007/bf00850375>.
- Bouchard, Frédéric. 2008. "Causal Processes, Fitness, and the Differential Persistence of Lineages." *Philosophy of Science* 75 (5):560–70. <https://doi.org/10.1086/594507>.
- Cadenasso, Mary L., Steward T. A. Pickett, Kathleen C. Weathers, and Clive G. Jones. 2003. "A Framework for a Theory of Ecological Boundaries." *BioScience* 53 (8):750–58. [https://doi.org/10.1641/0006-3568\(2003\)053\[0750:AFFATO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0750:AFFATO]2.0.CO;2).
- Carlquist, Sherwin. 1974. *Island Biology*. New York: Columbia University Press.
- Carpenter, Steve, Brian Walker, J. Marty Anderies, and Nick Abel. 2001. "From Metaphor to Measurement: Resilience of What to What?" *Ecosystems* 4 (8):765–81. <https://doi.org/10.1007/s10021-001-0045-9>.
- Clark, Colby J. 2024. "Geographical Boundaries and Historical Explanations of Within-Scale Resilience." *Ecological Complexity* 57:101062. <https://doi.org/10.1016/j.ecocom.2023.101062>.

- Colyvan, Mark, and Lev R. Ginzburg. 2003. "Laws of Nature and Laws of Ecology." *Oikos* 101 (3):649–53. <https://doi.org/10.1034/j.1600-0706.2003.12349.x>.
- Cumming, Graeme S. 2011. "Spatial Resilience: Integrating Landscape Ecology, Resilience, and Sustainability." *Landscape Ecology* 26:899–909. <https://doi.org/10.1007/s10980-011-9623-1>.
- Cumming, Graeme S., and Jon Norberg. 2008. "Scale and Complex Systems." In *Complexity Theory for a Sustainable Future*, edited by Jon Norberg and Graeme S. Cumming, 246–76. New York: Columbia University Press.
- Cummins, Robert. 1975. "Functional Analysis." *Journal of Philosophy* 72 (20):741–65. <https://doi.org/10.2307/2024640>.
- Dakos, Vasilis, Sonia Kéfi, Max Rietkerk, Egbert H. van Nes, and Marten Scheffer. 2011. "Slowing Down in Spatially Patterned Ecosystems at the Brink of Collapse." *The American Naturalist* 177 (6):E153–66. <https://doi.org/10.1086/659945>.
- Diamond, Jared M. 1975. "Assembly of Species Communities." In *Ecology and Evolution Communities*, edited by Martin L. Cody and Jared M. Diamond, 342–444. Cambridge, MA: Harvard University Press.
- Dussault, Antoine C. 2022. "Two Notions of Ecological Function." *Philosophy of Science* 89:171–79. <https://doi.org/10.1017/psa.2021.20>.
- Dussault, Antoine C., and Frédéric Bouchard. 2017. "A Persistence Enhancing Propensity Account of Ecological Function to Explain Ecosystem Evolution." *Synthese* 194:1115–45. <https://doi.org/10.1007/s11229-016-1065-5>.
- Elmqvist, Thomas, Carl Folke, Magnus Nyström, Garry Peterson, Jan Bengtsson, Brian Walker, and Jon Norberg. 2003. "Response Diversity, Ecosystem Change, and Resilience." *Frontiers in Ecology and the Environment* 1 (9):488–94. <https://doi.org/10.2307/3868116>.
- Folke, Carl, Steve Carpenter, Brian Walker, Marten Scheffer, Thomas Elmqvist, Lance Gunderson, and C. S. Holling. 2004. "Regime Shifts, Resilience, and Biodiversity in

- Ecosystem Management.” *Annual Review of Ecology, Evolution, and Systematics* 35:557–81. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105711>.
- Garson, Justin. 2017. “How to Be a Function Pluralist.” *The British Journal for the Philosophy of Science* 69:1101–22. <https://doi.org/10.1093/bjps/axx007>.
- Holling, C. S. 1973. “Resilience and Stability of Ecological Systems.” *Annual Review of Ecology and Systematics* 4 (1):1–23. <https://doi.org/10.1146/annurev.es.04.110173.000245>.
- Holling, C. S. 1996. “Engineering Resilience versus Ecological Resilience.” In *Engineering Within Ecological Constraints*, edited by Peter C. Schulze, 31–44. Washington, DC: National Academy Press.
- Holling, C. S. 2001. “Understanding the Complexity of Economic, Ecological, and Social Systems.” *Ecosystems* 4:390–405. <https://doi.org/10.1007/s10021-001-0101-5>.
- Holling, C. S., and Lance H. Gunderson. 2002. “Resilience and Adaptive Cycles.” In *Panarchy: Understanding Transformations in Human and Natural Systems*, edited by Lance H. Gunderson and C. S. Holling, 25–62. Washington, DC: Island Press.
- Holt, Robert D. 1993. “Ecology at the Mesoscale: The Influence of Regional Processes on Local Communities.” In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, edited by Robert E. Ricklefs and Dolph Schluter, 77–88. Chicago, IL: The University of Chicago Press.
- Holt, Robert D. 2004. “Implications of System Openness for Local Community Structure and Ecosystem Function.” In *Food Webs: At the Landscape Level*, edited by Gary A. Polis, Mary E. Power, and Gary R. Huxel, 96–114. Chicago, IL: The University of Chicago Press.
- Hubbell, Stephen P. 2005. “Neutral Theory in Community Ecology and the Hypothesis of Functional Equivalence.” *Functional Ecology* 19:166–72. <https://doi.org/10.1111/j.0269-8463.2005.00965.x>.
- Jax, Kurt. 2005. “Function and ‘Functioning’ in Ecology: What Does It Mean?” *Oikos* 111 (3):641–48. <https://doi.org/10.1111/j.1600-0706.2005.13851.x>.

- Jax, Kurt. 2006. "Ecological Units: Definitions and Application." *The Quarterly Review of Biology* 81 (3):237–58. <https://doi.org/10.1086/506237>.
- Jax, Kurt. 2010. *Ecosystem Functioning*. Cambridge: Cambridge University Press.
- Kolasa, Jerzy. 1989. "Ecological Systems in Hierarchical Perspective: Breaks in Community Structure and Other Consequences." *Ecology* 70 (1):36–47. <https://doi.org/10.2307/1938410>.
- Kolasa, Jurek, and Maciej Zalewski. 1995. "Notes on Ecotone Attributes and Functions." *Hydrobiologia* 303:1–7. <https://doi.org/10.1007/bf00034039>.
- Krohs, Ulrich, and Martin Zimmer. 2023. "Do Ecosystems Have Functions?" *Ecology and Evolution* 13:e10458. <https://doi.org/10.1002/ece3.10458>.
- Lawton, John H. 1999. "Are There General Laws in Ecology?" *Oikos* 84 (2):177–92. <https://doi.org/10.2307/3546712>.
- Lean, Christopher Hunter. 2018. "Indexically Structured Ecological Communities." *Philosophy of Science* 85 (3):501–22. <https://doi.org/10.1086/697746>.
- Lean, Christopher Hunter. 2021. "Invasive Species and Natural Function in Ecology." *Synthese* 198:9315–33. <https://doi.org/10.1007/s11229-020-02635-x>.
- Levin, Simon A. 1992. "The Problem of Pattern and Scale in Ecology." *Ecology* 73 (6):1943–67. <https://doi.org/10.2307/1941447>.
- Levin, Simon. 1999. *Fragile Dominion: Complexity and the Commons*. Reading: Perseus Books.
- Linquist, Stefan. 2015. "Against Lawton's Contingency Thesis; or Why the Reported Demise of Community Ecology Is Greatly Exaggerated." *Philosophy of Science* 82 (5):1104–15. <https://doi.org/10.1086/684024>.
- Lundberg, Jakob, and Fredrik Moberg. 2003. "Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management." *Ecosystems* 6:87–98. <https://doi.org/10.1007/s10021-002-0150-4>.

- MacArthur, Robert H. 1969. "Patterns of Communities in the Tropics." *Biological Journal of the Linnean Society* 1 (1–2):19–30. <https://doi.org/10.1111/j.1095-8312.1969.tb01809.x>.
- MacArthur, Robert H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. New York: Harper & Row.
- Maclaurin, James, and Kim Sterelny. 2008. *What Is Biodiversity?* Chicago, IL: The University of Chicago Press.
- Meentemeyer, Vernon, and Elgene O. Box. 1987. "Scale Effects in Landscape Studies." In *Landscape Heterogeneity and Disturbance*, edited by Monica G. Turner, 15–34. New York: Springer.
- Millikan, Ruth Garrett. 1989. "In Defense of Proper Function." *Philosophy of Science* 56 (2):288–302. <https://doi.org/10.1086/289488>.
- Millstein, Roberta L. 2020. "Functions and Functioning in Aldo Leopold's Land Ethic and in Ecology." *Philosophy of Science* 87 (5):1107–18. <https://doi.org/10.1086/710619>.
- Mikkelsen, Gregory M. 2003. "Ecological Kinds and Ecological Laws." *Philosophy of Science* 70 (5):1390–1400. <https://doi.org/10.1086/377416>.
- Mitchell, Sandra D. 2009. *Unsimple Truths: Science, Complexity, and Policy*. Chicago, IL: The University of Chicago Press.
- Morrow, Katie H. 2023. "A Causal-Role Account of Ecological Role Functions." *Philosophy of Science* 90:433–53. <https://doi.org/10.1017/psa.2022.95>.
- Mossio, Matteo, and Alvaro Moreno. 2010. "Organisational Closure in Biological Organisms." *History and Philosophy of the Life Sciences* 32 (2/3):269–88.
- Mossio, Matteo, Cristian Saborido, and Alvaro Moreno. 2009. "An Organizational Account of Biological Functions." *The British Journal for the Philosophy of Science* 60 (4):813–41. <https://doi.org/10.1093/bjps/axp036>.
- Neander, Karen. 1991. "Functions as Selected Effects: The Conceptual Analyst's Defense." *Philosophy of Science* 58 (2):168–84. <https://doi.org/10.1086/289610>.

- Nunes-Neto, Nei, Alvaro Moreno, and Charbel N. El-Hani. 2014. “Function in Ecology: An Organizational Approach.” *Biology & Philosophy* 29:123–41. <https://doi.org/10.1007/s10539-013-9398-7>.
- Nyström, Magnus, and Carl Folke. 2001. “Spatial Resilience of Coral Reefs.” *Ecosystems* 4 (5):406–17. <https://doi.org/10.1007/s10021-001-0019-y>.
- O’Neill, Robert V., Donald L. DeAngelis, J. B. Waide, and Timothy F. H. Allen. 1986. *A Hierarchical Concept of Ecosystems*. Princeton, NJ: Princeton University Press.
- Odenbaugh, Jay. 2007. “Seeing the Forest *and* the Trees: Realism about Communities and Ecosystems.” *Philosophy of Science* 74 (5):628–41. <https://doi.org/10.1086/525609>.
- Odenbaugh, Jay. 2010. “On the Very Idea of an Ecosystem.” In *New Waves in Metaphysics*, edited by Allan Hazzlett, 240–58. London: Palgrave Macmillan.
- Odenbaugh, Jay. 2019. “Functions in Ecosystem Ecology.” *Philosophical Topics* 47 (1):167–80. <https://doi.org/10.5840/philtopics20194719>.
- Paine, Robert T. 1966. “Food Web Complexity and Species Diversity.” *The American Naturalist* 100 (910):65–75. <https://doi.org/10.1086/282400>.
- Parker, V. Thomas, and Steward T. A. Pickett. 1998. “Historical Contingency and Multiple Scales of Dynamics Within Plant Communities.” In *Ecological Scale: Theory and Applications*, edited by David L. Peterson, and V. Thomas Parker, 171–91. New York: Columbia University Press.
- Pattee, Howard H. 1972. “The Nature of Hierarchical Controls in Living Matter.” In *Foundations of Mathematical Biology*, vol. 1, edited by Robert J. Rosen, 1–22. New York: Academic Press.
- Pickett, Steward T. A, and Peter S. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. San Diego: Academic Press.
- Potochnik, Angela. 2017. *Idealization and the Aims of Science*. Chicago, IL: The University of Chicago Press.

- Potochnik, Angela. 2021. "Our World Isn't Organized into Levels." In *Levels of Organization in the Biological Sciences*, edited by Daniel Stephen Brooks, James DiFrisco, and William C. Wimsatt, 61–76. Cambridge, MA: MIT Press.
- Pulliam, H. Ronald. 1988. "Sources, Sinks, and Population Regulation." *The American Naturalist* 132 (5):652–61. <https://doi.org/10.1086/284880>.
- Saborido, Cristian, Matteo Mossio, and Alvaro Moreno. 2011. "Biological Organization and Cross-Generation Functions." *The British Journal for the Philosophy of Science* 62 (3):583–606. <https://doi.org/10.1093/bjps/axq034>.
- Salthe, Stanley N. 1985. *Evolving Hierarchical Systems*. New York: Columbia University Press.
- Scheffer, Marten. 2009. *Critical Transitions in Nature and Society*. Princeton, NJ: Princeton University Press.
- Shrader-Frechette, K. Kristin S., and Earl D. McCoy. 1993. *Method in Ecology: Strategies for Conservation*. New York: Cambridge University Press.
- Simon, Herbert A. 1962. "The Architecture of Complexity." *Proceedings of the American Philosophical Society* 106 (6):467–82.
- Simon, Herbert A. 1973. "The Organization of a Complex System." In *Hierarchy Theory: The Challenge of Complex Systems*, edited by Howard H. Pattee, 1–27. New York: George Braziller.
- Sterelny, Kim. 2006. "Local Ecological Communities." *Philosophy of Science* 73 (2):215–31. <https://doi.org/10.1086/510819>.
- Sundstrom, Shana M., and Craig R. Allen. 2019. "The Adaptive Cycle: More Than a Metaphor." *Ecological Complexity* 39:100767. <https://doi.org/10.1016/j.ecocom.2019.100767>.
- Sundstrom, Shana M., Craig R. Allen, and David G. Angeler. 2022. "Panarchy, Cross-Scale Resilience, and Discontinuous Structures and Processes." In *Applied Panarchy: Applications and Diffusion across Disciplines*, edited by Lance H. Gunderson, Craig R. Allen, and Ahjond Garmestani, 29–50. Washington, DC: Island Press.
- Thompson, John N. 2005. *The Geographic Mosaic of Coevolution*. Chicago, IL: The University of Chicago Press.

- Ulanowicz, Robert E. 1986. *Growth and Development: Ecosystems Phenomenology*. New York: Springer.
- Ulanowicz, Robert E. 1990. "Aristotelean Causalities in Ecosystem Development." *Oikos* 57 (1):42–8. <https://doi.org/10.2307/3565734>.
- Ulanowicz, Robert E. 1995. "Network Growth and Development: Ascendancy." In *Complex Ecology: The Part–Whole Relation in Ecosystems*, edited by Bernard C. Patten and Sven E. Jørgensen, 643–55. Englewood Cliffs, NJ: Prentice Hall.
- Ulanowicz, Robert E. 1997. *Ecology, the Ascendent Perspective*. New York: Columbia University Press.
- Walker, Brian. 1995. "Conserving Biological Diversity through Ecosystem Resilience." *Conservation Biology* 9 (4):747–52. <https://doi.org/10.1046/j.1523-1739.1995.09040747.x>.
- Whittaker, Robert J. 1998. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford: Oxford University Press.
- Wiens, John A. 1989. "Spatial Scaling in Ecology." *Functional Ecology* 3 (4):385–97. <https://doi.org/10.2307/2389612>.
- Wiens, John A., Nils C. Stenseth, Beatrice Van Horne, and Rolf A. Ims. 1993. "Ecological Mechanisms and Landscape Ecology." *Oikos* 66 (3):369–80. <https://doi.org/10.2307/3544931>.
- Wilson, Edward O. 1961. "The Nature of the Taxon Cycle in the Melanesian Ant Fauna." *The American Naturalist* 95 (882):169–93. <https://doi.org/10.1086/282174>.
- Wimsatt, William C. 1972. "Complexity and Organization." *Philosophy of Science* 1972:67–86. <https://doi.org/10.1086/psaprocbienmeetp.1972.3698961>.
- Woodward, James. 2010. "Causation in Biology: Stability, Specificity, and the Choice of Levels of Explanation." *Biology & Philosophy* 25:287–318. <https://doi.org/10.1007/s10539-010-9200-z>.
- Wright, Larry. 1973. "Functions." *The Philosophical Review* 82 (2):139–68. <https://doi.org/10.2307/2183766>.