

Functional Biodiversity, Context-based Ecological Roles and the Function/Accident Distinction¹

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1. Introduction

In the last three decades, *functional biodiversity* has become a central focus in ecology and environmental conservation. This is especially the case in *biodiversity and ecosystem function* (BEF) research, an ecological subfield which studies the relationship between biodiversity and the functioning of ecosystems (Naeem 2002a; Loreau 2010; Tilman, Isbell, and Cowles 2014). The explanatory and predictive limitations of more traditional species richness measures of biodiversity has led an increasing number of researchers in this field to consider, alongside the number of species present in a community, the particular ecological *roles* or *functions* fulfilled by those species (Tilman and Lehman 2002, 11–14; DeLaplante and Picasso 2011, 173; Nunes-Neto, Do Carmo, and El-Hani 2016, 296–97). This has fostered among those researchers an interest in the ways in which organisms can be grouped on the basis of their *functional traits*, which are deemed to be of more direct ecological importance than those on which the more standard taxonomic classifications are based (e.g. Naeem 2002b; Lavorel and Garnier 2002; Hooper et al. 2002; Petchey and Gaston 2006). At the societal level, this interest in functional biodiversity is reinforced by a growing concern over how the Earth's

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ecosystems will respond to the current dramatic losses in biodiversity resulting from human-induced environmental changes, and over the potential impacts of those responses on human well-being (Naeem 2002a, 1540; Loreau 2010, 51; Laureto, Cianciaruso, and Samia 2015, 113).

As remarked by Jax (2010, 74) and DeLaplante and Picasso (2011, 179), however, a major philosophical issue raised by the notion of functional diversity is that of the *teleology* insinuated by the notion of *ecological role* underlying it.² To state the ecological function or role of an organism seems, in some sense, to state “what it is for” ecologically-speaking. Furthermore, statements about the ecological roles or functions of organisms seem undergirded by a form of *functional holism* about ecological communities and ecosystems. As DeLaplante and Picasso (2011, 181–85) observe, however, those notions of ecological-level teleology and functional holism seem to conflict with some central tenets of contemporary biological theorizing. More specifically, two central tenets of contemporary biological theorizing jointly seem to foreclose the use of functional concepts at community and ecosystem levels. The first tenet, which I will call *selectionism about function*, states that the teleological dimension of the notion of function is to be elucidated in terms of past natural selection. It states, in accordance with the *selected effect* theory of function advocated by many philosophers of biology (e.g. L. Wright 1973; Millikan 1989; Neander 1991; Godfrey-Smith 1994), that the function of a part or trait of a biological entity is the effect for which that part or trait was preserved under past episodes of natural selection operating on ancestors of that entity as a whole.³ The second tenet, which I will call *individualism about selection*, states that natural selection primarily operates at the level of individual organisms. It states, in accordance with the standard neo-Darwinian wisdom which prevails among biologists and ecologists since Maynard-Smith’s (1964) and Williams’s (1966) persuasive critiques of group selection, that natural selection may occur at supraorganismic levels of organization such as those of ecological communities and

² See also Calow (1987).

³ For critical overviews of philosophical theories of function, see McLaughlin (2001), Wouters (2005a), and Garson (2016).

ecosystems only under very stringent and therefore rarely realized conditions.⁴ Those two tenets jointly entail that genuine functional organization at community and ecosystem levels is an uncommon phenomenon, and so question the theoretical cogency of BEF research's generalized use of functional concepts at community and ecosystem levels. As we shall see, those two tenets jointly relegate the ascription of *roles* to organisms within communities and ecosystems at best to the status of a *heuristics*, which have little bearings on the real makeup of the ecological world. At the practical level, this, I will highlight, threatens to undermine ecosystem-focused approaches to environmental conservation by casting doubt on the very existence of ecosystems.

This implication raises foundational issues for BEF research. Can communities and ecosystems be conceived as functional wholes in any substantive sense, or is the use of functional language in BEF research merely heuristic? When ecological roles are ascribed to organisms with respect to “ecosystem functioning” or when organisms are classified into functional groups on the basis of those roles, does the identification of those roles and the delineation of those functional groups “carve the world at its joints” or does it simply pick up some features that ecologists and conservationists happen to find interesting?

This chapter aims to contribute to the tackling of those issues by assessing two philosophical defenses of the notion of ecological role. Those strategies consist in denying either one or the other of the two tenets of biological theorizing identified above, that is denying either *selectionism about functions* or *individualism about selection*. More specifically, my goal will be to reinforce the first argumentative strategy, by explaining how it can vindicate more than a heuristic use of the notion of ecological role despite its non-selectionist character. I will argue that functional organization can be recognized as a real feature of ecological units if one draws the appropriate connection between

⁴ As historians of ecology recall (Kimler 1986; Hagen 1992, chap. 8), although many early ecologists advocated the view that natural selection customarily operates at the levels of ecological communities and ecosystems as a whole (e.g. Allee et al. 1949, chap. 35; Dice 1952, chap. 22; Dunbar 1960), the critique of group selection has led most later ecologists to distance themselves from this view (see e.g. Whittaker 1975, chap. 8; Pickett, Kolasa, and Jones 2007, 160–61).

ecosystem-level functional organization and a phenomenon which is fundamental to the makeup of the ecological world: the association of organisms with one another into more or less resilient webs of *use* and *service* relations which generate cycles of nutrients and flows of energy between them. Thus, I will maintain that, in the context of ecology, functional roles are essentially constituted by regular *beneficiary relations* between organisms, which collectively undergird cycles of nutrients and flows of energy.

My discussion will be organized as follows. In section 2, I will argue—in line with the argumentative strategy that denies *selectionism about function*—that the notion of ecological role should be elucidated in a non-selectionist manner. My arguments will however diverge from those of previous proponents of this strategy in that they will be based on observations about ecologists' actual use of the notion of ecological role, rather than on claims about the uncommonness of community- and ecosystem-level selection. In section 3, I will identify a challenge seemingly faced by a non-selectionist account of ecological roles. This challenge derives from the well-known conventionalist stance on the difference between *functions* and mere *accidental effects* adopted by defenders of the most common alternative to the selected effect theory, namely the *causal role* theory of function (R. C. Cummins 1975, 2002; Davies 2001; Craver 2001, 2013). This conventionalist stance entails that a non-selectionist account of the notion of ecological role can at best ground a *heuristic* use of this notion, and therefore, I will highlight, implicitly concedes that only selection-based functions are *real* functions. In section 4, I will respond to this challenge in three steps. First, I will criticize an undefended assumption underlying selected effect theorists' take on the function/mere effect distinction. Second, I will draw upon a contrast attributed to Aristotle between two notions of teleology, in order to propose an alternative take on the function/mere effect distinction centered on the notion of cross-species benefit. Third, I will make two observations in favor of viewing those cross-species beneficial interactions as giving rise to genuine part-whole functional relations between organisms and the ecosystems they are part of.

2. Functional ecology's context-based notion of ecological role

Before delving deeper into the issues raised by the notion of ecological role, it must be remarked that not all the types of functional classifications used by ecologists involve the notion of *ecological role* (see Jax 2010, 54–55). Contemporary functional ecologists commonly distinguish two types of functional classifications: *functional response groups* (or types) and *functional effect groups* (or types) (Catovsky 1998; Lavorel and Garnier 2002; Hooper et al. 2002; Symstad 2002; Suding et al. 2008). *Functional response groups* classify organisms on the basis of their *functional response traits*, that is, traits that predict similar response to particular environmental factors, such as resource availability, disturbances, CO₂. In such groupings, the traits of organisms are generally used as *explanans* for the assembly of local ecological communities from a regional species pool and their response to disturbances and environmental variability (Grime 1974; Keddy 1992; Díaz, Cabido, and Casanoves 1999; Lavorel and Garnier 2002). The focus is on how organisms exhibiting particular traits are capable of surviving in a particular location given the prevailing biotic and abiotic environmental conditions. Thus, the notion of function associated with functional response traits is *organism-centered*. It ascribes functions to the traits of organisms to the extent that those traits explain (and/or allow to predict) the survival and reproduction of those organisms themselves (or in Darwinian terms, their *fitness*) (Violle et al. 2007, 887). In this respect, the notion of function associated with functional response groups has little to do with how organisms contribute to the functioning of their ecosystem, and so it is not concerned with eventual ecological roles they would fulfill within ecosystems.⁵ This notion thus seems to comply with the two tenets of contemporary biological theorizing mentioned above. It is both selectionist (i.e. defined in relation to an entity's fitness) and individualistic (i.e. applied at the level of individual organisms). Therefore, it eschews the philosophical issues associated with functional holism about ecosystems highlighted above.

⁵ However, it should be noted that functional response groups may indirectly involve the ascription of ecological roles to organisms when they are used in concert with functional effect groups to study the stability and resilience of ecosystems to environmental fluctuations (Naeem 1998; Walker 1995; Suding et al. 2008; see Jax 2010, 55).

The notion of function associated with *functional effect groups*, in contrast, *does* involve the ascription of roles to organisms within communities and ecosystems. Functional effect groups classify organisms on the basis of their *functional effect traits*, that is, traits that predict similar influence on ecosystem processes, such as biomass productivity, energy flow and nutrient cycling (K. W. Cummins 1974; Naeem 2002b; Petchey and Gaston 2006). In such groupings, the traits of organisms serve as *explanans* for those processes, in that ecologists are interested in how those traits determine the particular contributions of organisms to those processes, and how eventual changes in the species composition of an ecosystem will impact its functioning. This is why the notion of function associated with functional effect traits is the most directly relevant to *biodiversity and ecosystem function* (BEF) research. It is important to note that despite the emphasis on *effects* in the phrases “functional effect groups” and “functional effect traits,” the effects at issue are not *any* effect that organisms may have on their surroundings. The effects at issue are those that influence ecosystem-level process. Thus, the notion of function associated with functional effect traits is *ecosystem-centered* and *does* ascribe *roles* to organisms with respect to higher-level ecological entities (Catovsky 1998, 126; Symstad 2002, 23–24; Jax 2010, 54).

As I already mentioned, such ecological role ascriptions insinuate a form of ecological-level teleology and a form of functional holism about ecological communities and ecosystems, which conflict with two central tenets of contemporary biological theorizing. As DeLaplante and Picasso (2011, 181–84) observe, although many biologists and philosophers of biology acknowledge teleological concepts as legitimate in the life-sciences (counter to a wide-spread view according to which teleology is wholly incompatible with scientific thinking), their privileged *selectionist* way to elucidate those notions, jointly with the neo-Darwinian wisdom which states that natural selection more primarily operates at the level of individual organisms, seems to foreclose their use at community and ecosystem levels. For this reason, the notion of ecological role associated with functional effect traits will be my focus henceforth.

The way in which the two tenets of biological theorizing I identified jointly foreclose the idea that organisms fulfill roles within higher-level ecological entities and the

associated functional holism about communities and ecosystems can be summarized in the form of the following syllogism:

- (1) In biology, functional roles are selected effects and therefore functional holism at one level requires natural selection operating at that level (*selectionism about function*).
- (2) Natural selection does not customarily operate at the level of communities and ecosystems (*individualism about selection*).
- (3) Therefore, ecological function ascriptions and functional holism at community and ecosystem levels are unfounded.

This indicates two argumentative strategies available for rejecting (3): denying premise (1) or denying premise (2).

Proponents of the strategy that denies premise (1) (i.e. *selectionism about function*) have typically defended this strategy by invoking the standard challenges to community and ecosystem selection (Maclaurin and Sterelny 2008, 114; Odenbaugh 2010, 251; Gayon 2013, 77; Nunes-Neto, Moreno, and El-Hani 2014, 124). Community and ecosystem selection, they argue, would implausibly require a form of large-scale evolutionary altruism, and would unrealistically require that communities and ecosystems reproduce and form lineages (see Maynard-Smith 1964; Williams 1966).⁶ This line of argument, it should be noted, overlooks the defense of community- and ecosystem-level selection elaborated by David Sloan Wilson and Eliot Sober, which elaborates insightful ways to meet those challenges (see Wilson and Sober 1989; Wilson 1992, 1997).⁷

⁶ For an overview of the group selection controversy, see Shanahan (2004, chap. 2).

⁷ It also overlooks Bouchard's (2013, 2014) defense of ecosystem selection, which argues that those challenges need not be met and that natural selection can be conceived in terms of *persistence* rather than survival and reproduction. Bouchard's approach, however, neither grounds nor intends to ground the application of the *selected effect* theory of function to ecosystems (see Bouchard 2013, 93). For a recent elaboration upon Bouchard's approach and the understanding of ecological function associated to it, see Dussault and Bouchard (2017), and on the relationship between that approach and the one adopted in this chapter, see Dussault (under review).

Although Wilson and Sober do not explicitly refer to the selected effect theory of function, they contend that their defense of community and ecosystem selection also provides a legitimation for the idea that some communities and ecosystems are functionally organized.⁸ This, in their view, even provides a legitimation for the idea that those naturally selected supraorganismic entities constitute genuine *superorganisms*. This link between levels of functional organization and levels of natural selection entails an implicit endorsement of the selected effect theory of function—though it should be noted that, as Wilson and Sober (1989, 343, 352) themselves emphasize, their approach ascribes functional organization only to some very special cases of communities and ecosystems and not to communities and ecosystems in general.⁹ Thus, Wilson and Sober’s defense of community and ecosystem selection lends (restricted) support to a defense on the notion of ecological role which proceeds by denying *individualism about selection* (premise (2) above).

Nevertheless, as I argue in more details elsewhere (see Dussault under review), Wilson and Sober’s selection-based approach to functional holism at community and ecosystem levels does *not* offer the most promising legitimization for the notion of ecological role. This is because their selectionist take on the issue of community- and ecosystem-level functional organization, and their association of this issue with that of ecological-level superorganisms, diverge significantly from how ecologists approach it. Ecologists typically conceive ecological roles as *context-based* properties of organisms, which depend upon their ecological relations with other organisms, rather than as *historical-evolutionary* properties defined in relation to past natural selection (see Brennan 1988, chap. 8; Jax 2010, 78–80). Moreover, their context-based understanding derives, historically and conceptually, from the renowned community ecologist Charles Elton’s (1927, 1933) analogy between food interactions within ecological communities and economic exchanges in human societies, and his related understanding of the notion of *ecological niche*. In Elton’s coinage, the term “niche” referred to “what [an animal] is

⁸ Contrary to Jax’s (2010, 75) remark, Wilson and Sober’s approach seems able to yield cases of *ecosystem*-level as well as *community*-level selection (see Wilson 1997, 2021–22).

⁹ For more details, see Dussault (under review).

doing in its community”, and emphasized an animal’s “*relations to food and enemies*” in contrast to “appearance, names, affinities, and past history.” (Elton 1927, 63–64, emphasis original). It was “used in ecology in the sense that we speak of trades or *professions* or *jobs* in a human community.” (Elton 1933, 28, emphasis added) Thus, for Elton, the niche concept was meant to identify similarities between organisms pertaining to their ecological roles rather than of their phylogenetic affiliation (e.g. the arctic fox and the spotted hyæna in tropical Africa fulfill the same niche).¹⁰

Elton’s context-based and ahistorical understanding of ecological roles was thus tied to a *communitarian* picture of communities rather than a *superorganismic* one (as in Wilson and Sober’s approach). As Jax (2010, 78–82) explains, such a communitarian picture entails a looser form of part-whole integration than the one found in paradigmatic individual organisms. It is therefore more inclusive as to what can genuinely count as an ecological role. Under Wilson and Sober’s selected effect understanding of function, can count as ecological roles only effects that organisms have on other organisms as a result of past natural selection operating on their community or ecosystem as a whole. In other words, Wilson and Sober’s approach entails that genuine ecological roles must be community- or ecosystem-level *evolutionary adaptations* (on the equivalence between selected effect functions and evolutionary adaptations, see Brandon 2013). In contrast, many of the ecological roles identified by functional ecologists are *by-products* of activities that organisms achieve for their own evolutionary benefits (see Schulze and Mooney 1993, 500; Odenbaugh 2010, 251). For instance, an ecologist’s depiction of a rabbit as fulfilling the role of a prey with respect to a fox does not entail that rabbits were selected for serving as food for foxes. Rabbits just grow muscles to be able to run when they are chased by predators and, as a (somewhat paradoxical) by-product, acquire traits that make them nutritious and palatable for their predators. Likewise, an ecologist’s depiction of foxes as fulfilling the role of a regulator of rabbit population does not either

¹⁰ Elton’s understanding of the niche contrasted with the one adopted by Joseph Grinnell (1917), the other originator of the niche concept, who used the niche concept to denote a species’ particular *environmental requirements* (see Leibold 1995, 1372–73). For discussions of the contrast between Grinnell’s and Elton’s niche concepts, see also Schoener (1989), Griesemer (1992), and Pocheville (2015).

entail that foxes were selected for regulating rabbit populations. Foxes chase and eat rabbits to feed themselves and, as a by-product, exert a form of control over rabbit populations.

Contemporary functional ecology expands upon Elton's initial focus on food interactions in two ways. First, it expands upon this focus by integrating ecosystem ecology's thermodynamic and biogeochemical outlook on the ecological world (see Hagen 1992, chaps. 4–5). Thus, BEF research investigates how the interactions between organisms within food-webs undergird ecosystem-level cycles of nutrients and flows of energy (see K. W. Cummins 1974; Naeem 2002b). Second, contemporary functional ecology expands upon Elton's focus on food or trophic interactions by also considering ecological roles derived from *non-trophic* interactions, such as what ecologists call *ecosystem engineers* (Jones, Lawton, and Shachak 1994, 1997; Cuddington et al. 2007).¹¹ *Ecosystem engineers* are organisms which create, modify and maintain habitats in ways that affect the life of other organisms (e.g. beavers build dams and in so doing create habitats and make many resources available for numerous other organisms).¹² The ecological roles of ecosystem engineers contrast with those fulfilled by organisms through the direct provision of food to other organisms (in the form of living or dead tissues) (see Berke 2010). Other well-studied non-trophic ecological roles include those fulfilled by *pollinators* and *seed dispersers* (see Blondel 2003, 227–28).

Those two significant expansions notwithstanding, the Eltonian *context-based* understanding of ecological roles remains. For instance, an ecologist's saying that, by building a dam, a beaver fulfills the role of a pond provider with respect to the numerous

¹¹ Though, as Schoener (1989, 86) notes, Elton did not limit his discussion of niches to food interactions (see especially Elton 1927, 67, where he speaks of earth-worms and land-crabs as fulfilling the same soil-burrowing niche).

¹² The concept of ecosystem engineering is closely similar to that of *niche construction* developed in the context of evolutionary biology (Odling-Smee, Laland, and Feldman 2003), in that both concepts concern the changes made by organisms to their environment. The main difference is that studies of niche construction focus on the evolutionary effects of those changes for the organisms that generate them, whereas studies of ecosystem engineering focus on the ecological effects of those changes on other organisms and ecosystems as a whole (see Barker and Odling-Smee 2014, 195–96).

organisms for which the pond is a favorable habitat, and that such pond providing affects the flows of nutrients and energy in their ecosystems (see e.g. Jones, Lawton, and Shachak 1994, 373–74), does not entail that beavers were selected for serving as pond providers with respect to all those species or for their contributions to the cycling of nutrients and the flow or energy within their ecosystems. Beavers build dam and create ponds for their own evolutionary benefit and, as a by-product, provide a habitat for numerous organisms and contribute to nutrient cycling and energy flow within their ecosystem.

The way in which the context-based understanding of ecological roles diverges from the historical understanding adopted by the selected effect theory can be further illuminated by drawing its connection with Achinstein's (1977, 350–56) delineation of three distinct meanings of "function" in ordinary language: *design*, *use* and *service* functions. An entity's *design* function consists in what this entity was *designed* or *created* to do (e.g. the function of a mouse trap is to catch mice); whereas an entity's *use* function consists in what it is *used for* (e.g. this table is used for sitting), and an entity's *service* function consists in what it is *serves as* (e.g. a watch's second hand serves as a dust sweeper). This distinction between design functions on the one hand, and use and service functions on the other, is sometimes also expressed in terms of a contrast between the notion of *being the function of* (e.g. breathing is the function of the nose) and that of *functioning as* (e.g. the nose functions as an eyeglass support) (e.g. Boorse 1976, 76; Bedau 1992, 787–89). In light of Achinstein's triad, the selected effect theory of functions can be viewed as concerned with *design* functions, as is reflected in selected effect theorists' typical association of function with *design* (see e.g. L. Wright 1973, 164–65; Millikan 1984, 17). In contrast, functional ecology's context-based functions can be conceived as denoting *use* and *service* functions. For instance, a rabbit is *used as* food by a fox, thus fulfilling the role of a secondary consumer in an ecosystem, or a fox *serves as* a regulator of a rabbit population, thus fulfilling a regulative role within its community. Just like a table's functioning as a seat or the second hand of a watch's functioning as a dust sweeper do not entail any claims that tables and second hands were intentionally designed for those roles, a rabbit's functioning as a prey relative to a fox and a beaver's

functioning as a pond provider relative to numerous organisms do not entail that rabbits and beavers were evolutionarily designed for fulfilling those roles.

Thus, ecology's contextual understanding of ecological roles derives from different ordinary language uses of "function" than does the selected effect theory. This use thus seems to call for an alternative elucidation, and therefore the strategy that defends the notion of ecological role by denying *individualism about selection* (premise (2) above) seems wrongheaded. In search for an alternative elucidation of the notion of ecological role, most philosophers who have adopted the alternative strategy which denies *selectionism about function* (premise (1) above) have turned to the main alternative to the selected effect theory, namely the *causal role* theory of function (Maclaurin and Sterelny 2008, 114–15; Odenbaugh 2010, 251–52; Gayon 2013, 76–77).¹³ According to the causal role theory (e.g. R. C. Cummins 1975, 2002; Davies 2001; Craver 2001, 2013), the ascription of functions to the parts of a biological entity is entirely independent of the selective history of that entity. Function ascriptions serve to characterize how the activities and capacities of those parts contribute to the activities or capacities of that entity as a whole. This ahistorical use accords with functional ecology's understanding of the ecological roles of organisms as their contributions to ecosystem-level cycles of nutrients and flows of energy (which, along the lines of the causal role theory, can be understood as the *activities* of ecosystems) (see Cooper, El-Hani, and Nunes-Neto 2016, sec. 4; Dussault under review, sec. 4). Moreover, the causal role theory accords with functional ecology's context-based understanding of ecological roles, in that it does not discriminate between the notion of *being the function of* and that of *functioning as* (see R. C. Cummins 1975, 762; Craver 2001, 55), and so acknowledges context-based functional roles as genuine ones. This suggests that the strategy which denies *selectionism about function* (and the associated causal role elucidation of the notion of ecological role) is more promising than the alternative selectionist strategy. The former strategy, however, as the next section will show, faces a challenge.

¹³ An exception, which I will briefly discuss in section 4, is Nunes-Neto et al.'s (2014) organizational account of ecological functions.

3. Are contextual functions *real* functions?

A serious challenge faced by the context-based and ahistorical understanding of ecological roles concerns the very *existence* of functional relations and of ecological-level functional wholes. The challenge arises from the conflict between the seeming *accidentality* of context-based ecological roles, and the requirement, widely acknowledged among philosophers of biology, that theories of function be able to ground a distinction between *functions* and *mere effects* or *accidents* (see e.g. Hempel 1959, 279; L. Wright 1973, 141–42). For instance, pumping blood is the function of hearts, whereas their thumping noise effect is merely accidental. This non-accidentality requirement prompts the worry that the purported context-based ecological roles undergirded by use and service relations between organisms are *too accidental* to constitute genuine functions of those organisms. For instance, such a worry seems to underlay Ruse’s (1973, 183) suspicion with regards to function ascriptions such as “The function of long hair on dogs is to harbour flees”, which are based on the mere use of some organisms by other organisms. In any case, failing to explain the difference between functions and mere effects would trivialize function ascriptions by allowing that effects which are clearly not functional (e.g. the gravitational effect of Pluto’s satellite Charon) be ascribed functions.

The selected effect theory of function yields a principled way of distinguishing functions and mere effects. Functions are effects of parts or traits of biological entities which result from evolutionary design (i.e. which were favored under past selective pressures), and mere accidental effects are *any* other effect that those parts or traits may have (see L. Wright 1973, 165–66; Millikan 1993, 38; Godfrey-Smith 1993, 198; Neander 2017, 1151–52). Effects which result from evolutionary design are non-accidental in that they in part causally explain the *presence*—i.e. the *existence*—of the biological items which produce them, whereas accidental effects provide no such explanation.¹⁴ In contrast, the causal role theory, which, as I remarked, has been the

¹⁴ In Wright’s original etiological theory of function, which is the theoretical ancestor of the selected effect theory, the notion of explaining the *presence* of some biological items was not strictly equated to that of explaining the *existence* of that item. It could also mean explaining why a biological item is where it is or why an organism has it (see L. Wright 1973, 158). This aspect of Wright’s etiological theory has made it

preferred theory of function among philosophers who defend the notion of ecological role by denying *selectionism about function*, provides no such principled way of singling out functions from mere effects. Causal role theorists typically adopt a *conventionalist* or *perspectivalist* stance on the function/accident distinction, according to which this distinction can only be made relative to some explanatory interests or perspective adopted by particular researchers (see R. C. Cummins 1975, 762; Craver 2001, 71, 2013, 140–41, 143). As I mentioned, on the causal role theory, function ascriptions serve to characterize how the capacities or activities of the parts of an entity contribute to some activities or capacities of that entity as a whole. Causal role theorists' perspectivalism thus makes it legitimate to formulate functional explanations with respect to any systemic activity or capacity that researchers are interested in, provided that the relation between those activities or capacities and the individual contributions of the system's parts is complex enough.¹⁵ Therefore, on the causal role theory, some effect of an item's fulfilling a function (in contrast to being a mere effect) is ultimately a matter of perspective or explanatory interests. The explanatory perspective adopted by researchers on the entity that contains this item emphasizes some activities or capacities of this entity over others, and correspondingly singles out some capacities or activities of the parts as functional and some others as mere effects. In this respect, on the causal role theory, some part of a system's being *for* something is ultimately a matter of convention. Hence, a causal role elucidation of ecological roles would entail that those roles and the ecological-level functional wholes in which they occur are not *real* features of the world, but at best heuristically fruitful theoretical constructions. On such an elucidation, BEF researchers just happen to be interested in how organisms in ecological contexts contribute to ecosystem-level cycles of nutrients and flows of energy, and accordingly single out those

vulnerable to serious objections (see e.g. Boorse 1976, 72; Bedau 1992, 786), which have led subsequent selected effect theorists to explicitly couch the theory in selectionist terms (and accordingly restrict its application to entities which are part of reproductive lineages) (see Godfrey-Smith 1994, 345–46; Odenbaugh 2010, 249–50; Garson 2016, 40–41). On this reformulation, functions explain why a type of biological item was reproduced and therefore explain the *existence* of token function bearers.

¹⁵ For more details on how causal role theorists substantiate this complexity requirement, see Cummins (1975, 764), Davies (2001, chap. 4), and Craver (2001, sec. 3.2).

contributions as functional roles and the other effects of organisms as mere (non-functional) effects.¹⁶

To be sure, one could argue that this conventionalism must simply be embraced. Such a conventionalist stance is advocated by Jax (2010), on the basis of the observation (rehearsed above) that ecosystems are not typically units of selection and therefore exhibit a looser form of part-whole integration than organisms. According to Jax (2010, 82):

[t]eleological statements about ecosystems and their functioning thus must not refer to an internal teleology, as is legitimate when describing organisms. If we speak in a teleological manner about ecosystems we have to be clear that their purposiveness is only an external one, set by individual observers or by societal choices. [...] We can also ask what purposes (functions) specific species have for the continued performance of a system. This purpose, however, is one depending on us selecting the system and its reference state and not a purpose which nature, or the ecosystem, brings about.

I think that this conventionalist stance, however, raises three (interrelated) worries. First, it seems to significantly restrict the scope of the project of elaborating a non-selectionist defense of the notion of ecological role. Indeed, the conventionalist stance implicitly concedes to selectionists about functions that, in final analysis, only selected effect functions are *real* functions and only the communities and ecosystems that are units of selection are *really* functionally organized. This retains a difference of status between function ascriptions based on selective history—which denote *real* functions; and function ascriptions based on use and service relations between organisms—which are merely heuristic. Second, against the binary opposition between selectionist and perspectivalist functions assumed in Jax’s reasoning, there seems to be a genuine similarity between the ways in which organisms and ecosystems constitute functionally organized entities (though, as seen in section 2, ecosystems and organisms are not identical). More specifically, there is an obvious similarity between the way in which, through their interactions, the organisms which compose an ecosystem collectively

¹⁶ This implication is reinforced by the fact that Achinstein (1977, sec. 7) associates his delineation of design, use and service functions with a pragmatic view of explanation (I am indebted to Philippe Huneman for noticing this).

undergird the cycles of nutrients and the flows of energy which occur at the level of the ecosystem as a whole, and the way in which the parts of an organism, through their interactions, collectively undergird the metabolic processes which occur at the level of organism as a whole. Although ecosystems are characterized by a looser form of part-whole integration than organisms and, in this respect, are more similar to human economic associations than to organisms, they are nevertheless composed of differentiated parts which collaborate in such a way that they collectively uphold some higher-level processes (e.g. nutrient cycling, energy flow). In this respect, a binary contrast between, on the one hand, organisms recognized as real entities in virtue of being units of selective design, and on the other hand, ecosystems denied a similar ontological status because of not meeting this criterion would seem misguided. Non-selectionism about functions need not entail conventionalism. Consequently, locating organisms and ecosystems on a continuum of functional integration, with no preconception as to whether organisms and ecosystems are more or less real or conventional than each other, would seem to better reflect both their differences and resemblances. Lastly, and more pragmatically, downplaying ecosystems as mere conventional entities may reinforce some rampant (and arguably misguided) skepticism about more holistic ecosystem-focused approaches to environmental conservation (see e.g. Fitzsimmons 1999; Sagoff 2000, 2003, 2013; and for rejoinders, see Odenbaugh 2010; DeLaplante and Odenbaugh Unpublished manuscript). If ecosystems and their functioning do not really exist, why care preserving them? The choice between realism and conventionalism about ecosystems does not only concern theoretical commitments; it may also have decisive practical implications regarding the goals set for environmental conservation. It therefore seems critical that, before embracing conventionalist views of ecosystems and their functioning, we should at least make sure that no alternatives besides selection-based realism and perspectivalist conventionalism are available.

Thus, I contend that a satisfactory non-selectionist defense of the notion of ecological role should provide a more realist-leaning elucidation of the function/mere effect distinction. This elucidation should explain the sense in which ecosystems constitute real functional wholes, in contrast to mere constructs that can fruitfully be

regarded *as if* functionally organized relative to some epistemic perspective. Section 4 will propose a way to meet this challenge.

4. Ecological functions as beneficial effects

4.1 The function/accident distinction and the meaning of “accident”

A first step towards responding to the challenge identified in section 3 consists in uncovering an undefended assumption underlying selected effect theorists’ take on the function/accident distinction. This can be achieved by looking more closely at the meaning of “accidental” which implicitly underlies this take. It is evident that by “accidental”, those theorists cannot simply mean “contingent” in a broad sense. Insofar as evolution by natural selection is a historical process, all evolutionary results are *historical* results which might have been different if evolution had unfolded in a different way (Gould 1990; Beatty 1995). Those results—including, for instance, the fact that there exists hearts whose selected effect function is to pump blood—are thus, in this respect, contingent. As Wright himself (1973, 165) explicitly states, the fact that the traits of organisms in part result from “[o]rganismic mutations” which are in some alternative sense “paradigmatically accidental” does not disqualify them from functionhood. Neither can “accidental” simply mean “not regular” or “exceptional” for selected effect theorists, because many effects which they would consider non-functional because accidental, such as the thumping noise of hearts, occur regularly.

The sense of “accident” under which Wright and later selected effect theorists are contrasting functions and accidental effects, I submit, has more to do with the distinction between *accidental* and *essential* or *necessary* properties. Selected effect theorists intuitively think that there has to be a necessary connection between the existence of a function bearer and its bearing its function. Their view that functions contrast with mere effects in that functions causally explaining the existence of their bearers implicitly entails that function bearers cannot exist without bearing their function. This amounts to saying that function bearers bear their functions *necessarily*, and consequently, on some understandings of essential properties, that functions are *essential properties* of their

bearers.¹⁷ For instance, given the evolutionary context which has led to the appearance of hearts, token hearts come into existence because hearts in general pump blood; and for this reason, token hearts come into existence with the appointed function of pumping blood. No heart could possibly come into existence devoid of this appointed function. This, I submit, is the sense in which selected effect functions are *non-accidental*. They are properties that their bearers cannot fail to have, that is, *necessary* or *essential* properties of their bearers. This, indeed, is not to say that bearers of selected effect functions necessarily *fulfill* their appointed function. A well-known feature of the selected effect theory of function—which is what makes function ascriptions normative on this theory—is that it makes it possible for an item to bear a function while failing to fulfill it. Token function bearers necessarily bear their function as an *appointed* function, that is, a function that they are *supposed* to fulfill, but that they may in fact fail to fulfill.

If this reading is correct, then the selected effect theorist's take on the function/accident distinction rests on an assumption that functions must be *essential* or *necessary* properties of their bearers, properties that do not depend on present context. But why should this be the case? Certainly not in virtue of conceptual analysis of the ordinary notion of *function*, for Achinstein's discussion of use and service functions makes clear that context-based function ascriptions are part of ordinary language. Can it be so in virtue of theoretical definition or conceptual analysis of scientific language, in line with Millikan (1989) and Neander's (1991) respective defenses of the selected effect theory? Perhaps, but in this case, only relative to the particular biological subfield on which Millikan and Neander's discussions are centered—i.e. evolutionary biology—with no implications for other biological subfields such as, in the case that concerns us here, ecology (for related critiques of the selected effect theory in relation to other biological subfields, see Amundson and Lauder 1994; Griffiths 2006).¹⁸ Thus, unless we are willing to grant evolutionary biology a privileged bearing on biological ontology, the fact that functions are conceived as necessary properties of their bearers from the theoretical

¹⁷ For a discussion of necessary vs. accidental properties, see Robertson and Atkins (2016).

¹⁸ In this regard, it is relevant to note that Millikan (1989, 293–94) herself acknowledges the need for a parallel concept of function more focused on the notion of *functioning as*.

perspective of evolutionary biology should not be taken to entail that ecology's context-based functions are less real features of the biological world than evolutionary biology's history-based functions.

A less disputable sense in which functions in general should be distinguished from accidents is the one (already mentioned) which contrasts “accidental” with “regular” (see Boorse 1976, 80–81, 2002, 70–72). It would seem implausible to ascribe a function to an effect which occurs only once or too irregularly to have significant repercussions on the general functioning of a system. However, not all regular effects can be envisaged as functions, and therefore something more has to be said about what distinguishes context-based functions from mere effects. In section 4.2, I will propose that organisms acquire ecological functions within communities and ecosystems through affording regular benefits to other organisms.

4.2 Teleology weak and strong

Further illumination of the sense in which the context-based ecological roles of ecological items are to be distinguished from mere effects can be found in a distinction attributed to Aristotle between two notions of teleology.¹⁹ This distinction derives from two ways in which a thing A can be said to be *for the sake of* another thing B. Those two ways are the *goal* sense of teleology, in which B is the *intrinsic end* of A, what A *strives* to do, and the *beneficiary* sense of teleology, in which B is something to which A is beneficial (see Kullmann 1985). This distinction is emphasized by some Aristotle scholars in discussions of passages where Aristotle identifies seeming teleological relations between organisms from different species (e.g. Sedley 1991; Bodnár 2005;

¹⁹ Consistent with what has been observed at the end of section 4.1, i.e. that their being non-accidental (in the sense of regular) is not the only aspect which demarcates functions from non-functions, from now on I will speak of a distinction between functions and *mere effects* rather than of one between functions and *accidents*.

Pellegrin 2011).²⁰ The most well-known of those passages, in which Aristotle describes a very simplified food chain, is from *Politics* I.8 1256^b15-20:

Hence it is equally clear that we should also suppose that, after birth, plants exist for the sake of animals, and the other animals for the sake of men—domesticated animals for both usefulness and food, and most if not all wild animals for food and other assistance, as a source of clothing and other utilities. If, then, nature makes nothing incomplete or pointless, it is necessary that nature has made them all for the sake of men. (quoted from Sedley 1991, 180)²¹

In order to reconcile those statements with the general notion that, for Aristotle, the primary end of each being is the development of its own potentialities, many Aristotle scholars invoke Aristotle's *beneficiary* sense of teleology (see Sedley 1991; Lennox 2001, 341; Bodnár 2005, sec. 3; Pellegrin 2011, 36–39). In their reading, what Aristotle is saying in those passages is not that serving the needs of animals is the *intrinsic end* of plants and that serving humans is the *intrinsic end* of animals, as would be the case if he was invoking the *goal* sense of teleology. In other words, he is not saying that plants and animals *strive* to feed the next links in the food chain. Plants, *qua* plants, strive to achieve the life-cycles characteristic of their kind, and animals, *qua* animals, strive to achieve the life-cycles characteristic of their kind. What Aristotle is saying, rather, is that, as a rule, plants, animals and humans interact in such a way that each of those beings *benefit* the next link in the food chain. Their serving as food is an *extrinsic function* of plants and animals, which they bear not as a result of their own internal striving, but as a result of being co-opted by other organisms for their own strivings.

This reading of Aristotle suggests an explanation of the sense in which the ecological interactions on which the ascriptions of ecological use and service functions are based

²⁰ It should be noted that those scholars disagree over the implications of those passages for the interpretation of Aristotle's general views on teleology. Those disagreements need not concern us here.

²¹ Another discussed passage is from the *Parts of animals* IV.13 696^b27-8, where Aristotle states that the mouth of dolphins and selachians is placed in such a way that they are slower at catching their preys, in part for the sake of those preys' preservation (see Lennox 2001, 341; Bodnár 2005, 27n34).

involve more than mere causal relations.²² It suggests that what essentially differentiates functional ecological interactions from mere causal interactions is the regular *beneficiary relation* that occurs between the organisms involved. Such beneficiary relations are a form of teleological relation, although a weaker one than that involved with the *goal* sense of teleology. As such, they are more than mere cause-effect relations and therefore involve more than mere effects. Those teleological relations are also ecologically fundamental, in that they are that by which organisms fulfill their contributions to ecosystem processes. It is through benefiting some other organism (e.g. through direct consumption in Aristotle's food chain description) that an organism contributes to the circulation of nutrients and energy within its ecosystem. For instance, by feeding a rabbit, hay and grass circulate nutrients and energy through the food cycle and, by so doing, fulfill their ecological role of primary producers (or autotrophs). Likewise, by feeding a fox, the rabbit, in turn, circulates nutrients and energy further in the food cycle and, by so doing, fulfills its ecological role of a primary consumer. If those types of interactions occur regularly between ecologically similar organisms, they will (jointly with other regular interactions occurring between other organisms) contribute to determining the regular way in which nutrients cycle and energy flows within the ecosystem in which they occur. Thus, the beneficiary relations that take place between organisms within ecological communities and ecosystems are not just relations that some researchers happen to be interested in; they are what upholds the very existence of ecosystems. In this respect, I submit that Aristotle's beneficiary sense of teleology as applied to ecological interactions within communities and ecosystems yields an observer-independent basis for distinguishing ecological roles from mere effects.

Consistent with what has been observed in section 2 regarding contemporary functional ecology's expansion upon Elton's initial focus on food interactions, the beneficiary relations in virtue of which organisms can be ascribed roles within ecosystems can not only involve *trophic* interaction (as in Aristotle's simple food-chain

²² Here my point is only to use the Aristotelian distinction to illuminate functional thinking in ecology, and I do not take stance on the more historical issue of whether Aristotle should be considered as an early contributor to the science of ecology (see e.g. Bodenheimer 1954; Acot 1988, 11–14).

depiction), but also *non-trophic* ones, such as *ecosystem engineering*, *pollination* and *seed dispersal*. Aristotle's beneficiary sense of teleology also offers some illumination as to what unifies those non-trophic interactions as ones that ground the ascriptions of ecological roles. Those are interactions in which some organisms benefit other organisms through other means than direct consumption, or to use ecologists' technical term, interactions which involve forms of *facilitation* (Callaway 1995, 2007; Bruno, Stachowicz, and Bertness 2003). Ecosystem engineers do not acquire their ecological roles from the mere fact that they modify their environments, but from the fact that those modifications create opportunities for other organisms.²³ Likewise, pollinators and seed dispersers acquire their ecological roles from the benefits generated by their activities for the plants they pollinate and whose seeds they disperse. Those benefits mainly consist in the creation of conditions which improve the benefited organisms' access to needed resources or habitats.²⁴

In contrast to the benefits provided through being consumed, which have *direct* repercussions on ecosystem-level cycles of nutrients and flows of energy, the benefits provided by some organisms to other organisms through non-trophic interactions have *indirect* (though nonetheless crucially important) repercussions on those cycles and flows. Those indirect repercussions result from the way in which facilitators inflect the direct contributions of the facilitated organisms to those processes. For instance, by improving other organisms' access to needed resources or habitats, ecosystem engineers

²³ Although facilitation and ecosystem engineering are similar in that they both involve non-trophic interactions, they differ in two significant respects. First, some facilitative interactions do not involve ecosystem engineering (e.g. pollination and seed dispersal). And second, facilitation is *by definition* a beneficial interaction, whereas ecosystem engineering may have positive and negative effects (see Jones, Lawton, and Shachak 1997).

²⁴ As Bruno et al. (2003, 119–21) remark, facilitative interactions can make the realized niche of a species larger than it would be if those interactions did not occur (in contrast competitive interactions, which reduce the range of a species' fundamental niche that this species can in fact occupy). It should be noted that this applies to the *requirement* (Grinnellian-Hutchinsonian) niche rather than to the *role* (Eltonian) niche (see note 10 above).

facilitate those other organisms' accomplishment of their life cycle and, by so doing, promote their ability to achieve their direct contributions to ecosystem-level cycles of nutrients and flows of energy. Likewise, by fertilizing some plants or helping their seeds to reach propitious environments, pollinators and seed dispersers facilitate those plants' accomplishment of their life cycles and, by so doing, further their ability to fulfill their direct contributions to ecosystem processes.²⁵ Thus, although indirectly rather than directly affecting ecosystem processes, facilitative interactions are nonetheless (complementarily to trophic ones) significant determinants of ecosystem functioning (see Cardinale, Palmer, and Collins 2002; Callaway 2010, 4–7; A. J. Wright et al. 2017).

At this stage, it is important to point out that by emphasizing *beneficiary* relations, I do not mean to paint an idyllic portrait of nature as being devoid of conflict, nor do I even claim that beneficial interactions are prevalent in the ecological world. The benefits provided by organisms to other organisms through trophic interactions (i.e. direct consumption) indeed involve high costs for the consumed organisms. Moreover, ecosystem engineering may have negative as well as positive local effects (Jones, Lawton, and Shachak 1997, 1950–51), and facilitative interactions are known to frequently incur indirect costs to the facilitator (Callaway 2007, 2). What I am claiming is that for a given ecological interaction to contribute to flows of nutrients and energy within ecosystems, this ecological interaction must ultimately favor the growth, survival or reproduction of some organisms. Nutrients and energy flows can occur within ecosystems only if there are some channels—the biotic segments of those channels being organisms—within which those flows can circulate. For most organisms (and, certainly, all heterotrophs), being able to exist and circulate nutrients and energy requires living off conditions of existence provided by other organisms. Thus, my emphasis of beneficiary relations does not amount to a denial of the presence of conflict in the ecological world.²⁶

²⁵ It should be noted that, insofar as facilitated organisms may also themselves be facilitators (besides fulfilling trophic-based functions), the indirect benefits provided by organisms to other organisms can be manifold and therefore a single organism can fulfill many ecological roles at the same time.

²⁶ The take on the function/mere effect distinction proposed in this section, centered around the notion of *benefit*, is similar to that adopted by many defenders of *contribution to fitness* or *life chances* theories of

4.3 From cross-species teleological relations to ecological functions

So far, the current discussion has shown how organisms from different species can be viewed as entertaining teleological relations in virtue of use and service relations. How does one move from such cross-species teleological relations to *part-whole* functional relations between organisms and the ecosystems they are part of? Two observations can illuminate this question.

First, it should be remarked that the ecosystems formed by cross-species beneficiary relations perform activities (nutrient cycling and energy flows) which are not the mere linear sum of the activities achieved by their component organisms. The particular way in which nutrients and energy circulate in a given ecosystem depends not only on the intrinsic abilities of their component organisms to metabolize those nutrients and energy, but also on how those intrinsic abilities are, *in context*, facilitated or inhibited by the presence of other organisms (Loreau and Hector 2001; Mikkelsen 2011, 400–405). Moreover, the interactions between organisms not only generate cycles of nutrients and flows of energy, but they also maintain those cycles and flows with some degree of *robustness*, or *resilience*, to use ecologists' preferred term (see e.g. Holling 1973, 1996; Pimm 1984; Desjardins et al. 2015).²⁷ According to many ecologists, the presence in an ecosystem of many types of organisms which are able to fulfill similar ecological roles but differ from each other in their ability to respond to changes in environmental conditions increases the resilience of ecosystem processes (Naeem 1998; Walker 1995; Suding et al. 2008).

function (e.g. Boorse 1976, 2002; Bigelow and Pargetter 1987; Walsh 1996; Wouters 2005b, 2013; see Garson 2016, chap. 4, for a discussion). An important difference between those theories and my present proposal, indeed, is the *cross-species* nature of the beneficiary relations in my proposal. According to contribution to fitness and life chances theorists, functional traits are traits that are advantageous to the organisms which bear them, not to other organisms they interact with. Yet, once one accepts that, as I argued, functions need not be necessary properties of the items which bear them, there seems to be no reason why functional relations could not arise from cross-species interactions.

²⁷ It should be noted that resilience and robustness may or may not be equivalent depending on which meaning of “resilience” is adopted. Discussing the various notions of resilience and their importance for community and ecosystem ecology lies beyond the scope of this chapter.

Second, it should also be remarked that insofar as the organisms that constitute to an ecosystem are interdependent (i.e. an organism lives off benefits provided by other organisms which themselves live off benefits provided by other organisms and so on), ecological roles do not only afford benefits to the organisms they affect directly. Their fulfillment also indirectly benefits many other organisms and, ultimately (though to a lesser degree), the whole network of organisms which constitute the ecosystem. In this respect, the cross-species teleological relations discussed above, when considered in their broader ecological context, are almost *ipso facto* organism-ecosystem functional relations. This is not to deny that, in some cases, an organism's benefiting another organism may have an overall negative effect on the whole ecosystem, and even lead to its collapse. Such overall negative effects occur, for instance, when invasive species facilitate each other in a way that leads to "invasional meltdown" (Simberloff and Von Holle 1999; see also Callaway 2010, 7–9). Yet such collapse-fostering facilitative interactions, precisely because they foster collapse, are not sustainable and so cannot become *regular* beneficiary relations. Thus, they cannot count as genuine ecological roles under the account of ecological roles articulated above.

Those observations, in conjunction with the Aristotelian contrast between the *goal* and the *beneficiary* sense of teleology, sheds some light on the way in which organisms and ecosystems constitute different, though equally real, types of functionally organized entities (see Kullmann 1985, 172–73). Within paradigm organisms, which exhibit a fairly strong degree of part-whole integration, the two types of teleology coincide. That is, the *benefit* provided by the parts to the whole is identical to their *intrinsic goal*. For instance, pumping blood is both what the heart contributes to the body and the goal it has been evolutionarily designed to fulfill. In contrast, within ecosystems, which exhibit a looser form of part-whole integration, the two types of teleology diverge. That is, the benefits that organisms provide to their ecosystem (by which they acquire their use and service ecological functions) are not identical with their intrinsic goals (their evolved design functions). The two types of teleology, in fact, almost inevitably conflict in the case of trophic roles, in that providing food to organisms situated at the next trophic level necessarily reduces, and in many cases puts an end to, an organism's ability to achieve its naturally selected activities. Conflict is less obvious and inevitable in the case of

facilitation-based functions (though, as remarked above, facilitation does not exclude conflict). For instance, a beaver's ability to profitably use its pond need not conflict with other organisms' also using it.

The coincidence between the two types of teleology in the case of paradigm organisms and their non-coincidence in the case of paradigm ecosystems, I contend, constitutes the main contrast between those two types of entities. Paradigm organisms are composed of parts whose intrinsic evolved goals coincide with the services they provide to the organism as a whole, whereas ecosystems are typically composed of parts (organisms) whose intrinsic evolved goals diverge from (and often conflict with) the services they provide to their ecosystem. This contrast illuminates the way in which ecosystems may be acknowledged as real functional wholes, despite being characterized by a looser form of part-whole integration than paradigm organisms. Ecosystems are not functional wholes in virtue of being superorganisms shaped by ecosystem-level natural selection, but because they constitute *trophic* and *facilitation networks* (Barker and Odling-Smee 2014, 198; see also Sterelny 2005, 321–22). That is, they are functional wholes through being networks of organisms which are directly or indirectly interdependent for their growth, survival and reproduction, in such a way that they collectively uphold cycles of nutrients and flows of energy between them.²⁸

The observations made in this section so far resonate with Nunes-Neto et al.'s (2014) proposal to elucidate the notion of ecological function through the prism of the *organizational* theory of function—a theory which has recently been advocated as an alternative to both the selected effect and the causal role theories of function (Mossio, Saborido, and Moreno 2009; Moreno and Mossio 2015). This theory defines functions as contributions of a system's parts to the maintenance of that system's organization, which

²⁸ The contrast made here between paradigm individual organisms and ecosystems may have to be revised in the light of the research on *holobionts*, which considers the importance of symbiotic bacteria for the physiology and development of many multicellular organisms. This research suggests that, somewhat turning on its head the historical controversy over whether ecosystems are organisms, many “individual” organisms are in fact more adequately envisioned as ecosystems, or even webs of ecosystems (Gilbert, Sapp, and Tauber 2012; Hagen 2014, 189–90).

in turn maintains the required conditions for the existence of those parts. Thus, on the organizational theory of function, fulfilling their functions allows the parts of a system to promote their own persistence through promoting that of the system they are part of. In this respect, on an organizational account of the notion of ecological role, saying that the ecological role of rabbits is to feed foxes would amount to saying that, by feeding foxes, rabbits contribute to the maintenance of their ecosystem's organization, which, in turn, maintains the conditions for their own existence (a very simplified scenario would conjecture that the fox's dung somehow nourishes the hay and grass that the rabbit eats) (see Nunes-Neto, Moreno, and El-Hani 2014, 133–36, for their own example of an ecosystem involving a bromeliad plant and its associated organisms).

An important difference between Nunes-Neto et al.'s (2014) proposal and the one developed in this chapter is that Aristotle's beneficiary sense of teleology does not require that function bearers be maintained by the system they contribute to. All that is required is that they contribute to the system's maintenance. In the rabbit-fox case, for instance, rabbits acquire their primary consumer ecological role essentially in virtue of providing a regular benefit to their predators, irrespective of whether the ecosystem they contribute to maintaining by doing so also provides conditions favorable to their existence. While this theoretical difference may be inconsequential in this case (and in the case of many organisms) insofar as rabbits require resources provided by their ecosystem to survive, it has important implications regarding the possibility that *abiotic* components fulfill ecological roles within ecosystems. As many Aristotle scholars have emphasized, Aristotle's beneficiary sense of teleology also legitimates the extension of teleology to non-living phenomena (Furley 1985; Sedley 1991; Bodnár 2005). For instance, it legitimates the assertion that, in the beneficiary sense of teleology, rain falls *for the sake of* crop growth (although rain has no *telos* in the *goal* sense).

Such a view accords with Odenbaugh's (2010, 251–52) argument that an adequate elucidation of the notion of ecological role should legitimate the ascription of ecological functions also to *abiotic* items which contribute to ecosystems processes. For instance, Odenbaugh remarks that, although living organisms achieve most of the nitrogen fixation occurring in the ecological world, lightning and volcanoes also achieve some not-

insignificant amount of nitrogen fixation, and therefore contribute to the nitrogen cycle in a way comparable to nitrogen-fixing organisms. Such contributions to ecosystem processes are easily accounted for by Aristotle's beneficiary sense of teleology. This beneficiary sense allows one to assert that, although lightning strikes and volcanoes erupt for no *intrinsic* purpose, they nevertheless fulfill the ecological role of nitrogen-fixation in virtue of the benefit they provide to many organisms which need fixed nitrogen. And to revisit the water-cycle case, much-discussed in the function literature (e.g. Millikan 1989, 294; Davies 2001, chap. 4; Nunes-Neto, Moreno, and El-Hani 2014, 128–29), Aristotle's beneficiary sense of teleology (as suggested by the above interpretation of Aristotle's rainfall example) also allows one to assert that, even though clouds form, rain falls and rivers flow for no intrinsic purpose, clouds, rain and rivers nevertheless fulfill the ecological role of water-provision in virtue of the benefit they provide to *all* living organisms (insofar as they *all* need water). In contrast, Nunes-Neto et al.'s (2014) organizational approach would entail that those abiotic components' contributions to ecosystem processes are mere accidental effects because they are not maintained by the ecosystems they contribute to.

Thus, I submit, my own proposal fares better than Nunes-Neto et al.'s (2014) with respect to the ecological roles of abiotic factors. Though space does not allow me to develop this idea here, the observations made in this section lean towards an understanding of ecological roles along the lines of either Boorse's (1976, 2002) *goal-contribution* or Wouters's (1995, 2005b, 2013) *life chances* theory of functions. Whereas those theories define functions as contributions to organisms' ability to *survive*, it seems conceivable to develop ecological-level versions of them which define ecological roles as contributions to ecosystems' ability to *maintain themselves*.

5. Conclusion

This chapter brought further support to defenses of the notion of ecological role that proceed by denying *selectionism about functions* (the view that this notion should be elucidated along the lines of the *selected effect* theory of function). It did so by showing how alternative *non-selectionist* elucidations of the notion can vindicate more than its use as fruitful heuristics. Section 2 argued that defenses of the notion of ecological role that

attempt to extend the selected effect theory of function to communities and ecosystems conflict with ecologists' context-based understanding of ecological roles. There, I have maintained that a non-selectionist elucidation which rejects *selectionism about functions* would better agree with that understanding. Section, 3, however, identified a challenge seemingly faced by non-selectionist elucidations of ecological roles. This challenge concerns their seeming inability to offer more than perspectivalist and conventionalist grounds for distinguishing ecological roles from mere effects. I have emphasized that failing to do so would implicitly grant *selectionism about functions* by conceding that, in final analysis, only selection-based functions are *real* functions. This, I observed, would implausibly and problematically entail that context-based ecological roles, as well as the ecological-level functional wholes in which these roles occur, are not *real* features of the world, but heuristically fruitful constructions at best. Section 4 offered a three-steps response to this challenge. First, I have showed that selected effect theorists' casting of the function/mere effects distinction as one between functions and *accidents* conceals an undefended assumption that functions must be necessary properties of their bearers. Second, I proposed an alternative take on this distinction articulated around the notion of *regular benefit*, according to which ecological roles are effects of organisms which afford regular benefits to other organisms in such a way that their association undergirds cycles of nutrients and flows of energy. Third, I contended that those cross-species beneficial relations can legitimately be conceived as organism-ecosystem functional relations for two main reasons: (1) the ecosystems formed by those relations perform activities which are genuine ecosystem-level activities, i.e. which differ from those which would result from the mere aggregation of the activities of their component organisms; and (2) the ecological roles fulfilled by organisms in fact do not only afford benefits to the directly affected organisms, but also to the whole network of organisms which constitutes their ecosystem.

The above discussion, I hope, strengthens the theoretical foundations of biodiversity and ecosystem function research, by illuminating how the ecological roles of organisms and the ecosystems in which they occur can be acknowledged as real features of the biological world, while avoiding any commitment to the pervasiveness of ecosystem-

level natural selection or to the existence of community- or ecosystem-level superorganisms.

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