A PERSISTENCE ENHANCING PROPENSITY ACCOUNT OF ECOLOGICAL FUNCTION TO EXPLAIN ECOSYSTEM EVOLUTION[*]

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We argue that ecology in general and biodiversity and ecosystem function (BEF) research in particular need an understanding of functions which is both ahistorical and evolutionarily grounded. A natural candidate in this context is Bigelow and Pargetter's (1987) evolutionary forward-looking account which, like the causal role account, assigns functions to parts of integrated systems regardless of their past history, but supplements this with an evolutionary dimension that relates functions to their bearers' ability to thrive and perpetuate themselves. While Bigelow and Pargetter's account focused on functional organization at the level of organisms, we argue that such an account can be extended to functional organization at the community and ecosystem levels in a way that broadens the scope of the reconciliation between ecosystem ecology and evolutionary biology envisioned by many BEF researchers (e.g. Holt 1995; Loreau 2010a). By linking an evolutionary forward-looking account of functions to the persistence-based understanding of evolution defended by Bouchard (2008, 2011) and others (e.g. Bourrat 2014; Doolittle 2014) and the theoretical research on complex adaptive systems (Levin 1999, 2005; Norberg 2004), we argue that ecosystems, by forming more or less resilient assemblages, can evolve even while they do not reproduce and form lineages. We thus propose a Persistence Enhancing Propensity (PEP) account of role functions in ecology to account for this overlap of evolutionary and ecological processes.

Keywords

Ecology, evolution, philosophy of ecology, philosophy of biology, function, ecological function, biodiversity, ecosystem, complex adaptive systems, reticulate evolution.

1. Introduction

An implicit consensus has recently emerged in the philosophy of ecology to the effect that the selected effect theory of functions (e.g. Wright 1973; Neander 1991a; Millikan 1989a) cannot adequately account for the use of functional language in ecological science (Nunes-Neto,

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Moreno, et al. 2013). Since this theory elucidates functions in terms of the evolutionary history of their bearers, many have argued, based on the practice of ecologists, that function ascriptions in ecology are better captured by ahistorical theories that define functions in terms of contributions to the activities and organization of a higher-level system. Accordingly, some philosophers of ecology (Maclaurin and Sterelny 2008; Odenbaugh 2010) lean towards an account of ecological functions that draws on Robert Cummins's (1975) causal role theory, while others (Nunes-Neto et al. 2014) have proposed an account that utilizes the more recently developed organizational theory of functions (Mossio et al. 2009; Saborido et al. 2011). These accounts accommodate in many ways the use of functional language by ecologists. By doing so, they significantly reinforce the theoretical foundations of the *biodiversity and ecosystem function* (BEF) research program, a nascent and very promising ecological approach which seeks to provide a better understanding of the importance of biodiversity for the functioning of ecosystems (e.g. Naeem 2002; Loreau 2010a, 2010b).

This constitutes a significant import of these accounts, since BEF research is arguably the domain of ecology where the concept of ecological function is the most central and essential. As Nei Nunes-Neto, R. S. Do Carmo and Charbel El-Hani. (2013, pp. 22–3) rightly note, in BEF research the concept of functional diversity, to which the concept of ecological function is intimately linked, plays the role of a conceptual bridge between the effects of biodiversity and its components, on the one hand, and their contribution to ecological processes which maintain ecosystems and their properties, on the other. For this reason, and also because the BEF research program seems well suited to achieve the long awaited unification of the often isolated theoretical perspectives of community and ecosystem ecology, our discussion will, like Nunes-Neto, Alvaro Moreno and El-Hani (2014), pay special attention to the BEF research program. BEF researchers strive for unification by investigating how the specific traits of organisms and other biological items contribute to the maintenance and functioning of ecosystems. Their approach thereby reaches beyond both the conventional aggregate "species richness" measures of biodiversity in earlier community ecology, and the abstract "black box" approach of classical ecosystem ecology which tended to reduce biological items to their thermodynamic properties (see Naeem 2002, p. 1539). This warrants a special focus on BEF research, since achieving a synthesis of the community and ecosystem ecological perspectives is now increasingly considered necessary by ecologists and policy makers to generate the knowledge required for humanity to meet the challenges of the current biodiversity crisis.

An important limitation of the causal role and organizational accounts, however, with respect to BEF research's unificatory project, is their dissociation of the concept of function from evolutionary considerations. Since evolutionary theory is an important component of the theoretical framework used in community ecology, many BEF researchers conceive of their attempted synthesis of the sub-disciplines of community and ecosystem ecology as involving the reintroduction of evolutionary considerations into ecosystem studies (e.g. Loreau 2010a, 2010b). Reintroducing these considerations would resolve an enduring theoretical incommensurability, deplored by many, between the two biological sub-disciplines (e.g. Loehle and Pechmann 1988; N. B. Grimm 1995; Holt 1995), and dovetails with the plea of many evolutionary biology theorists for a reintegration of ecological considerations into evolutionary thinking (e.g. Odling-Smee et al. 2003; Bouchard and Rosenberg 2004; Barker and Odling-Smee 2013). Hence, insofar as this unification of ecological and evolutionary thinking is desirable, an account of the concept of ecological function which helps illuminate the relation between biodiversity and its components' ecological roles and adaptive evolutionary change would seem preferable to alternative ones with no evolutionary import.

In this context, we will argue in this article that ecology in general and BEF research in particular require an understanding of functions which is both ahistorical *and* evolutionarily grounded. We suggest that the most plausible and fruitful account of functions in ecology is an enriched version of John Bigelow and Robert Pargetter's (1987) evolutionary forward-looking account of functions. This account assigns functions to parts of integrated systems regardless of their past history—in this it is similar to causal-role accounts—but adds an evolutionary dimension which relates functions to those systems' ability to thrive and perpetuate themselves in the future. Linking ecological research programs to a persistence-based account of evolution defended by Frédéric Bouchard (2008, 2011) and others (e.g. Bourrat 2014; Doolittle 2014), we label our proposal the Persistence Enhancing Propensity (PEP) account of functions in ecology.

We introduce this proposal as follows. In section 2, we add support to the implicit consensus about the limitations, for ecology, of the selected effect theory of functions, but argue that James MacLaurin and Kim Sterelny's (2008) and Jay Odenbaugh's (2010) proposal to define ecological functions in terms of Cummins's causal role account is in tension with some central tenets of the BEF research program. In section 3, we show how a persistence-based account of evolution which eschews reproduction and lineage formation as conditions for natural selection makes the evolution of communities and ecosystems more easily conceivable and tractable than is usually assumed. And finally, in section 4, we show how our PEP account better accommodates the use of functional language by BEF researchers and ecologists in general than Nunes-Neto et al.'s (2014) organizational account. Furthermore, we argue that this is a necessary theoretical step towards the unification of ecosystem ecology and evolutionary biology sought by BEF researchers and many other ecologists.

2. Ecological and evolutionary functions

The use of functional language has been one of the most important subjects of dissension between ecosystem ecologists and evolutionary theorists (see Hagen 1989, 1992, chap. 8). At least since George C. Williams (1966), many evolutionary theorists and philosophers of biology (Wright 1973; Millikan 1989a; Neander 1991a, 1991b) have defined functions in relation to past natural selection. According to this view, to which we will refer, following Ron Amundson and George Lauder (1994), as the "selected effect" theory (or SE for short), a trait's function is an effect of that trait which explains why its transmission was favored under past selective pressures. This backward-looking approach to functions, however, has not been the one favored by ecosystem ecologists. Since the demise of Clementsian organismic ecology in the 1950s, the understanding of functional integration in ecosystem ecology has tended to be more in line with Charles Elton's (1927, 1930) "economy of nature" metaphor for ecological units; this understanding leaves room for migrations, as well as what Elton acknowledged as the selection of their environment by animals, among the factors that explain the composition of communities (see Hagen 1992, pp. 55–62; Jax 2010, pp. 79–80). Hence, function ascriptions in ecology focus on how the species in an ecosystem *currently* interact, regardless of where and how they evolved in the past. To use Peter Achinstein's (1977) helpful delineation of three types of function statements, the selected effect theory of functions characterizes *design functions*, that is, functions defined in terms of what something was designed or created to do (e.g. a mouse trap's function is to catch mice); whereas functional talk in ecology denotes *use functions* and *service functions*, that is, respectively, functions defined as what something is used for (e.g. this table is used as a seat) or what something serves as (e.g. a watch's second hand functions as a dust sweeper). For instance, in an ecological context, a rabbit can be used as food by a fox and so acquire a use function, and the fox, in turn, may acquire a service function with respect to the overall ecosystem's dynamic by regulating the rabbit's population. Thus, functions in ecosystem ecology are not intrinsic evolved properties of species and organisms but rather contextual and relational ones (see Brennan 1988, chap. 8), akin to what Amundson and Lauder (1994), characterizing Cummins's (1975) account, would refer to as "causal role" functions (or CR for short). Functions thus defined translate into mere accidental by-products from the standpoint of the SE theory.

Even in the last decades, where the theoretical incommensurability between ecosystem ecology and evolutionary biology has increasingly been found problematic (see e.g. Loehle and Pechmann 1988; Holt 1995), and many ecologists (some of them involved in the BEF research program) pursue the project of unifying the two disciplines' divergent outlooks (e.g. Loreau 2010a, 2010b), the use of functional language in ecology has remained mostly ahistorical. For instance, Nancy B. Grimm (1995, p. 8) notes that, although the term "'function' implies to some an evolutionary origin," in ecology, "it remains a useful term for describing what a system does in the context of its surroundings" (see Nunes-Neto, Do Carmo, et al. 2013, for a review of BEF work which demonstrates its ahistorical use of functional language). This, as Nunes-Neto, Moreno and El-Hani (2013) remark, has led to an implicit consensus among philosophers of ecology that SE functions cannot account for how functional language is used in ecology (see Maclaurin and Sterelny 2008, pp. 114–6; Odenbaugh 2010, pp. 248–52).

According to Kurt Jax's (2005, pp. 641–2, 2010, pp. 62–5) comprehensive review and analysis of function ascriptions in ecology and BEF research, "function" in those contexts is used in four different and complementary ways (here we paraphrase Jax's texts):

[1] A process or interaction: A purely descriptive meaning referring to a change of state or what happens between two biotic or abiotic objects, e.g. a prey-predator interaction or the assimilation of nutrients by plants.

[2] The functioning of a whole ecosystem: The network of processes constituting the performance or operating of a whole ecosystem. It can be focused on single processes, or, more holistically, focused on the overall performance of the ecosystem, and on what sustains it.

[3] The role functions of parts of ecosystems: The roles of biotic and abiotic components in relation to the functioning of a whole ecosystem (defined by meaning 2), e.g. a plant's role of primary producer within an ecosystem. These roles are connected to the ideas of functional types or functional groups in ecology, which classify organisms or species on the basis of their effects on ecosystem processes. This is what Elton called their "professions" in the biotic community, regardless of their taxonomic properties.

[4] Ecosystem services: A subset of ecosystem processes which fulfill some human needs or purposes (e.g. water purification, oxygen production).

Jax notes that meaning [1] is a purely descriptive sense of "function" and is therefore philosophically unproblematic, and that meaning [4] can be interpreted as a subset of meaning [2]. Following that analysis, we will focus here on meanings [2] and [3], which call for further philosophical investigation insofar as they seem to involve more than pure descriptions. At first sight, these observations plead in favor of Maclaurin and Sterelny's (2008, pp. 114–6) and Odenbaugh's (2010, pp. 251–2) proposal to interpret ecologists' ascription of role functions to components of ecosystems (Jax's functions meaning [3]), in accordance with Cummins's CR theory. Odenbaugh (2010, p. 251) reformulates the CR theory of function as such (where *x* is a part of a system *S* and *C* is a capacity of *S*):

> The [CR] function of *x* in a system *S* is to *F* if, and only if, *x* is capable of *F*-ing and *x*'s capacity to *F* in part accounts for *S*'s capacity to *C*.[1]

This, as he notes, applies well to typical function ascriptions in ecology, such as the function of fungi to decompose woody products, defined in relation to an ecosystem's capacity to recycle carbon, or the function of *Rhizobium* (a kind of bacteria) to fix nitrogen, defined in relation to an ecosystem's capacity to recycle nitrogen. Moreover, this interpretation is consistent with Jax's observation that function ascriptions to biotic and abiotic components of ecosystems (functions meaning [3]) serve the purpose of analyzing some activity of an ecosystem (functions meaning [2]) in terms of the causal contributions of its parts. The CR interpretation is also congruent with the fact that many philosophers of biology have adopted a pluralistic stance regarding the function debate (e.g. Brandon 2013; Bouchard 2013a; Amundson and Lauder 1994; Godfrey-Smith 1993; Millikan 1989b). If, as Amundson and Lauder (1994), Paul Griffiths (2006) and Christopher Boorse (1976, pp. 85–6) respectively argue, the SE account applies well neither to functional anatomy, developmental biology, nor to physiology, then it would not seem problematic for ecology to be just one more “orphan” of the SE theory (see Bouchard 2013a, p. 93).

Yet, although the pluralistic strategy and the CR theory of function may satisfyingly account for some uses of functional language in ecological contexts, and although, like Odenbaugh (2010) and Maclaurin and Sterelny (2008), we will propose an account which analyses ecological role functions (Jax’s function meaning [3]) in terms of their causal contribution to some activity of an ecosystem (functions meaning [2]), we worry that an unrestricted CR account of ecological function may reveal itself insufficient with respect to some important aspects of the BEF research program. The first of these aspects is the interest shared by many BEF researchers in the relationship between biodiversity and ecosystem stability and resilience (Naeem 1998; Loreau et al. 2002; Loreau 2010b, chap. 5). As Kevin deLaplante and Valentin Picasso (2011, p. 170) and Michel Loreau et al. (2002, pp. 79–82) note among others, BEF research can in part be seen as reviving the research on the diversity-stability hypothesis, that is, the hypothesis that ecosystems with higher species diversity tend to be more stable, by implementing new theoretical and experimental approaches to it. While classical formulations of that hypothesis focused on aggregate “species richness” measures of biodiversity, BEF researchers tend to focus more on the specific features of the species which play functional roles in ecosystems (Jax 2010, pp. 53–5; DeLaplante and Picasso 2011, pp. 170–3). Given this focus on stability and resilience, it would seem inconsistent with BEF research to assign functions to components of ecosystems in relation to *any* activity occurring at the ecosystem level, including even their collapse or their decrease in resilience. For instance, assigning functional roles to some pollutants or invasive species on the grounds of their contributions to ecosystem fragilization or collapse would seem to run counter to BEF researchers’ focus on stability and resilience. Ecosystem functioning (function meaning [2]), in other words, implicitly suggests *sustainability* of ecosystem functioning, whence its alleged relevance for human sustainability and the maintenance of ecosystem services (Millennium Ecosystem Assessment 2005). Hence, the general worry that the CR theory is too liberal (McLaughlin 2001, pp. 119–24; Wouters 2005, pp. 135–6) also applies to the case of CR ecological functions. Since it significantly relativizes functional analysis to the interests of researchers, that theory would readily allow defining some ecological functions relative to ecosystem fragilization or collapse, as long as doing so holds some scientific fruitfulness (see Nunes-Neto et al. 2014, pp. 137–8). Thus, if ecologists wish to distinguish such merely heuristic use of functional language from more genuine ones linked to ecosystem sustainability and resilience, their science requires an analysis of function more discriminating than the CR theory (for similar reasons, evolutionary theorists eschewed CR functions, see Godfrey-Smith 1994).[2]

Another consideration which pleads against a CR interpretation of ecological functions is the explicit aim endorsed by some BEF researchers to overcome the traditional theoretical incommensurability between ecosystem ecology and evolutionary biology (e.g. Loreau 2010a, pp. 55–7, 2010b, chap. 8). Unifying these two scientific disciplines has long been seen as desirable by many evolutionary biologists (e.g. Wilson 1976; Odling-Smee et al. 2003) and ecologists (e.g. Hutchinson 1965; Loehle and Pechmann 1988; Holt 1995), and BEF research holds some promise for enabling the unification in a way that does justice to the theoretical contributions of both disciplines. Yet, since the CR theory typically refuses to assign any privilege to evolutionary considerations in the ascription of functions (see Cummins 1975, pp. 755–7), a CR interpretation of ecological functions may counter-productively limit the scope of this unification. Moreover, some very promising trends in BEF research integrate the insights of *complex adaptive systems* (CAS) theory to the study of the link between biodiversity and ecosystem functioning (e.g. Levin 1999, 2005; Norberg et al. 2001; Norberg 2004; Leibold and Norberg 2004). But as some critics have argued (e.g. Jax 2010, pp. 81–2), given CAS theorists' willingness to dissociate their theory from ideas of ecosystems as units of selection (in keeping with Williams (1966) and others' anti-group selection arguments), the notion of systems as being "adaptive" in CAS theory remains rather obscure, since it remains unclear in what non-evolutionary sense ecosystems adapt to their environment. Thus, the notion of system adaptiveness involved in CAS theory and its use in BEF research could be made advantageously clearer if its connection with the evolutionary notion of adaptiveness could be illuminated. These observations, to be sure, do not definitively rule out any CR interpretation of ecological role functions, since one could insist that ecological functions need not be assigned an evolutionary significance for a synthesis of ecology and evolution to be achieved. Nevertheless, we think that these observations at least suggest that an evolutionarily grounded interpretation of ecological role functions would be more fruitful with respect to some important theoretical endeavors of BEF research. Some of the payoffs of adopting a more evolutionarily grounded functional perspective will be more clearly highlighted in section 4 of this paper.

In this context, we propose that role functions in ecology (functions meaning [3]) should be interpreted according to a modified version of the evolutionary forward-looking account of functions developed by Bigelow and Pargetter (1987). The latter account, being the main evolutionarily grounded alternative to the SE theory, is well-suited to lay the theoretical underpinnings for achieving the unification of ecosystem ecology and evolutionary biology sought in BEF research. In contrast to the SE account which focuses on what an organism's traits have been selected for in the past, Bigelow and Pargetter's account focuses on how the traits of an organism enhance its *present* fitness and therefore its propensity to survive and reproduce (whence its "forward-looking" label). This forward-looking character resonates well with the focus of BEF research on the relationship between biodiversity and ecosystem resilience and sustainability. Transposed to ecosystems, which do not reproduce, this propensity can be interpreted as a propensity to *persist*, understood in terms of ecosystem stability and resilience (Bouchard 2013a, 2014), linking the notion of ecological role function to the research on resilience in ecology (Gunderson and Holling 2002; Beisner et al. 2003; Gunderson et al. 2009; Desjardins et al. 2015). Bigelow and Pargetter's forward-looking theory of functions is often referred to as the Survival Enhancing Propensity (SEP) account of functions (e.g. Bardon 2007;

Bertrand 2013). Correspondingly, we label our proposal the Persistence Enhancing Propensity (PEP) account of role functions in ecology (in what follows, we will simply speak of "functions" in ecology but it should be understood that our focus is on role function, that is, Jax's function meaning [3]). According to our proposed PEP account, ecological function may be defined as such:

> The function of *x* in an ecosystem *E* is to *F* if, and only if, *x* is capable of doing *F* and *x*'s capacity to *F* contributes to *E*'s propensity to persist.

The shift from survival to persistence is not trivial given that survival is an organism-centric concept. But more importantly, because persistence is more genuinely time-comparison relative, one should not focus exclusively on the maintenance of the *stability* of a given system defined as its ability to return to its equilibrium state after disturbance. In the spirit of C. S. Holling's (1973, 1996) emphasis on *ecological* resilience over *engineering* resilience (stability), and in line with the work of hierarchy theorists (O'Neill et al. 1986; Allen and Hoekstra 1992), ecological functions should be defined relative to an ecosystem's more general ability to persist, often by "tolerating" and "absorbing" change, given a succession of different states on different temporal scales (more on this below).[3] This, as we will show, will link the notion of ecological function to the ahistorical concept of evolutionary adaptation highlighted by Brandon (1990, 2013) and central to "extended adaptationist" approaches to evolution like the niche construction and extended organism perspectives (Odling-Smee et al. 2003; Turner 2004; Barker 2008; Bouchard 2010; Barker and Odling-Smee 2013).

This enrichment of Bigelow and Pargetter's forward-looking account of functions rests on a strong analogy between the fitness of organisms understood in terms of survival and reproduction and the adaptiveness of ecosystems understood as their potential to persist (often referred to in ecology as their resilience); yet most proponents of the view of ecosystems as adaptive systems (e.g. Levin 1998, 1999, chap. 9, 2005; Allen et al. 2003, chap. 6) have shied away from such a strong analogy, motivated by classical anti-group-selectionism arguments (see DeLaplante 2005, pp. 402–6; DeLaplante & Odenbaugh Unpublished manuscript, pp. 19–22). Precisely because it is evolutionarily grounded, in that it defines functions in relation to the evolutionary concept of fitness, Bigelow and Pargetter's account of functions can only be applied to entities which can properly be said to evolve through natural selection. Yet, since the work of Williams (1966), the idea that ecosystems are units of selection has been at best controversial. Although this controversy is the main reason why philosophers of ecology have considered that the SE theory cannot account for ecological functions (Maclaurin and Sterelny 2008, p. 114; Odenbaugh 2010, pp. 249–51; Nunes-Neto, Moreno, et al. 2013, pp. 49–51; Nunes-Neto et al. 2014, p. 124), a more fundamental reason, we think, is the more specific observation that ecosystems do not *reproduce* and so do not form *lineages*. The SE theory of function, as it seeks to explain the production (through ontogeny) of token traits by their function (and thereby to naturalize teleological explanations), requires a clearly defined generational bottleneck between past token traits which were selected because of their advantageous effects, and the current ones to which functions are ascribed. This makes reproduction a necessary condition for functionality independently of whether it is, as commonly conceived, also necessary for evolution. But since Bigelow and Pargetter's forward looking account does not purport to explain the production of functional traits, it allows for token traits to have functions regardless of their origin, as long as they are favored by *current* natural selection. Indeed, if one assumes that reproduction and lineages are necessary conditions for natural selection, then one will conclude that ecosystems cannot have functions so understood. In response to this, the next section will argue (building on Bouchard 2008, 2010, 2011, 2013a, 2013b, 2014) that this orthodox reproductive and lineage-bound understanding of Darwinian evolution is problematic, in many respects, in the light of recent developments in biological research.

3. Ecology and evolution and their (promiscuous) common fate

The most broadly accepted reconstruction of the process of natural selection is Richard Lewontin's (Levins and Lewontin 1985, p. 76):

> A sufficient mechanism for evolution by natural selection is contained in three propositions:
>
> 1. There is variation in morphological, physiological, and behavioral traits among members of a species (the principle of variation).
>
> 2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals, and, in particular, offspring resemble their parents (the principle of heredity).
>
> 3. Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness).

As pointed out by Bouchard (2011, p. 107, 2014, pp. 382–3), natural selection in this reconstruction is, essentially, a process in which successful variants in a population are passed on to a new generation through an inheritance mechanism. This reconstruction, which has been assumed in most discussions of community and ecosystem evolution (e.g. Whittaker and Woodwell 1972; Futuyma 1986; Bambach and Bennington 1996), imposes rather stringent conditions on ecosystem selection. First, since it makes differential reproduction the key measure of evolutionary success and since gene transmission is usually conceived of as the main mechanism through which successful variants are reproduced, Lewontin's reconstruction implies that most ecosystems cannot evolve, to the extent that they neither reproduce nor have a unified genome. Second, since it characterizes evolution by natural selection as occurring on relatively homogeneous populations belonging to unified monophyletic groups, Lewontin's reconstruction entails that ecosystems could evolve only if there were lineages of ecosystems, that is, if there were populations of token ecosystems unified by a common phylogeny. Ecologists, however, have come to think ecological units do not meet this condition (Whittaker and Woodwell 1972; Whittaker 1975, pp. 353–363; Allen et al. 1993). These, as we will see, are the main reasons for the widespread dismissal of early accounts of community and ecosystem evolution (e.g. Dunbar 1960, 1972) and, more recently, for many ecologists' adoption of non-Darwinian theories of ecosystem organization, such as complex adaptive systems theory (see DeLaplante 2005, pp.

402–6; DeLaplante & Odenbaugh Unpublished manuscript, pp. 19–22). Drawing from Sober and Wilson's (1994; see also Wilson and Sober 1989) notion that, in order for an entity to constitute an evolutionary unit, its parts must share a *common fate*, this section revisits these two challenges in the light of recent developments in the biological research on clonal and symbiotic entities, as well as on the microbial world. Our discussion will build on Bouchard's take on these recent developments and his argument that variation, which Lewontin rightly emphasizes as necessary to evolution by natural selection, is to be found not only among the members of populations, but also among the parts of complex evolving entities (see Bouchard 2008, 2014). This, we will argue, makes a case for downplaying reproduction and lineage formation as conditions for the evolution of communities and ecosystems.

3.1 The reproduction challenge

As many have argued (e.g. L. W. Buss (1983), André Ariew and Richard Lewontin (2004), Bouchard (2008, 2013a, 2011) and Peter Godfrey-Smith (2009, 2013)) the reproduction criterion for natural selection is problematic for many life forms. For instance, the evolution of protists, fungi and some plants results in large part from a selection on somatic changes that do not affect the germ line. Moreover, for many plants, the line between reproduction and growth is often blurred, since asexual reproduction and vegetative growth both involve the formation of ramets, and differ only in that the ramets become physiologically distinct in the former while they remain physiologically connected in the latter. For instance, while a quaking aspen (*Populus tremuloides*) grove looks like a standard forest, its trunks are in fact branches that are connected underground; the grove thus forms a functionally integrated whole (see Bouchard 2008, pp. 562–6). Although quaking aspens can reproduce sexually, that strategy is often inefficient since most seeds die before germination because of lack of water and light (Mitton and Grant 1996). Moreover, while quaking aspen ramets often split, those that remain metabolically integrated with the grove usually fare better, because they can share nutrients with each other (Gough et al. 2001). This suggests that *not* reproducing is a better evolutionary strategy for many quaking aspen, and so relativizes the reproduction component of fitness by suggesting that, depending on the selective pressures at play, sexual reproduction, asexual reproduction and vegetative growth can all be successful strategies. Based on similar observations to the effect that reproductive accounts of fitness do not apply well to many clonal entities, insect colonies and symbioses, Bouchard (2008, 2011) proposes that evolutionary fitness should be recast in terms of *differential persistence* rather than *differential reproductive success*, thereby making reproduction a non-necessary component of evolution.

Such an understanding of fitness, as Bouchard (2013a, 2014) and others (e.g. Partridge 2000; Blandin 2007) have argued, makes ecosystem evolution more easily conceivable, and partly rehabilitates Dunbar's (1960, 1972) earlier account of ecosystem selection in terms of differential persistence through stability (see Cropp and Gabric 2002 for a recent defense of a similar account). However, important developments in ecological theory in the last decades indicate that a persistence-based account of ecosystem evolution should adopt a broader view of how ecological units persist and de-emphasize stability defined as an ecosystem's ability to return to its equilibrium state after disturbance. As many commentators have noted, the use of stability concepts and terms in ecological theory has often been very messy and confused (see Shrader-Frechette and McCoy 1993, section 2.2; and Odenbaugh 2001 for discussions), but an important improvement in the understanding of how ecosystems persist is C. S. Holling's distinction between *engineering* and *ecological* resilience (Holling 1973, 1996; Beisner et al. 2003; Desjardins et al. 2015). As Holling (1996; in Gunderson et al. 2009, pp. 53–4) defines these terms, *engineering* resilience, which is the more traditional notion of stability on which earlier ecologists have tended to focus, "concentrates on stability near an equilibrium steady state, where resistance to disturbance and speed of return to the equilibrium are used to measure the property"; whereas *ecological* resilience

> emphasizes conditions far from any equilibrium steady state, where instabilities can flip a system into another regime of behavior—that is, to another stability domain. In this case the measurement of resilience is the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior.[4]

This advance in ecological theory is important for our purpose, since it bears on how one should understand the link between biodiversity and the persistence of ecosystems. From the perspective of classical engineering resilience, the co-evolutionary adaptation of species to each other, which could in time dampen their fluctuations in abundance, was seen as the main source of stability in communities and ecosystems (Dunbar 1960, 1972). From the more contemporary perspective of ecological resilience, the overspecialized relationships which result from such coevolution are seen as undermining, rather than reinforcing, the ability of ecosystems to persist (Holling 1986; in Gunderson et al. 2009, pp. 93–8). According to ecological resilience theorists, the increased species connectedness that occurs through ecological succession, although it tends to make a system more stable in the engineering sense, makes it at the same time more fragile and vulnerable to perturbations (Desjardins et al. 2015, pp. 150–1). Therefore, ecological resilience theorists conceive of the persistence of ecosystems as favored by weaker interactions, in which redundancy in functional biodiversity plays a key role (more on this below). Hence, overspecialized ecological relationships, according to resilience theorists, often threaten the persistence of a system, and so often render it less functional according to our account.

However, for this very same reason, one might resist our proposed extension to ecosystems of the persistence-based understanding of evolutionary fitness. One might reply that this emphasis on weak interactions makes ecosystems too transient to constitute assemblages of parts which could meet, if only in spirit, Sober and Wilson's common fate criterion. One might even reject our persistence-based understanding of evolutionary fitness while essentially conceding our definition of ecological functions in terms of contribution to ecosystem persistence. The resulting theory would have some commonality with Christopher Boorse's (1976, 2002) account of function in terms of contribution to an organism's natural goals of survival and reproduction (which could be reinterpreted for ecological purposes as contribution to persistence), where those natural goals are not given direct evolutionary underpinnings. In favor of this sort of happy medium concession, some appealing theoretical reasons could be invoked for retaining coevolution as a precondition for ecosystem-level evolution (and thus denying the evolutionary significance of weak interactions). As David Hull (1980, pp. 326–7) states:

> The major stumbling block in the path of treating such systems as interactors is the independence of their constituent replicators. […] The organisms that comprise an ecological community may interact with the environment of the community as a cohesive whole, but the effects of these interactions on their constituent replicators are not unitary.

Such an observation may have inspired Patrick Blandin and Maxime Lamotte's account, which states that ecosystem evolution can take place on some associations of species which interact cooperatively insofar as some prior co-evolution coordinates their genomes and thereby binds their evolutionary fates together (Lamotte and Blandin 1985, p. 188; Blandin and Lamotte 1989, p. 40; Blandin 2007, p. 43). Such genome coordination enables Blandin and Lamotte to formulate a persistence-based account of ecosystem evolution which meets Lewontin's other necessary condition for natural selection: the formation of lineages. Hence, one could grant our definition of ecological functions in terms of contribution to persistence, but insist that only those ecological functions which originate in the kind of co-evolutionary episodes depicted by Blandin and Lamotte enhance ecosystem persistence in an evolutionary significant way.

To tie this in with recent conceptual work on evolution at the microbial scale, it could be noted that Blandin and Lamotte's criteria resonate with John Dupré and Maureen O'Malley's (2009) more recent account of evolutionary individuality, which identifies *metabolic collaboration* and *lineage membership* as its two defining components. A central tenet of Dupré and O'Malley's work is their aim to embrace the unruliness of interactions as they occur in the microbial world (in the spirit of Dupré's (1993) defense of *promiscuous realism* about biological ontology). This unruliness in many respects resembles the intricateness of ecological interactions at more macroscopic levels. Yet, in building bridges between theoretical work on evolution at the microbial and ecological scales, we will argue in section 3.2 that evolutionary theorists should go even further than Dupré and O'Malley in embracing the promiscuity of the biological world, and relativize the lineage coordination criterion. This will underscore that, although it is conceptually possible to accept our account of functions in terms of contribution to persistence while denying it an evolutionary significance, this would underestimate fruitful and novel explanatory approaches in evolutionary microbiology (e.g. Doolittle 2000; Doolittle and Bapteste 2007; Bapteste et al. 2012).

3.2 The lineage challenge

Another, and perhaps more serious, challenge to the idea of community and ecosystem evolution is neo-Gleasonian ecology's observation that species associations in ecosystems do *not* typically form coordinated lineages (Whittaker and Woodwell 1972; Whittaker 1975, pp. 353–363; Allen et al. 1993). Neo-Gleasonian ecology has become established in the 1950s, while growing skepticism regarding Frederic Clements's (1916, 1936) strong analogy between ecological units and living organisms has led many ecologists to adopt his historical rival Henry Gleason's (1917, 1926) more population-reductionist picture of the ecological world. Accordingly, neo-Gleasonian ecologists (e.g. Whittaker 1951, 1975; Curtis and McIntosh 1951) characterize typical ecological communities as composed of species which have evolved independently and combined through chance immigration and individual suitability to ecological contexts. As the neo-Gleasonian ecologists Robert Whittaker and G. M. Woodwell (1972, p. 141) emphasize :

> A community is not simply the lineal descendent of some past community; it comprises species of diverse evolutionary histories in diverse past communities. […] Communities are related by a blurred reticulateness of many intersecting strands (i.e., species) relating a present community to many past communities. The evolutionary relationship is more like the genetic relationship of human families to one another than of species to one another.

What Whittaker and Woodwell call the "reticulateness" of community evolution alludes to the fact that change at the community level typically results from the lateral movement of species between communities through migrations, in contrast to evolution at the population level where traits are characteristically transferred vertically through reproduction (as illustrated in Figure 3.1). As Whittaker (1975, pp. 358–9) argues, this reticulateness, which implies that "[p]resent and past communities are not arranged by ecologists in evolutionary trees," entails that "[c]are is needed in discussing evolution of characteristics of communities as a process separate from the evolution of their species." According to Whittaker (1975, p. 362), in other words, the net-like, rather than tree-like, structure of evolutionary relationships in ecological communities implies that they cannot be said to evolve in the standard sense. Thus, according to neo-Gleasonian ecology, most ecological units do not

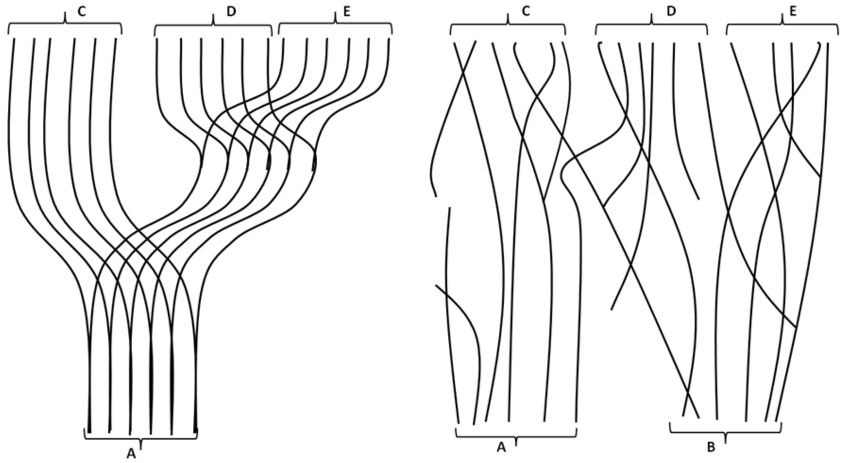

Figure 3.1: Clementsian and Gleasonian views of community evolution. On the Clementsian view (left), communities C, D, and E are clear descendents of community A, while on the Gleasonian view (right), no clear lineage can be found between communities A and B and communities C, D, and E (inspired from Whittaker 1975, p. 358).

Working copy: may differ from final version. Contact author for questions or comments:antoine.cdussault@clg.qc.ca, f.bouchard@umontreal.ca meet Blandin and Lamotte's lineage criterion.[5] However, it is important to emphasize that, contrary to common misinterpretations, Gleasonian or neo-Gleasonian ecology does not deny the kind of community-level functional organization depicted by Elton's trophic model of ecological communities and later studied by ecosystem ecology. Although Gleason and his followers adopt a population-reductionist stance concerning the migration and establishment of species in a location, they do not deny that these species interact once they are established (Nicolson and McIntosh 2002; Eliot 2011). Hence, while neo-Gleasonian ecology does not conceive ecological units as forming lineages, it nevertheless acknowledges the form of metabolic collaboration between components of ecological units whose study, as the historian of ecology Joel Hagen (1989, 1992, Chapters 4–6) highlights, is the main unifying subject of ecosystem ecology. The question, hence, is whether metabolic collaboration is sufficient for communities and ecosystems to be potential units of evolution.

The idea that natural selection can only operate on entities that form clear lineages is grounded in the classical "Tree of Life" image of evolutionary history, which states that, in the absence of extinction, species diversity increases over time and no reticulation occurs between evolutionary branches. This picture, however, has been seriously queried by researchers in the field of microbiology (e.g. Doolittle 2000; Doolittle and Bapteste 2007; Bapteste et al. 2012), where a form of reticulateness akin to the one observed at the level of communities and ecosystems by neo-Gleasonian ecologists is rampant. As noted by Bouchard (2010, pp. 623–4), this sort of reticulateness results from at least two phenomena that are widespread in the microbial world: endosymbiosis (the interdependent living of some organisms in other ones or their cells) and lateral gene transfer (the transmission of genes between phylogenetically distant organisms). These phenomena blur the Tree of Life picture in that they involve new forms of life with emergent adaptations, which evolve from exchanges between lineages, so that taking these into account turns the tree picture into that of a network. In such a network picture, genealogical patterns are only a subset of evolutionary patterns, and clear-cut lineages, when they obtain, are contingent evolutionary products rather than a necessary condition for evolution (Bapteste et al. 2012, p. 82). Proponents of the Tree of Life picture, as emphasized by Bapteste et al. (2012, p. 96) carve the biological world in a way that gives absolute (and perhaps illegitimate) ontological priority to genealogical change in monophyletic groups, and blinkers evolutionary models into ignoring natural phenomena that have deep consequences for the process of adaptation.

A similar critique of gene-centric views of adaptation has been formulated by proponents of what Gillian Barker (2008) terms "extended adaptationist" views of evolutionary change, such as niche construction theory and symbiosis research. As Barker (2008, p. 4) indicates, extended adaptationists take issue with the standard Williamsian view, according to which an adaptation in the Darwinian evolutionary sense must be the result of natural selection's effect on previous generations of an entity's lineage, and acquired by this entity through genetic inheritance. Extended adaptationists expand this view by acknowledging non-genetic means by which evolutionary entities acquire and propagate adaptations. Acknowledging the importance of these alternative means of adaptation, as noted by Bouchard (2009, 2010, 2013b, 2014), reveals a sort of clumping, similar to that observed by Bapteste and others, in the "macrobial" world. For instance, in many non-obligate symbioses, symbionts share some time of their lives but retain independent reproductive fates. In such interactions, the symbionts collaborate with each other in a way that enhances each other's ability to persist. Those interactions can thus be conceived as cases of laterally transferred adaptations (in an extended sense of *adaptation* which no longer restricts the notion to traits whose current presence is explained by past selective history, see section 4 for precisions) (Bouchard 2010, pp. 629–32, 2014, pp. 387–8). Moreover, niche construction research reveals that laterally transferred adaptations can also be acquired though interaction with abiotic structures. This research highlights that many organisms increase their chances of survival by modifying the properties of the environments they live in, or by interacting with some parts of their environment instead of others (Odling-Smee et al. 2003; Barker and Odling-Smee 2013). When these interactions increase those organisms' chances of survival and reproduction, they may be seen as involving cases of lateral adaptation transfer.

Hence, although Dupré and O'Malley (2009) retain the lineage membership criterion for evolutionary individuality, this criterion turns out not to be as inclusive as even ‘‘promiscuous’’ realists about evolutionary individuality wish it to be. Embracing the manifold variety of the biological world also requires that we assign evolutionary significance to the transient and ephemeral associations epitomized by many microbial and symbiotic entities.[6] As Bouchard (2014) argues, downplaying the lineage membership criterion significantly broadens Sober and Wilson's notion of common fate and emphasizes Dupré and O'Malley's metabolic collaboration (over lineage membership) as the key feature of evolutionary individuality. This also requires the recognition that a common fate need neither involve reproductive bondage nor engage partners "'til death do us part," and, we argue, also reinstates neo-Gleasonian (reticulately evolving) ecological entities as candidate units of natural selection. If ephemeral non-obligate symbiotic associations can be said to evolve together even when they do not beget a lineage, there is no reason why the larger-scale contingent collaboration found in neo-Gleasonian ecosystems could not as well. If this is correct, then ecosystems may be seen as evolving by natural selection even when, in conformity with the neo-Gleasonian ecological picture, they acquire their functional components laterally, that is, even when the traits of the components which have current functional roles in an ecosystem have evolved before that ecosystem was formed. Admittedly, this extended notion of common fate and the associated argument that ecosystems may evolve do not, in themselves, constitute a full defense of our proposal to define ecological functions in relation to ecosystem evolution. The next section will supplement this argument by highlighting some of the payoffs of our proposal, with respect to the unification of ecology and evolutionary biology sought by many ecologists and BEF researchers.

4. Ecological functions as forward-looking adaptations

Behind Blandin and Lamotte's and earlier ecologists' co-evolutionary accounts of ecosystem evolution lies the assumption that the ecosystem-level functional organization requires that the functions performed by the organisms involved should be intrinsic evolved properties of those organisms. It requires that the ecological functions of species be ingrained in their intrinsic natures by natural selection, so that they can be said to perform their function *for the sake of the ecosystems* they are part of. Thus, for these authors, the concept of function is tied to the classical Williamsian concept of adaptation which, as Robert Brandon (2013, pp. 100–1) notes, restricts the notion to traits whose current presence is explained by past selective history (see also Brandon 1990, section 1.7). But as we have seen in section 1, functions in ecology are conceived as relational and contextual rather than intrinsic evolved properties. Therefore, functions in ecology, although they, as we argued, have evolutionary underpinnings, are tied to what Brandon (2013, pp. 100–1) identifies as the ahistorical concept of adaptation, which refers to traits that contribute to the current fitness of an entity in its present environmental context. Hence, our proposal turns on its head the usual (i.e. Williamsian) understanding of the explanatory link between function ascriptions and adaptations. Ever since the neo-Darwinian synthesis, many evolutionary biologists take the concept of adaptation to be more fundamental than the notion of function; as a result, stories about adaptations are what informs function ascriptions (whence the SE account of function). In our proposal, since ecological functions typically are relational properties that their bearers would cease to have if their ecological context were to change, this explanatory relation is reversed: the understanding of functional roles, conceived as contributions of the parts to an entity's metabolic collaboration, is what informs statements about adaptations. In other words, the fitness of an entity, understood as a propensity (S. K. Mills and Beatty 1979; Brandon 1990, section 1.5), can be assessed by looking at how well its parts contribute functionally to the entity's ability to persist (even though the goal of propensity interpretations of fitness was not to provide an account of function). One could see our approach to fitness assessment as an extension of the ecological interpretation of the propensity theory of fitness, which, as many have argued (e.g. Bouchard and Rosenberg 2004; Rosenberg and Bouchard 2005; Sterelny 2005), is necessary to make the concept explanatory. It gives explanatory priority to ecological considerations about how an entity manages to persist, over evolutionary-historical ones about how its parts have come to acquire the adaptive traits they have.

Reversing the explanatory link between functions and adaptations provides theoretical grounds for the notion of lateral adaptation transfer between evolutionary entities introduced in section 3 in relation to extended adaptationist evolutionary approaches (Barker 2008; Bouchard 2010; Barker and Odling-Smee 2013). Among the genes that are laterally transferred between microbes, the symbionts that move between symbiotic entities, and the environments that organisms choose to live in, some, as we have argued, generate adaptations in the extended sense. What distinguishes those adaptations (in the ahistorical sense) from non-adaptive acquired traits is the former's functional character. Under the ecological interpretation of the propensity theory of fitness, a trait increases the fitness of an entity insofar as it contributes to that entity's ability to persist in the face of the challenges posed by its environment. Hence, under this interpretation, a trait of an entity's component which bears a function with respect to that entity's continued integrated operating (or to revert to O'Malley and Dupré, an entity's metabolism) constitutes an adaptation for that entity. Adaptations at the ecosystem level can be understood in a similar way. Among the constituting species of an ecosystem, those whose traits have positive effects on the ecosystem's ability to maintain the metabolic collaboration of its components in the face of environmental challenges (e.g. invasive species, perturbations) can be said to have functions in the ecosystem. The acquisition of these traits by the ecosystem can thus be conceived of as a form of laterally transferred adaptation. An important upshot of this relational understanding of ecological functions is that a species may have a function in an ecosystem without having evolved its functional traits *for the sake of the ecosystem's persistence*. As Brandon (2013, p. 101) notes, the ahistorical concept of adaptation includes what Stephen J. Gould and Elisabeth Vrba (1982) insisted on calling "exaptations" rather than "adaptations," which for them includes only the historical sense. Exaptations, as Gould and Vrba define the term, involve traits that serve some current functions but have not evolved for this purpose, and happen to serve their current function by chance or by being co-opted for a new use (e.g. feathers were most plausibly not originally selected for their aerodynamic effects but for thermoregulation, and were then co-opted for flight by early flying dinosaurs). Although, like Brandon, we do not think it necessary to adopt Gould and Vrba's term, we emphasize the evolutionary significance of the kind of functional co-optation it denotes.[7]

Acknowledging the evolutionary importance of these co-optations explains how new functions and adaptations (in the relational sense) can emerge through lateral transfer, as is the case for ecosystems. Ecological functions, as characterized by the PEP account, can emerge as relational properties through co-optation episodes similar to those described by Gould and Vrba. Typical Gleasonian immigration events, where a species establishes in an ecosystem and some of its traits, which did not evolve for the ecosystem's benefit, happen to increase that ecosystem's ability to maintain itself, constitute such episodes. Similarly to feathers in Gould and Vrba's case of early flying dinosaurs, an immigrating species acquires its ecological function by being co-opted in the ecosystem's evolution. Moreover, similarly to the evolution of lineages of organisms, which, as we have seen, can often involve the functional use of non-living components of the organisms' environment, the evolution of ecosystems can, as we shall see below, also involve the co-optation of *abiotic* features of the ecosystems' environment (like disturbance regimes and habitat heterogeneity). Neither for organisms nor for ecosystems, of course, should the intentional connotations of the term "co-opted" be understood as more than metaphorical.

The reversal of the explanatory relationship between functions and adaptation dovetails with Arno Wouters's (2003) response to an objection raised by Ruth Millikan (1989b) regarding the counterfactual references made by SEP accounts of function to the fitness value an entity *would* *have* if it had not had one of its alleged fitness-enhancing trait. As Millikan (1989b, p. 174) objects: "But exactly in this sort of context counterfactuals are most notoriously indeterminate in truth value. If a given individual with a certain trait were not to have it, what would this individual have instead? There is no such thing, for example, as being simply not monogamous." Wouters notes, in response, that the kind of counterfactual comparisons derided by Millikan are in fact commonplace in biology, and reports how biologists ground such comparisons in specific empirical knowledge about the life-styles of the studied species and the specific environmental challenges that they face. Thus for Wouters (2003, p. 656), "[t]he solution is to relativize advantages to a well-specified counterfactual situation, not to deny counterfactual comparison as such" (see also his recent Wouters 2013 where some of these arguments are further developed). This solution comports with Bigelow and Pargetter's (1987, p. 190) own understanding of the propensity notion of fitness as a property which "supervenes on the morphological characters of the individual (or species)." To view functions as explaining adaptations, rather than the other way round, allows our PEP account to escape a similar counterfactuals objection applied at the ecosystem level. A central motivation for the notion of functional diversity in BEF research is the aim of formulating counterfactual comparisons about how an ecosystem's performance and resilience would be affected if some species were added or removed. BEF researchers, using insights from complex adaptive systems theory, have made impressive progress in this direction (more on this below). Hence, presumably, as BEF research progresses, the fitness (resilience) of ecosystems will become even less counterfactually intractable.

As to how it accommodates the use of functional language by ecologists, our PEP account offers something of a middle way between Maclaurin and Sterelny's (2008) and Odenbaugh's (2010) too liberal Cumminsian accounts, and Nunes-Neto et al.'s (2014) recently proposed organizational account, which, as we shall now argue, is too restrictive to accommodate current ecological theories. Nunes-Neto et al's account is derived from Mossio, Saborido, & Moreno's (2009) *organizational theory of functions*, also often called the *systems account of functions* (see also Schlosser 1998; McLaughlin 2001; Christensen and Bickhard 2002; Saborido et al. 2011). This theory, in Mossio et al.'s version, states that traits have functions relative to what its proponents call the *organizational closure* of a system, which is a causal loop that occurs when the parts of a far-from-equilibrium system contribute to its self-maintenance, and the system, in turn, maintains those parts. While Nunes-Neto et al.'s account focuses on self-maintenance, and so presumably shares our account's focus on resilience and the collaboration of ecosystem components into a persisting whole, their account's adoption of the closure criterion makes it more restrictive than ours. This increased restrictiveness, as we shall see, renders it unable to accommodate some key aspects of contemporary ecology and BEF research. First, compared to the organizational theory, our PEP account accommodates better the role that BEF researchers attribute to biodiversity for the resilience of ecosystems. As noted by Nunes-Neto et al. (2014, p. 126; see also Nunes-Neto, Do Carmo, et al. 2013, p. 23) themselves, BEF researchers assign functions to both biodiversity as a whole and items of biodiversity. The former, however, cannot be accommodated by the organizational account. Indeed, biodiversity in an ecosystem, rather than being maintained by the system itself, is in large part the result of species-level evolution and contingent factors like the immigration of species from the ecosystem's regional species pool (Whittaker and Woodwell 1972; Levin 1999, chap. 7). Hence, in order to make their account plausible, Nunes-Neto et al. must adopt a revisionist stance with respect to BEF researchers' attribution of functions to biodiversity itself. Accordingly, they downplay biodiversity itself as a possible bearer of function (see Nunes-Neto et al. 2014, p. 126n2; Nunes-Neto, Do Carmo, et al. 2013, pp. 23–4).

This move is problematic, however, since according to the most promising models elaborated by BEF researchers, it is often biodiversity as a whole, rather than specific items of it, that promotes the maintenance and resilience of ecosystem properties. As Sterelny (2005, pp. 323–7) summarizes, two main mechanisms by which diversity enhances the resilience of ecosystems have been identified: the "sampling effect" and the "compensation effect," among which the latter is a collective effect of biodiversity (for detailed surveys on the diversity-stability relationship, see also Ives 2005; McCann 2005; and Mikkelson 2009). The former attributes the increased resilience of species-rich ecosystems to the statistical fact that they have more chances to contain species whose functional performance will remain unaffected by a given environmental variation. In this case, the positive link between diversity and the stability of ecosystem functioning can be seen as a statistical (non-causal) correlation, and the causal contribution to ecosystem maintenance can be attributed to the specific items of biodiversity rather than to biodiversity as a whole. The compensation effect, however, attributes the increased resilience of species-rich ecosystems to a particular kind of biodiversity: response diversity. The key idea is that the presence of many species which are different in the way that they respond to environmental variation, but are able to perform similar functional roles in an ecosystem, generates a compensatory dynamics between species. When an ecosystem's environment varies in such a way that a formerly dominant species decreases in abundance, a species which is functionally equivalent but different in the way it responds to the new environmental condition can compensate for the first species' decrease in functional performance. This sort of compensation reduces the likelihood that environmental variations will lead to the complete interruption of some functional performance. This idea was explored and developed both by researchers on the diversity-stability relationship (e.g. Tilman 1999; Lehman and Tilman 2000) and by complex adaptive systems theorists (e.g. Folke et al. 2004; Mori et al. 2013), and was integrated by BEF researchers in their theoretical framework (e.g. Naeem 1998; Norberg et al. 2001; Loreau et al. 2002; Loreau 2010b, chap. 5). So, although Nunes-Neto et al. are right that a division of labor occurs in ecosystems, such that many *items* of biodiversity make specific contributions to the overall functioning of an ecosystem, the collective stabilizing function of response biodiversity should not be left out of an adequate account of ecological function. In contrast to the organizational account, our PEP account can accommodate the ecological function of diversity simply by acknowledging the mechanisms by which diversity promotes the ability of ecosystems to persist through responding adaptively to perturbations. Hence, with respect to the collective function of response biodiversity, our PEP account accommodates ecologists' use of functional language better than the organizational one.[8]

Second, our PEP account accommodates better than the organizational one the ascription of functions to abiotic components of ecosystems. This makes our account more compatible with "non-equilibrium" approaches to ecology, and their observation that many populations in ecosystems are maintained by abiotic factors like disturbance regimes and habitat heterogeneity (Pickett and White 1985; Pickett and Ostfeld 1995; Pickett et al. 1999; White et al. 1999). The classical equilibrium or balance of nature ecological perspective focuses on biotic processes like competition and predation, which are deemed to be the main factors regulating the abundance of populations and the structure of communities (see Cooper 2003, chap. 3). This perspective fits well with Nunes-Neto et al.'s closure criterion, since it pictures populations as both contributing to the maintenance of the ecosystem through competition and predation, and maintained by these very processes. The closure criterion, however, is not met in the occurrence of non-equilibrium ecological dynamics in which populations are determined by abiotic factors, since those factors are usually not maintained by the ecosystems they affect. Odenbaugh (2010, p. 251) argues, convincingly we think, that if some abiotic process has the same effect on an ecosystem as a biotic process to which an ecological function is ascribed (e.g. the fixation of nitrogen by lightning and volcanoes), those abiotic processes should be ascribed a function as well.

The study of abiotic disturbances by non-equilibrium ecologists reveals that cases of abiotic contributions to ecosystem maintenance are anything but exceptional. Perhaps the most documented case is the role of fires in many forest ecosystems. Fires play a key role in those ecosystems due to the fact that some of their dominant species can reestablish only when fire opens them some access to light in the canopy and when sufficient heat allows their cones to burst and disperse their seeds (Gauthier et al. 1996; Schwilk and Ackerly 2001). The fact that such fires are often conceived as "keystone disturbances" (Keane et al. 2002; Brown and Cook 2006) by analogy with the concept of *keystone species*, and that keystone species are paradigm cases of ecological function bearers, suggests we should assign functions to fires in those forest ecosystems. Moreover, that the contribution of abiotic disturbances to the maintenance of ecosystems is a wide-spread phenomenon is indicated by the *intermediate disturbance hypothesis* put forth by many ecologists (Grime 1973; Connell 1978; Huston 1979; Biswas and Mallik 2010). This hypothesis states that the occurrence of disturbances of moderate intensity at moderate frequency often favors biodiversity in ecosystems by preventing the competitive exclusion of many species occupying similar niches. By thus mitigating the effect of competitive exclusion, moderate disturbances contribute to maintaining many species in ecosystems, some of which presumably assume functional roles. Such indirect maintenance of species is akin to the effect of keystone predators in many ecosystems, which, by controlling the abundance of many populations, prevent them from becoming invasive and competitively excluding other populations (Paine 1966, 1995; L. S. Mills et al. 1993). Again, the fact that keystone predators (a paradigm case of keystone species) are typical cases of ecological function bearers suggests we should assign functions to moderate disturbances in many ecosystems. Yet, since forest fires and other disturbance regimes are, in many cases, not themselves maintained by the ecosystems that they affect, they lie outside those ecosystems' closure as defined by organizational theorists, and so cannot be ascribed functions according to their theory.

Here, proponents of the organizational theory may object that at least some disturbance regimes are in fact under biotic control. For instance, ecologists have observed that some fire-adapted species have traits that promote flammability and, by this means, influence the frequency of fires (Mutch 1970; Schwilk and Ackerly 2001). Thus, the organizational theorist may attempt to argue that only disturbances that are under biotic control can legitimately be assigned ecological functions, and that disturbances that are not should instead be interpreted as external features constraining an ecosystem from the outside. This move, however, would run counter to the tendency in contemporary ecosystem ecology to include disturbance regimes into the dynamic of ecosystems irrespective of whether they are under biotic control, in part because of the epistemic difficulty of determining whether they are, and because many of them are most probably on a continuum between being biotically controlled and uncontrolled (Pickett and White 1985, pp. 8–9).[9] Moreover, this move seems even more problematic with regard to another important case of contributions to ecosystem maintenance by components that defy the closure criterion. This case originates from a phenomenon often called *source-sink dynamics* (Amarasekare and Nisbet 2001; Loreau et al. 2003), which involves the migration of organisms between ecosystems that are relatively isolated by the heterogeneity of their environment. These dynamics explain the maintenance of many "sink" populations, that is, populations which would run extinct if not kept afloat by constant immigration from "source" populations, as well as the maintenance of many "source" populations, whose abundance would often inflate considerably if not relieved by emigration to "sink" populations. The effects of source-sink dynamics are in fact often indistinguishable from those of more conventional density-dependent regulative processes (see Sterelny 2006, pp. 219–20 for a discussion), which, as we mentioned, meet the closure criterion, and so would warrant ecological function ascriptions according to the organizational theory. This makes a case for assigning ecological functions to source and sink populations regardless of the fact that they lie outside of the organizational closure of the ecosystems to which they contribute.

Hence, given the inability of the organizational account to assign ecological functions to response diversity as a whole, to ecological disturbances and to source and sink populations, despite their obvious contributions to the functioning of many ecosystems, we think that our PEP account is more appropriate for ecological contexts. By focusing on how some components, be they biotic or abiotic, contribute to an ecosystem's resilience without imposing any requirement as to how these components themselves are maintained, our PEP account accommodates the use of functional language by ecologists better than the organizational one.

Admittedly, not all versions of the organizational theory of functions are as restrictive as Mossio et al.'s (2009) one, on which Nunes-Neto et al.'s (2014) account of ecological functions is based. For instance, Wayne Christensen and Mark Bickhard (2002, pp. 24–5), who defend an account similar to Mossio et al.'s, seem willing to conceive as a matter of degrees the kind of autonomy achieved through what Mossio et al. call the organizational closure of a system. This would presumably make Christensen and Bickhard's account more easily applicable to ecological contexts.[10] Moreover, as we already mentioned, some essential tenets of our proposal to define functions as contribution to persistence could be adopted even while denying the evolutionary significance of such contributions. Hence, what ultimately warrants the adoption of our evolutionary forward-looking account over non-evolutionary alternatives is its payoff with regard to BEF researchers' and other ecologists' aim to reconcile the perspectives of ecology and evolutionary biology. In other words, besides navigating better than the alternative CR and organizational accounts of functions between the Scylla of excessive liberality and the Charybdis of unnecessary restrictiveness, our account, by building a conceptual bridge between the concept of resilience studied in complex adaptive systems theory and the evolutionary concept of fitness, also broadens the scope of the reconciliation of ecosystem ecology and evolutionary biology sought by BEF researchers and many ecologists.

BEF researchers who have integrated the insights of complex adaptive systems theory have themselves noted the close resemblance between their account of the biodiversity-resilience relationship and the process of natural selection (e.g. Loreau 2000, p. 14; Loreau et al. 2002, p. 83; Loreau 2010a, p. 52, 2010b, p. 234; Norberg et al. 2001, p. 11376; Norberg 2004, p. 1270). Central to this resemblance is the role of species diversity, maintained mainly through migrations between communities, which mimics the adaptive role of allele variation in species evolution, and implies that species which migrate in a location form with their environments more or less resilient assemblages that persist differentially from one another. Hence, our PEP account of ecological functions allows the reconciliation of two apparently conflicting aims of complex adaptive systems theorists and BEF researchers. It allows the disassociation of their models from group selection ones—which focus on explaining how the components of ecosystems can evolve traits for the sake of their benefit for ecosystems—while at the same time providing theoretical grounds for their idea that complex systems can be genuine bearers of adaptations. If, as we argued, functions, and therefore adaptations, can be transferred laterally between evolutionary entities, then complex ecological systems can legitimately be conceived to respond adaptively to the environmental challenges they face, even when they mainly do so by co-opting the traits of their components rather than by constraining those components into evolving traits which serve their higher-level advantage. In other words, according to the broadened view of evolution introduced in section 3, a common fate need not imply common goals, and so a species may collaborate in an ecosystem even while it still pursues its individual evolutionary interest.

The broad scope of the reconciliation between ecosystem ecology and evolutionary biology offered by our PEP account of ecological function can be made salient by recalling Robert D. Holt's (1995, p. 278) early remark on the limited prospects for such reconciliation:

> There are some clear circumstances when evolutionary perspectives would not appear to be very useful [in ecosystem studies]. For instance, if a community were comprised of species assembled hodge-podge, without prior contact (as on some islands heavily disturbed by humans), a purely phenetic approach would seem to suffice. As a second example, if an organism is an ecological engineer […] but experiences little or no feedback from its effects on the ecosystem to its own fitness, there would be a decoupling of ecosystem effect from organismal fitness (in contrast to, say, nutrient uptake).

Our account indicates that decoupling ecosystem effects from *organismal* fitness need not entail any dissociation whatsoever of ecosystem effects from ecosystem-level evolutionary considerations. If, as we argued, the evolutionary play includes adaptive phenomena at many levels of organization where adaptations at one level need not be correlated to adaptations at other ones, then a component of an ecosystem may, in taking on a role in an ecological context, acquire an adaptive function in an ecosystem without being itself changed from that role-taking by a downward effect of the selection occurring at the ecosystem-level.

Conclusion

We argued for a Persistence Enhancing Propensity (PEP) account of ecological functions which links ecosystem studies and BEF research to a persistence-based account of ecosystem evolution. We showed in section 2 that the function concept used in ecology refers to a relational and contextual property, rather than an intrinsic evolved one as in the SE theory of function. We argued, moreover, that Maclaurin and Sterelny's (2008) and Odenbaugh's (2010) proposal to interpret ecological functions in terms of the CR theory of function stands in tension with the focus of many BEF researchers on the relationship between biodiversity and the resilience of ecosystems, and with their and many ecologists' willingness to bridge the historical gap between ecosystem ecology and evolutionary biology. In section 3, we showed that a persistence-based account of evolution that abandons reproduction and lineage formations as conditions for natural selection is necessary to encompass the evolution of several biological entities, and explained how it renders the evolution of communities and ecosystems more easily conceivable than more orthodox accounts. And finally, in section 4, we linked the notion of ecological functions as relational properties, introduced in section 1, to Brandon's (1990, 2013) ahistorical notion of adaptedness. This allowed us to show how our account better accommodates the use of functional language by BEF researchers and ecologists in general than alternative accounts, and how it offers a profitable conceptual contribution to the synthesis of ecosystem ecology and evolutionary biology sought by BEF researchers and many other ecologists.

Three important issues have however not been undertaken in the above discussion. Although the full treatment of these issues will have to be deferred to a later occasion, we would nevertheless like to ease some of the worries they may raise by concluding with some hints at how we think they might be tackled. The first one is the issue of the normativity of ecological functions according to our account, and its ability to ground a notion of ecological *dysfunction*. Although generating normativity has not been the purpose of all the proposed theories of function, this issue seems particularly crucial in the case of functions in ecology, given the importance that such normativity may have for environmental conservation. In line with our observation in section 1 that functions in ecology are *relational* rather than *intrinsic* properties, we think that notions of ecological dysfunctions should also be understood relationally. On such an understanding, an ecological item cannot be *in itself* dysfunctional, but can only be so relative to its detrimental effect on the overall functioning of the ecosystem it is part of. This departs considerably from the way normativity has been approached in SE accounts, and so would require some further elaboration in order to show how this would apply in ecological contexts; nonetheless, some promising resources for doing so can be found in Christensen and Bickhard (2002) and Ulrich Krohs (2010). Note that although, as we argued, ecological functions are to be defined as contributions to ecosystem persistence, we leave the possibility open that dimensions other than persistence may have to be considered in a full-fledged account of the ecological function/dysfunction contrast which can adequately inform environmental conservation.

A second issue, which follows from our adoption of the forward-looking approach to functions, is that of the reference environment relative to which the fitness (resilience) of ecosystems is to be assessed. In the same way as to be fit in the usual Darwinian sense is to be fit to some particular environment (see Brandon 1990), to be resilient, as some resilience theorists have emphasized (e.g. Carpenter et al. 2001), is to be resilient to some range of background environmental variation (for no system can be resilient to everything). Hence, our PEP account faces the same issue as the standard SEP accounts, that is, that of specifying a reference environment with regard to which the functional contributions to an entity's fitness must be weighed (on this issue as it pertains to the SEP account, see Mitchell (1993), Godfrey-Smith (1994), Walsh (1996), McLaughlin (2001, chap 6), Bardon (2007) and Bertrand (2013)). In contrast to Bigelow and Pargetter (1987, p. 192), who relativize function attributions to a creature's "natural habitat," the above discussion assumed a version of the forward-looking account where the functions of ecosystem components are defined in relation to the *present* environment of an ecosystem. This is motivated in part by the fact that what ecologists seek to characterize is how an ecosystem functions in its actual context, not how it would function if placed in other background conditions. At the more theoretical level, this goes in line with the idea that fitness comparisons in the persistence account are temporal scale relative, so that two entities are compared in their potential to persist relative to a specific temporal scale, while there isn't a single temporal scale over which all fitness comparisons will be made. To be sure, this is a significant departure from Bigelow and Pargetter's initial formulation, which would require a more substantial treatment than what we can provide here.

A third issue, which raises the venerable Heraclitean problem of an entity's sameness through change, is that of the self-identity of ecosystems (see Jax et al. 1998; V. Grimm 1998; Sagoff 2003, pp. 536–9; Collier and Cumming 2011). This issue is made inescapable by the fact that all ecosystems change over time, which often makes their identity unclear. While death draws a clear contrast between many organisms' being and non-being, ecosystems typically shade gradually into new ones; no clear demarcating event signals when an ecosystem has ceased to exist. Accordingly, as Jax et al. (1998) have remarked, ecologists have elaborated a plurality of ways to define the identity of ecosystems, none of which seems to be more commanding than the others. This raises a significant issue for our account, since it emphasizes that, in the case of ecosystems, persistence may remain a non-operational concept until some identity conditions are specified: these conditions would enable one to determine, regarding a particular ecosystem change, whether the ecosystem has persisted and adapted to its new environmental conditions or whether it has collapsed and been succeeded by a new one. What gives us some hope that this issue, albeit serious, is not an insurmountable one, is the fact that it is, as noted by John Collier and Graeme Cumming (2011, p. 208) and DeLaplante and Odenbaugh (unpublished manuscript, p. 13-4), not unrelated to one that has concerned biologists and philosophers of biology regarding the biological concept of species. The problematic ontology of species and the pluralism about species concepts has not barred biology from fruitfully using species concepts and has instead prompted theoreticians to rethink those concepts. Thus, we are hopeful that some conceptual resources deployed with regard to the species concept can be fruitfully mobilized to tackle the ecosystem identity issue. More specifically, we think that the pluralism about ecosystem ontology exposed by Jax et al. (1998) and the affinities between our views on ecosystem evolution and Dupré's (1993) promiscuous realist stance regarding biological ontology invite a similar promiscuous realist treatment of this issue.

Debates about theories of function sometimes seem stale and out of touch with actual scientific concerns. Yet, despite the further elaborations that our account still obviously requires, we hope to have shown that theoretical work on the function concept is key to understanding the relation between the distinct endeavors of biological subdisciplines such as ecology and evolutionary biology.

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[1] See Cummins (1975, p. 753) for his initial formulation of the CR theory.

[2] As an anonymous referee recalled, Paul Davies's (2001, chap. 4) discussion does significant work at easing the worry of excessive liberality attached to the CR account, by restricting its application to hierarchically-organized systems. Despite this, however, Davies's reinterpretation of the CR theory would, it seems, still admit the functional ascriptions, criticized in the above paragraph, to ecological items relative to ecosystem fragilization or collapse. This, at least, is suggested by Davies's willingness to assign to the "unwieldy tusk of the narwhal whale" the function of reducing the animal's mobility, despite the presumable fact that such reduced mobility is detrimental to its survival (Davies takes this example from Mohan Matthen (1988)). Hence, Davies's revised CR account remains more liberal than would seem to be allowed by ecologists' focus on stability and resilience.

[3] Note, for precision, that on this account of fitness, the mere existence of something, although it is the *consequence* of past propensity to persist, should not be conflated with a present propensity to persist in the future.

[4] In an earlier paper, Holling (1973) simply uses *stability* to denote engineering resilience and *resilience* simpliciter to refer to ecological resilience. Other theorists denote the same distinction through a different terminology, e.g. Loreau (2010b, p. 126; Loreau et al. 2002, p. 81) and Stuart Pimm (1991, pp. 13–4), use "resilience" for what

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Holling calls *engineering* resilience and use respectively "robustness" and "persistence" for what he calls *ecological* resilience. In line with an anonymous reviewer's remark, we must point out that the difference between engineering and ecological resilience may be ultimately a matter of time-scale (see, for instance, Beatrix Beisner et al. (2003, p. 378) for remarks along these lines).

[5] Blandin (2007, pp. 44–6) himself acknowledges, that his and Lamotte's account rests on a notion of the general trajectory of ecosystems as moving from "Gleasonian" situations where interacting species contingently happen to be compatible but have not yet co-evolved, to "Darwinian" situations where co-evolution has reinforced their interdependence.

[6] An alternative way of doing this, as Godfrey-Smith (2009) suggests, is to see a broad spectrum of individuality where some are in some sense fully-fledged individuals (e.g. some Metazoans) while other individuals are much less fixed and much less formed (e.g. microbial colony) with all the rest of the spectrum occupied by individuals with different degrees of individuality. While there is appeal to this view, we aren't sure that this shading-off view will be sufficient to account for the complexity and pervasiveness of symbiotic interactions in the biological world.

[7] See Barker (2008) for an extended discussion of the notion of co-optation as it pertains to extended adaptationist research programs, and of the related concept of "biological lever" which she coins to denote cases where an organism co-opts another one by interfering with its regulatory processes. Although space does not allow us to develop on this here, the process of biological leverage should, we think, undoubtedly play a key role in an understanding of ecosystem evolution like ours.

[8] Sterelny (2005, pp. 323–7) characterizes the compensation effect as an emergent top-down effect. We do not here take a stand on emergence and top-down causation in ecology, but see Gregory Mikkelson (2004) for an insightful discussion.

[9] The epistemic difficulty identified here is similar to that identified by Amundson and Lauder's (1994) objection to the SE theory of functions, on the grounds of the epistemic difficulty of knowing sufficiently the evolutionary history of a trait to know exactly what its selected effects are.

[10] We are thankful to an anonymous referee for noticing this.

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