

Biodiversity and ecosystem functioning: an analysis of the functional discourse in contemporary ecology

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Abstract: The functional discourse is both ubiquitous and central in contemporary ecology, mainly in the context of the researches about biodiversity and ecosystem functioning, which emerged in the 1990s amidst a growing social recognition of the biodiversity crisis. However, in spite of this strong presence, the functional discourse has not been adequately investigated in ecology and many related fundamental problems remain without clear answers. Starting with this assumption, we performed a conceptual analysis of “function” in studies relating biodiversity to ecosystem properties, which allowed us to identify four salient uses of this concept and to discuss their epistemological assumptions and consequences. These four uses are associated to the entities to which function is ascribed: biodiversity, the items of biodiversity, the ecosystem as a whole, and, finally, the ecosystem as a part embedded in a larger whole.

Key-words: function, biodiversity, ecosystem, ontology

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Biodiversidade e funcionamento ecossistêmico: uma análise do discurso funcional na ecologia contemporânea

Resumo: O discurso funcional é tanto ubíquo quanto central na ecologia contemporânea, principalmente no contexto das pesquisas sobre biodiversidade e funcionamento ecossistêmico, que surgiram na década de 1990 em meio a um crescente reconhecimento social da crise da biodiversidade. No entanto, apesar desta forte presença, o discurso funcional não foi adequadamente investigado em ecologia e muitos problemas fundamentais relacionados permanecem sem respostas claras. A partir desse pressuposto, foi realizada uma análise conceitual de “função” em estudos que relacionam a biodiversidade às propriedades dos ecossistemas, o que nos permitiu identificar quatro usos mais salientes deste conceito e, também, discutir os seus pressupostos epistemológicos e consequências. Estes quatro usos estão associados às entidades a que a função é atribuída: a biodiversidade, os itens da biodiversidade, o ecossistema como um todo, e, por fim, o ecossistema como uma parte incorporada em um todo maior.

Palavras-chave: função, biodiversidade, ecossistema, ontologia

1 INTRODUCTION

Ecological science is marked by a great deal of theoretical and philosophical problems, some of which only recently discussed from the viewpoint of history, sociology, and philosophy of science. Some of these problems are linked to the very definition of the domain or general aims of ecology (e.g. Pickett, Kolasa & Jones, 2007), including the central problem of the validity and meaning of the functional language, that is, the descriptions of explanations using function or derivatives, or even, expressions of the teleological semantic domain, such as goal or purpose¹ that pervades this science² since its origins in the end of the 19th century (McIntosh, 1985, p. 69). In recent years, functional language has become even more central to ecology, in the context of the Biodiversity and Ecosystem Functioning research program (from now on, BEF). This leads us to an odd situation: while the concept of

¹ For more details about the teleological and functional language in the biological sciences, in the broad sense, see Nunes-Neto & El-Hani, 2009.

² As can be known in Jax, 2005; Nunes-Neto & El-Hani, 2006, 2011; Caponi, 2010; Nunes-Neto, Carmo & El-Hani, 2013; Nunes-Neto, Moreno & El-Hani, 2014; Cooper, El-Hani & Nunes-Neto, 2016; Dussault & Bouchard, 2016.

function is much and even increasingly used in ecology, with different meanings and theoretical or epistemological assumptions, it is rarely the object of analytical efforts that may provide it with theoretical and philosophical consistency.

In order to reach more clarity about this subject one possibility is to follow Kurt Jax's (2005) advice, building a classification system of "function" in ecology:

[...] What is urgently needed is to construct a thorough classification of different types of 'functions' and systems. For such more restricted domains of theory it is much more likely that generalizations will emerge. (Jax, 2005, p. 646)

This is a call for an ontology of ecology, concerning the functional objects and systems that matter for ecological research. Here it is important to say something about the relationship between ontology and epistemology of science. We think that one scheme about the ways that scientists use functional language (which can be, for instance, an epistemological typology) can help in the building of a clear set of phenomena that are studied by the scientists (which, in turn, is an ontology or a metaphysics). That is to say, here we do not aim at approaching the ontology or metaphysics of ecology directly. This decision follows from an important reason. The ontology or metaphysics of a given science is always assumed in dependence of a given epistemology (and, contrariwise, epistemology is also dependent on ontology, in a dialectical relationship). Methodologically, we focus, thus, on how ecologists use the concept of function and consider, then, how this generates some ontological categories (where, for instance, some items are assumed as observable, others as unobservable, yet others as parts or wholes). In sum, our intention is to clarify the ontology of the BEF by clarifying the epistemological uses of function in this research program.

With this background in mind, our goal in this paper is to analyze the uses of the concept of function by the ecologists involved in the BEF through a critical study of the literature. This literature was surveyed by means of a search for scientific papers in the SCOPUS database covering the period from 2002 to 2012, with the following combination of keywords: (Role OR Function*) AND (Biodiversity OR Diversity) AND Ecosystem*. The search resulted in 10,145 papers, from which we selected the 10 most cited papers per year. Among the

10 most cited papers, we then selected those well suited for an examination of the problem of functional language in ecology (for the list of the examined papers, see Table 1 and the marked papers in the list of references). The criteria adopted for this selection were the occurrence of several different uses of function in the paper, or the occurrence of circularities in the definition of function employed (when there was one), or a treatment of function by the authors of the paper as a self-evident concept, requiring no explanation or definition.

Table 1. List of the works submitted to the analysis, according to the first author(s) of the work, journal and year. For the complete references, see the reference list in the end of this paper.

Authors	Journal	Year
Doney, S. <i>et al.</i>	<i>Annual Review of Marine Science</i>	2012
Mace, G., Norris, K. & Fitter, A.	<i>Trends in Ecology & Evolution</i>	
Maestre, F. <i>et al.</i>	<i>Science</i>	
Cardinale, B., <i>et al.</i>	<i>American Journal of Botany</i>	2011
Estes, J., <i>et al.</i>	<i>Science</i>	
Gessner, M., <i>et al.</i>	<i>Trends in Ecology & Evolution</i>	2010
Wiens, J., <i>et al.</i>	<i>Ecology Letters</i>	
Cavender-Bares, J. <i>et al.</i>	<i>Ecology Letters</i>	2009
Sutherland, W.J., <i>et al.</i>	<i>Conservation Biology</i>	
Van Der Heijden, M., Bardgett, R. & Van Straalen, N.	<i>Ecology Letters</i>	2008
Cardinale, B. <i>et al.</i>	<i>Proceedings of the National Academy of Sciences – USA</i>	
Duffy, J. <i>et al.</i>	<i>Ecology Letters</i>	2007
Balvanera, P., <i>et al.</i>	<i>Ecology Letters</i>	
Petchey, O. & Gaston, K.	<i>Ecology Letters</i>	2006
Hughes, T. <i>et al.</i>	<i>Trends in Ecology & Evolution</i>	
Tscharntke, T. <i>et al.</i>	<i>Ecology Letters</i>	2005
Wardle, D., <i>et al.</i>	<i>Science</i>	2004
Sax, D. & Gaines, S.	<i>Trends in Ecology & Evolution</i>	2003
Lavorel, S. & Garnier, E.	<i>Functional Ecology</i>	2002
Torsvik, V. & Ovreas, L.	<i>Current Opinion in Microbiology</i>	

In order to keep clear the focus in the analysis of the literature the following guiding questions were used: (i) Is there any philosophical ground to the uses of function in the examined paper? (ii) What is the item (entity or activity) to which function is ascribed in the paper?

Based on this analysis, we searched for a general taxonomy of the uses of function in the BEF, which resulted in four salient uses. This taxonomy of the uses of function allows us to map the different objects to which function is ascribed in this research program, clarifying also the epistemological presuppositions of each use. As a consequence, it becomes more likely that generalizations regarding the uses of function by practicing ecologists emerge, as suggested by Jax (2005).

The paper is structured as follows. In the next section we will point to some reasons to perform an epistemological work on function in ecology. Then, after it, we offer a general presentation of the functional discourse in ecology and how this discourse reemerged in the BEF. In the sequence, based on the analysis of the scientific literature, we will expose the different uses of the concept of function in the BEF, with a discussion of the epistemological presuppositions assumed in each. After the presentation of our typology we discuss it in relation to other approaches found in the literature. And finally, we will advance our final remarks, pointing to perspectives for future works concerning metatheoretical analyses of the scientific practices of the BEF.

2 REASONS TO PERFORM AN EPISTEMOLOGICAL WORK ON FUNCTION IN ECOLOGY

Before proceeding directly to our object, we need to say some words about the importance of doing an epistemological work on the uses of the concept of function in ecology. Very briefly, we point to three reasons.

First, as we will show below, function is often simply taken for granted by ecologists. This implies that the current scientific debates involving notions such as function or role have problems from the very beginning, because it is not generally clear what each author means by these terms. A straightforward way to contribute to the resolution of some theoretical debates in science is to establish the meanings of the fundamental concepts as clearly as possible, and the case of functional language in ecology illustrates this. Clearly established meanings for key concepts are important because they allow us to know whether scientific debates are indeed about the same subject, and, particularly in our case, about the same use of the concept of function.

Second, as we have already pointed out elsewhere (Nunes-Neto, Carmo & El-Hani, 2013; Nunes-Neto, Moreno & El-Hani, 2014) at least one use of the concept of function plays the role of a conceptual bridge between community and ecosystem ecology, in the context of the theoretical integration proposed by the BEF. Then, to shed some light, from an epistemological point of view, on the concept of function in the BEF can contribute to the work of theoretical integration in ecology. This is important, in turn, to achieve good understanding, high predictability, and the building of consistent models (Pickett, Kolasla & Jones, 2007).

Third, there is a relevant link between function and environmental or ecosystem services, which directly points to the implications of the epistemological work to ethical and political issues and the management of natural resources or processes. For instance, Loreau (2010) pointed to one articulation between functions and services (see also De Groot, Wilson & Boumans, 2002):

[...] *services are derived from the normal functioning of ecosystems*, raising the important question of whether impoverished ecosystems may in some way *function* less efficiently than the more species-rich systems from which they are derived, and hence gradually lose their ability to deliver ecosystem services to human societies (Loreau, 2010, p. 51, emphasis added).

Notice that, as Loreau puts it, the services are derived from the “normal functioning of ecosystems”. Therefore, if we have to understand what are the services, the way they can or should be classified, measured and conserved, or even whether or not the jump from function to service is a well justified one from the point of view of environmental ethics (Luck *et al.*, 2012; Jax *et al.*, 2013) we should know beforehand *what function is*. However, function is simply taken for granted by Loreau in his paper, as well as in most of the contemporary ecological literature.

Besides these reasons, we should notice that the lack of clarity concerning central concepts in ecology is not restricted at all to function, but is also important in other closely related concepts, mainly in the BEF, such as “biodiversity” (Oksanen & Pietarinen, 2004) and “ecosystem” (Jax, 2007), both with serious scientific and social implications. Unsurprisingly, the need of conceptual clarity is in general recognized

by the very community of ecologists, which has taken advantage of the contributions from the philosophy of science (Pickett, Kolasa & Jones, 2007). As Naeem once suggested,

[...] the history and philosophy of ecology are as important to its development and progress as advances in natural history, technology, mathematics, modeling, experiments, and statistics. (Naeem, 2002, p. 1539)

But, despite this attention to philosophical studies related to ecology, the same is not true with regard to the uses of function in the BEF, which received much less philosophical attention than other problems such as, say, the nature of laws or generalizations in ecological science (Cooper, 1998).

3 FUNCTION IN ECOLOGICAL THOUGHT: FROM CLEMENTS TO THE BEF

In general, functional explanations (explanations that appeal to some notion of biological function, role or goal) or functional ascriptions (statements that ascribe function to some object or activity) are very common in ecology, as we can deduce from a brief analysis of the works of influential scientists, associated to different approaches within this discipline (Frederic Clements, [1916], 2000; Charles Elton, 1927; Eugene Odum, 1988, among others).

One hundred years ago, Clements ([1916], 2000) already used a functional language in his superorganismic perspective on the transformation of the vegetation. For him, the only adequate view of the vegetation was one that treated it as a complex organism (Clements [1916], 2000, p. 35). He advanced a strong analogy between ecological succession and the development of an organism, with functions being performed by the components of the plant community (analogically to organismic functions).

Another ecologist who used functional discourse was Charles Elton (1927) through his notion of functional niche. It was in the Odum brothers' ecosystem approach, however, that the notion of function became more salient in ecology. In the fifth edition of *Fundamentals of Ecology*, one of the classic texts for the ecosystem approach to ecological systems (the first edition was written by the Odum brothers in

1953), Odum & Barrett (2005, p. 2) offer the very definition of the science of ecology in functional terms.

Although these authors are not the only ones that use a functional discourse in the context of ecology, they are representative of different perspectives in this science, some more mainstream, others more marginal or outdated. Anyway, it is implicitly shared by them that the ascription of function to components of ecological systems (say, organisms, the plant community, etc.) is an important part of ecological explanations. Caponi (2010, p. 350) goes even further, holding that the main cognitive goal of ecology is to explain how some processes and regimes of order of the biosphere can be maintained, despite their relatively high improbability. According to him, the functional analyses of ecological systems are performed by ecologists in order to show how a given continuous maintenance of the improbable is kept in these systems, by analyzing the systemic capacities exhibited by them in terms of the causal contributions (the functions) of their component parts.

Despite the relevance of functional discourse since the early days of ecological research and its influential use in ecosystem ecology, it was only around the beginnings of the 1990s that function arose as a much stronger element in ecological discourse. It is worth noticing that in this reappearance the notion of function is detached from a strong organicist thought such as that found in Clements' ideas, for instance. In other words, while for Clements the concept of function was to be understood in a strong analogy with the individual organism, which by the way is a result of a process of design (natural selection), in the new context, this analogy – if present – is much softer or even irrelevant.

More precisely, this recent (re)appearance is closely linked to the notion of biodiversity. Then, in order to clarify the current place of function in ecology we have to examine some problems in the traditional conception of biodiversity. Traditionally, biodiversity is conceived as variety of species (Magurran, 2004), more precisely, as richness and abundance of species (Hubbel, 2001). These definitions generate, however, some ambiguities and inaccuracies, as discussed in the contemporary literature (Tilman & Lehman, 2002).

For instance, imagine two ecological communities, A and B. While A is composed by three species of bees of the same genus, B is composed by one species of bee, one of an ant and a third one of a spider.

Consider, also, that the three species in A and B have the same relative abundances. Then, if we apply the traditional notion of biodiversity as richness and abundance of species, formalized in an index like Shannon's, we will obtain exactly the same value for both communities. But this is a very counterintuitive conclusion, since in their dynamics the communities are indeed very different. On the one hand, community A is composed by functionally equivalent species, that is, different species performing one and the same function. On the other hand, community B includes species that are not functionally equivalent and, therefore, can present a larger variety of functions compared to A.

These diverging features in the composition and biodiversity of the two communities can result in very different performances of the ecological systems at stake. Thus, we can say, following Tilman & Lehman (2002) among others, that a concept of biodiversity as richness and abundance of species as well as the application of an index such as Shannon's – compatible with that definition – result in an ambiguity concerning the understanding of the ecological dynamics or operation of the ecosystem. In other words, the physical conception and measure of biodiversity (richness and abundance of species, mathematically measured in Shannon's index, for instance) is ambiguous to provide per se a good, sophisticated, and adequate understanding of the ecological *explanandum* (that is, the fact to the explained). The mere counting of species and relative abundances, and the application of an index that measures a physical variable (entropy) taken as a proxy for biodiversity, cannot adequately grasp the degree of differences among the species, as well as the organization of the ecological systems (conceived as the way that parts interact within them and the resulting order at the level of the whole). In order to properly understand what is happening in the ecological systems at stake we need an ecological discourse which employs a functional conception or point of view on these systems. The traditional, narrow conception of biodiversity (and the measures derived from it) neglects the existence and relevance of functions (Naeem, 2002). That is, it neglects the activities or roles performed by the species in the ecosystems of which they are part and, as a consequence, also their contributions to some properties of the ecosystems, such as decomposition of organic matter and primary productivity.

We are not claiming, however, that the definition of biodiversity as richness and abundance of species is not useful at all. Despite all the problems presented by it, it is still a very operational concept. We should not stop using it in our efforts to describe, understand, and protect ecological systems. Rather, the point is that this concept is not enough if we want to understand in a deeper way the dynamics and organization of the ecological systems. In sum, it is necessary to broaden the repertoire of definitions and measures of biodiversity, and functional discourse plays an important role in this broadening of our conceptions of biodiversity.

Around the beginnings of the 1990s, the limitations of the conception of biodiversity as richness and abundance of species showed the need of a more systemic and dynamic approach for a proper understanding of ecological systems. This approach was taken as a way to better account for the complexity of ecological systems, as a requisite, among other things, to build more precise and consistent conservation strategies. The BEF then emerged as an answer to this double challenge, in both scientific and practical sides (Naeem, 2002; Loreau, 2010).

As part of its scientific agenda, the BEF explicitly seeks to integrate ecosystem ecology to community ecology. These two ecological fields have been historically separated – in methods, terminology, and ontology (Pickett, Kolasa & Jones, 2007; Loreau, 2010; Nunes-Neto, Carmo & El-Hani 2013; Nunes-Neto, Moreno & El-Hani, 2014) – and are conceived in the BEF, instead, as parts of an integral and integrated science of ecology. Both traditions deal with central questions for the understanding of ecological systems, but which were approached by theories and models in isolation until very recently. On the one hand, community ecology has studied the biological interactions, and the biodiversity and distribution of organisms in space and time. On the other, ecosystem ecology has studied the flows of matter and energy in ecological systems, typically representing organisms as black boxes in the modeling (Naeem, 2002, p. 1547). This large integration in ecological science is only at the beginnings, as pointed out by Loreau (2010, p. 55). Not surprisingly, as any great synthesis in science, decades, not years, are necessary in order to build strongly integrated knowledge

(see, for instance, the time for building the synthetic theory of evolution from around the 1920s to the 1950s; see Mayr & Provine, 1980).

In this integration between two major ecological fields the concept of function has a fundamental role to play, although this is not adequately acknowledged in the present day (an exception is in Petchey & Gaston, 2006, pp. 750-752). At least one use of the term “function” plays the role of a conceptual bridge in the BEF. More precisely, the ascription of function to the biodiversity or to its components (such as the traits, populations, functional groups, etc.) aims at explaining the maintenance of ecosystem properties (nutrient cycling, primary productivity, resistance to invasions, etc.). To put it differently (see, for example, Loreau, 2010; Mace, Norris & Fitter, 2012), the BEF recognizes that there is some functional action of the objects of community ecology (biodiversity or its components) on the object of ecosystem ecology (the flow of matter and energy). As Petchey and Gaston (2006) put it:

[...] functional diversity is a link between species traits [community ecology] and ecosystem processes [ecosystem ecology], including evenness in its measurement forces an assumption about the relative importance for ecosystem processes of variation in traits among species and variation in their abundances. (Petchey & Gaston, 2006, p. 750)

4 IN THE BEF FUNCTION IS SAID IN FOUR WAYS

In the BEF function can be said in four ways. And this is common even inside one given paper. That is to say, the papers in the BEF literature cannot be clearly split up in different categories of uses of function. On the contrary, the uses of function discussed below typically overlap within a single work.

We can now mobilize the guiding questions presented in the introduction. The answer to the first guiding question (Is there any philosophical ground to the uses of function in the examined paper?) which emerged from the analysis of the papers is that none of them presents a philosophical ground to the uses of function. By philosophical ground here, we mean the elaboration around or even some reference or mention to the debates on theories of function from philosophy of biology. More precisely, we have in mind three large and influential

theoretical landmarks in the field: the etiological theories (Wright, 1973; Godfrey-Smith, 1993); the systemic theories (Cummins, 1975; Craver, 2001) and the organizational theories (Collier, 2000; Mossio, Saborido & Moreno, 2009)³. In sum, all the papers simply take the concept of function for granted, although some define it in connection to other concepts such as biodiversity (this is the case of Petchey & Gaston, 2006, for instance) or ecosystem (see, for instance, Sax & Gaines, 2003).

By its turn, the second guiding question (What is the item - entity or activity - to which function is ascribed in the paper?) was more crucial to our study, because it allowed us to map the different uses in the literature. In what follows we present our typology, emphasizing the second question; and in the sequence, we compare it with the typologies proposed by Jax (2005) and De Groot, Wilson & Boumans (2002). For a graphic scheme, see Figure 1, and for some direct examples, see Table 2.

4.1 The function of biodiversity: function of an unobservable entity

To consider biodiversity as a functional entity is linked to one of the central features of the BEF: this research program conceives biodiversity as a causal agent in the ecosystem, differently from the traditional knowledge in community ecology. For instance, for Mace, Norris & Fitter (2012, p. 22), “the biological composition of ecosystems, measured as biodiversity, has a key role in ecosystem service delivery”. Very often, the ascription of function to biodiversity is linked, then, to the delivery of services. In this context it is important to make a distinction between the BEF (Biodiversity and Ecosystem Functioning) and the BES (Biodiversity and Ecosystem Services) approaches, as put forward by Cardinale *et al.* (2012). While the BEF is a body of knowledge interested in the understanding of how biodiversity or its components affect ecosystem processes, the BES is more focused on the provisioning and regulating services of ecosystems (Cardinale *et al.*,

³ In other works we have elaborated a more detailed analysis of the topic from the point of view of philosophy of biology (Cooper, El-Hani & Nunes-Neto, 2016). In particular, we have developed an organizational approach to ecological functions (Nunes-Neto, Moreno & El-Hani, 2014).

2012, p. 59). Both areas use functional language, but in different contexts. This distinction helps systematizing the different domains for the uses of function (see Figure 1).

In connection with this use of function it is important to elaborate more on the ontological nature of biodiversity. First of all, we should highlight an important point: since biodiversity implies, generally speaking, variety, and also, since variety is not something observable, but only inferred (from the observation of entities or processes that vary), then, we can deduce, it cannot be an object of functional ascription in an ecological context.

We can mathematically capture variety in ecological systems, as an inferred property, through indexes such as Shannon's. The possibility that two very different ecological communities – in composition and functional aspects – show the same value for biodiversity as indicated by the Shannon's index helps supporting the idea that variety cannot be functional in the same way as the variants can. Variety is measured in numbers, and we cannot ascribe function to such entities, unless they are embedded in a sociocultural domain. This does not mean, however, that mathematical entities such as numbers show no functional roles at all, but only that the kind of function performed by such entities is not the same kind of function that interests ecologists in their work to understand ecological phenomena. Mathematical entities present functions in the context of the sociocultural human world, not in the natural world *per se*.

At the same time, notice that this indicates that biodiversity can have functions, but from another perspective. Although it cannot play functional roles in the ecological world – as an inferred, theoretical entity (for instance, Almeida & El-Hani, 2006, p. 35) – it has relevant functions in the sociocultural domain of human practices. It performs important functions, for instance, in the education of new biologists, in the education of children about environmental issues, and in the management of environmental resources, through the strategy of environmental services, for instance (Mace, Norris & Fitter, 2012). This means that biodiversity can only emerge as a legitimate object of functional ascription as an idea, what really captures the original intentions behind this concept: in 1986 when Walter Rosen coined the word “biodiversity” during the organization of a scientific and political meeting in Washington, DC, biodiversity came to the fore as a social construction, even though intended to refer to some natural phenomena by the participants (Takacs, 1996, pp. 38-39). Moreover, it emerged with a very relevant role to play in the conservation and management of resources in a world in crisis.

In order to avoid mistakes in the ascription of function to biodiversity, it is always necessary to be clear about what is the system which provides the context to the performance of the function. After all, while biodiversity is a concept to which one can ascribe a functional role in a sociocultural context, in an ecological context to ascribe function to biodiversity implies to assume that unobservable entities, which are only inferred, can have a functional action on ecosystem properties. Since ecologists usually assume that functional action is a concrete feature of ecological systems, then the functional entity should also be concrete, observable in those systems. But it is very odd to assume that biodiversity can be such a concrete entity. It is rather a theoretical entity, the reification of which is extremely problematic in both scientific and epistemological terms. It is true that in the context of ecological research biodiversity has been often reified, transformed in a material thing, a substance, but this can be regarded as a mistake of the scientific practice, an example, in ecology, of the epistemological obstacle of substantialization (Bachelard [1938], 1996).

4.2 The function of the items of biodiversity: observable entities as the objects of functional ascription

In the context of strictly ecological explanations, a legitimate locus of the functional ascriptions seems to be, very often, what we have called the items of biodiversity⁴, the entities or activities which can be biodiverse (traits, organisms, populations, guilds, functional groups, etc.). They are assumed, thus, as functional agents in an ecosystem context.

More traditionally, only species have been treated as items of biodiversity in ecology. But, since around the end of the 1980s, following the Convention on Biological Diversity (UN, 1992) and the efforts of the BEF to overcome limitations of the traditional notion of biodiversity, more items came to be considered as components of the biodiversity, resulting in a pluralism. This pluralism does not entail a denial of species as items of biodiversity, but, instead, the building of a wider perspective, encompassing more entities or activities than species only.

Indeed, species continue to be important items of biodiversity, as we can see in Gessner *et al.* (2010, p. 378): “diversity effects can only arise when species differ in their functional characteristics relevant to the studied process”. But we also find in these same authors a strong emphasis on functional effect traits, that is, phenotypic features of organisms that have implications for ecosystem processes such as decomposition (e.g. feeding preference, consumption rate, mouth part morphology, enzymatic capabilities, litter quality parameters such as C:N ratio) (*ibid.*, p. 372).

⁴ In the context of an organizational approach of ecological functions, proposed by Nunes-Neto, Moreno & El-Hani (2014, p. 132), we have defined the expression item of biodiversity as referring to “morphological or physiological traits, organisms, populations, species and functional groups”. The reference is not only to species composition, but is wider, reaching entities or activities which are considered biodiverse, in contemporary ecology, especially BEF (Naeem 2002; for a more detailed analysis see Nunes-Neto, Carmo & El-Hani, 2013). Moreover, following Cooper and colleagues (2016), it is interesting to highlight that the abstract concept of item of biodiversity can be conceived as intrinsically hierarchical and scale-free (just as the ecosystem concept), which allows a heuristically powerful flexibility in the building of hierarchical sets by biodiversity scientists (with a community composing an organism, for instance). Significantly, this is in accordance with Allen & Hoekstra’s hierarchy theory ([1992], 2015).

Guilds or functional groups also appear as relevant objects of functional ascription in the BEF:

The concomitant quantitative and comparative analyses of expressed rRNA genes and genes for key enzymes in relation to environmental factors can be used to obtain information about the phylogeny and ecology of *functional bacterial groups* responsible for processes like denitrification, nitrification and methane oxidation. (Torsvik & Ovreas, 2002, p. 241, emphasis added).

And, finally, even genes are mentioned as objects of functional ascription in the BEF:

Thus, to link microbial diversity to ecosystem function it is necessary to focus on functional traits and *functional genes* that are important for biogeochemical processes. (Van der Heijden, Bardgett & Van Straalen, 2008, p. 307, emphasis added)

Notice that function is ascribed here also to the ecosystem, pointing to a different use of the concept, and to two items of biodiversity (traits and genes).

The scope of the concept of items of biodiversity seems to be an open issue in contemporary ecology. In order to define this scope, it is necessary to explicitly take into account several factors: (i) what is the phenomena to be explained in the particular ecological context (e.g. the dynamics of the ecosystem? the occurrence, interactions or distribution of the items of biodiversity?); (ii) the particular biome under study and its geological, chemical, and physical boundary conditions (e.g. tropical megadiverse environments? Species-poor environments, such as tundras? Environments with high functional redundancy?); (iii) the pragmatic interests of the researchers at stake (e.g. explanation? Prediction? Model building? Intervention?). We think that these are only some factors to be addressed in the definition of the scope of the items of biodiversity.

4.3 Ecosystem Function/Functioning: the functions of the ecosystems as parts or the dynamics of the ecosystem as a whole?

The concept of function in the BEF is also directly linked to the ecosystem concept, which is found in the very label given to the research program (Biodiversity and Ecosystem Function / Functioning). Perhaps for this latter reason, this is a very widespread and common use. It requires, however, an important distinction. As correctly noticed by De Groot, Wilson & Boumans, there is some ambiguity in the literature concerning the understanding of what are “ecosystem functions”:

In the ecological literature, the term “ecosystem function” has been subject to various, and sometimes contradictory, interpretations. Sometimes the concept is used to describe the internal functioning of the ecosystem (e.g. maintenance of energy fluxes, nutrient (re)cycling, food-web interactions), and sometimes it relates to the benefits derived by humans from the properties and processes of ecosystems (e.g. food production and waste treatment). (De Groot, Wilson & Boumans, 2002, p. 394)⁵

We propose that these two ways of understanding the expression “ecosystem function/functioning” are connected to different hierarchical levels in which the ecosystem can be located. For this reason, in what follows, we suggest to separate these two uses.

4.3.1 *It is better to avoid talking about function when referring to the ecosystem as a whole*

The use of “ecosystem functioning” and some uses of “ecosystem functions” presuppose a hierarchical perspective on the ecosystem seen as a whole composed of parts. For instance, Naeem proposed that,

[...] physical and chemical conditions of the environment are increasingly recognized as driven, at least in part, by ecosystem function (e.g. nutrient cycling and energy flow). (Naeem, 2002, p. 1539)

When he exemplifies ecosystem function by referring to nutrient cycling and energy flow, Naeem makes it clear that he is not talking

⁵ See also Jax, 2005, p. 644 and Fisher, Turner & Morling, 2009, p. 645.

about some activity of the biota or the organisms in separate, as parts of the ecosystem, but rather about processes at the ecosystem level of organization. Another example is provided by Petchey & Gaston:

Dominance of ecological processes, such as character displacement, environmental filtering, and assembly rules [...] would lead to a weaker impact of phylogeny on community structure and *ecosystem functioning*. (Petchey & Gaston, 2006, p. 754, emphasis added)

From our point of view, in these cases, it is more adequate to talk about ecosystem dynamics, performance or operation, instead of ecosystem function/functioning, in order to avoid the conflation with the other use of function associated to the ecosystem, discussed in the following subsection.

4.3.2 *The ecosystem as part: function of the ecosystem within larger wholes*

In the second use of “ecosystem functions”, ecosystems are assumed to be functional parts within larger wholes. Mace, Norris & Fitter offer a good example in their definition of ecosystem service:

Ecosystem service: an activity or *function of an ecosystem that provides benefit (or occasionally disbenefit) to humans* [...] (Mace, Norris & Fitter, 2012, p. 19, emphasis added)

Here the authors ascribe function to the ecosystem – through the direct reference to its services – in the context of a larger system, the human socioeconomic system. Of course it could be argued that, at the scale of the biosphere, the human systems are parts of a natural system (the Earth as a whole). This is correct, but at a more local scale it is perfectly possible to assume that ecosystems are nested parts within a socioeconomic system. For instance, the ecosystems in the Brazilian Atlantic rain forest can be seen as component parts of the entire Brazilian socioeconomic system, although, of course, the whole global ecosystem cannot be contained by the Brazilian socioeconomic system. In sum, this particular use of function seems to be a legitimate one.

In this context, it is important to make a reference for a general analysis made by Cummins (1975), who argues that function is the contribution of a part to some capacity of a whole which contains it. In these terms, there is no sense in ascribing function to an uncontained system: we always ascribe function to some entity or process which is

contained within a larger whole, in order to understand the performance or dynamics of that whole. It is important to notice that, although clearly pointed by Cummins (1975), this consideration is not limited to his approach to function. Rather, it is shared by the three chief approaches to function in current philosophy of biology, the etiological, systemic and organizational. Generally speaking, to ascribe function is only meaningful if we are considering a relationship between the item of functional ascription and some whole (or some aspect of some whole), which contains the item. This can be the evolutionary lineage which contains and engenders the very item of functional ascription, for the etiological approaches (Wright, 1973); a complex capacity of the containing system, for the systemic approaches (Cummins, 1975); or the organization of the system, according to the organizational approaches (Mossio, Saborido & Moreno, 2009).

Anyway, if we assume this view about the meaningfulness of function ascriptions shared by the three chief approaches to function in philosophy of biology, we will see why to ascribe function to the ecosystem within a larger context is a legitimate use of function. At the same time we will see why it is misguided to ascribe function to the ecosystem seen as a whole. Of course, part-whole relationship is always relative, not absolute. Something is a whole or a part depending on the context into which it is embedded. But this context-dependency of the part-whole relationship is not always noticed and made explicit in the scientific discourse of the BEF, particularly concerning the ecosystem as an object of functional ascription.

In sum, it is important to notice that the concept of function cannot be legitimately used unless one specifies a containing system for the entities or activities to which one ascribes a function. Normally, ecosystem functions are thought in the context of socioeconomic systems and are mobilized in the discourse about environmental or ecosystem services. For this reason, this legitimate use of ecosystem functions is more adequate within the framework of the BES, and not so much within the BEF (see Figure 1).

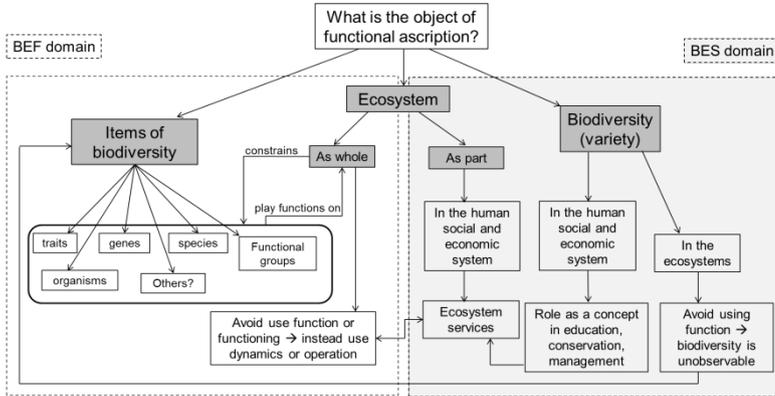


Fig. 1. Scheme for the uses of function in the BEF, according to the objects of functional ascriptions, which are represented by the darker boxes. This scheme is intended to apply to the uses of function in the BEF (Biodiversity and Ecosystem Function) and BES (Biodiversity and Ecosystem Services) approaches. The distinction between BEF and BES is due to Cardinale *et al.* (2012) and is adequate for systematizing the two larger domains, for uses of function, based on our analysis.

5 COMPARISON WITH OTHER TYPOLOGIES OF FUNCTION IN THE LITERATURE

Now it is time to compare our analysis to those put forward by De Groot, Wilson & Boumans (2002) and Jax (2005), who made important efforts for systematizing the uses of the concept of function in current ecology and ecological economics.

Let us begin with De Groot, Wilson & Boumans (2002), to whom ecosystem functions can be grouped in four categories, very briefly described as follows: (i) regulation functions: linked to the capacity of the natural and semi-natural ecosystems to regulate essential ecological processes; (ii) habitat functions: linked to the capacity of natural systems to offer refuge and reproductive conditions to plants and animals; (iii) production functions: linked mainly to primary productivity by autotrophs; and finally (iv) information functions: linked to human health, spiritual enrichment, aesthetic experience and education, for instance.

Although these authors provided a useful and influential taxonomy of ecosystem functions (which conceives ecosystems as functional parts of larger wholes), they did not provide such a classification for the broader category of ecological functions in general. This is perfectly understandable, since they speak from the field of ecological economics, where the functions that matter are primarily those performed by the ecosystems within socioeconomic contexts. But in this manner all the discussion is limited to only one item of functional ascription, the ecosystem. To put it differently, De Groot, Wilson & Boumans (2002) offer a contribution that is more suitable to the BES (and, hence, seems particularly relevant to the economic and social sciences) than to the BEF perspective (that is to say, more specifically in the context of the ecological sciences).

Jax's (2005) analysis, in turn, is more relevant for the ecological uses of the concept within the BEF and encompasses more items of functional ascription. According to him, there are four meanings of function in ecology:

[i] Function refers, in a descriptive sense, to processes and the causal relations that give rise to them, [ii] to the role of organisms within an ecological system, [iii] to the overall processes that sustain an ecological system (which together determine its "functioning") and finally [iv] to the services a system provides for humans or other organisms. (Jax, 2005, p. 646)

The first meaning is not easy to understand, at least as expressed in Jax's words. Anyway, it seems better to avoid ascribing such a meaning to function, since what seems to be at stake in this case is simply a relationship, an interaction.

The second meaning, in turn, is associated with our second use of function (function of the items of biodiversity). However, our category is broader in the sense that it includes not only organisms as possible items of functional ascription, but also other entities, such as genes, traits, and functional groups. We must remember that in the BEF – which is, by the way, taken by Jax to illustrate his scheme of classification – the items of biodiversity do not encompass only organisms or species, as traditional community ecology used to conceive, but also those other entities. As a consequence, if we want to adequately cap-

ture the uses of function in the BEF we cannot limit ourselves to organisms or species as items of biodiversity, as Jax does. It seems necessary to adopt a broader perspective, as we assume here.

Jax's third meaning is associated with our third use of function, that is, ecosystem function/functioning, which, for us, is an inadequate use of function unless we are talking about ecosystems as components of larger, containing systems, such as human socioeconomic systems. If we are talking about ecosystems themselves as containing entities, it seems more adequate to replace function by performance, dynamics or operation. Jax seems to agree with this latter point (Jax, 2005, pp. 642-644).

Finally, Jax's fourth use of function can be associated with our fourth use, that is, the function of ecosystems within larger wholes, which is more suitable to the BES, as already noticed. This is a legitimate use of function and, generally speaking, we agree with the formulation of this category in Jax's typology. However, it seems important to build a broader image of the possible systems inside which an ecosystem can be functional. Jax (2005) and, also, De Groot, Wilson & Boumans (2002) assume that the functions of ecosystems within larger wholes should be qualified as services. Although this identity between function and service is common in this particular use, it is possible (and perhaps even interesting) to conceive that an ecosystem can have a function also within an ecological (and not human) context; for instance, a function within a landscape, a biome, a larger ecosystem (since ecosystem is a scale-free concept). Again, a crucial point here is to be precise about the hierarchical context into which function is ascribed to the ecosystem, that is, we should be clear about the containing systems of which the ecosystem is taken to be a part.

Moreover, Jax's analysis does not capture the ascriptions of function to biodiversity, the first use in our typology. Although not legitimate in a strictly ecological context – according to our analysis – since the term biodiversity refers to an unobservable, this is an important use in sociocultural and socioeconomic contexts, as already noticed.

Perhaps because Jax's classification does not take into account epistemological landmarks about functional and teleological explanations (such as the long debate about function; see Wouters, 2005); it does not capture many important epistemological assumptions linked to

each use or meaning of function. Our typology, in turn, considers basic philosophical differences among the uses. For instance, it answers clearly to the following basic questions, all directly linked to the guiding question (ii), above: what is the item (entity or activity) of functional ascription?; Is the item of functional ascription an observable or unobservable?; Is the item of functional ascription seen as part or whole, in the particular functional ascription at stake?

Table 2. Some examples of functional discourse in the examined papers. The statements or expressions with a functional discourse are highlighted.

Function of biodiversity	Function of items of biodiversity	Function of Ecosystem as part	Ecosystem Function/ Functioning (as whole)
The decline of biodiversity may affect ecosystem functioning and yield [...], although the <i>functional role of biodiversity</i> is little known [...] (Tscharrntke <i>et al.</i> , 2005, p. 859, emphasis added)	Combined comparative analyses of core house-keeping genes like rDNA and <i>functional genes</i> may provide information on both phylogenetic diversity and the potential <i>functional diversity of microbial communities</i> . (Torsvik & Ovreas, 2002, p. 241, emphasis added)	Nonetheless, as the <i>benefits of ecosystem function to humans become more apparent</i> [...] and as we come to appreciate the complex, often indirect ecological effects of our activities, the conservation spotlight has shifted away from individual species (Sutherland <i>et al.</i> , 2009, p. 564, emphasis added)	<i>Ecosystem functioning is the end result</i> of the operation of multiple environmental filters in a hierarchy of scales which, by selecting individuals with appropriate responses, result in assemblages with varying trait composition (Lavorel & Garnier, 2002, p. 545, emphasis added)

Here, we have stressed scale issues and the	Fertile soils also support soil food webs in which the	[...] biodiversity does indeed regulate	Nowhere has this view been more apparent
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<p><i>functional roles of biodiversity</i> for discerning crucial components of marine resilience. (Hughes <i>et al.</i>, 2005, p. 384, emphasis added)</p>	<p><i>bacteria-based energy channel, microfauna (nematodes and protozoa), and earthworms play an important role</i> in nutrient cycling, whereas infertile soils tend to support food webs dominated by fungi and arthropods [...]. (Wardle <i>et al.</i>, 2004, p. 1631, emphasis added)</p>	<p>several processes that are essential to the functioning of <i>ecosystems</i> and that many of <i>these functions are important for humanity</i> (Cardinale <i>et al.</i>, 2011, p. 589, emphasis added)</p>	<p>than in the recent body of research addressing the ‘diversity–ecosystem function’ debate. The premise for most of this work has been to examine the consequences of declines in diversity on <i>ecosystem functioning</i>. (Sax & Gaines, 2003, p. 561, emphasis added)</p>
<p><i>The role of biodiversity</i> in buffering environmental variation and thus providing consistent service delivery has received extensive theoretical treatment (Balvanera <i>et al.</i>, 2006, pp. 1154–1155, emphasis added)</p>	<p>A consequence of this definition, one that pervades this review, is that measuring functional diversity is about measuring functional trait diversity, where <i>functional traits are components of an organism’s phenotype that influence ecosystem level processes</i>. (Petchey & Gaston 2006, p. 742, emphasis added)</p>	<p>The aggregate effect of these interactions constitutes <i>ecosystem function</i> (e.g., <i>nutrient cycling, primary and secondary productivity</i>), through which <i>ocean and coastal ecosystems provide the wealth of free natural benefits that society depends upon</i> [...] (Doney <i>et al.</i>, 2012, p. 12, emphasis added)</p>	<p>The vast majority of empirical tests of whether functional diversity informs about <i>ecosystem level functioning</i> use an <i>a priori</i> functional classification to produce functional groups. (Petchey & Gaston, 2006, p. 750–751, emphasis added)</p>

These are relevant questions for several reasons: to establish the item to which function is ascribed is a crucial point in each and every ascription of function, as stressed, for instance, by Wright (1973); to

clarify the metaphysical nature of the item of functional ascription can show misuses of the concept of function, as we argued above in relation to the ascription of function to biodiversity; and to make explicit the hierarchical position of the item avoids ambiguities in the use of functional language, as we have shown in the case of functional ascription to ecosystems.

Jax's (2005) work indeed brought important insights to a theoretical or philosophical reflection about function in ecology. As he himself noticed:

Distinguishing these meanings can increase the usefulness of terms and make the different lines of research, e.g. on biodiversity and ecosystem functioning much clearer. To bring science forward we need both a precision of data and a precision of concepts and theories. (Jax, 2005, p. 646)

Based on this backdrop, we believe, that our typology is a contribution – alongside De Groot's and Jax's – towards an ontology of ecology, concerning function.

6 FINAL REMARKS

As we discussed in this paper, in the BEF, function is commonly said in four salient ways: function of biodiversity, function of the items of biodiversity, ecosystem function/functioning (even though in this case we argue that the reference to function should be avoided), and function of ecosystems within larger wholes. Any of the proposed uses of function has each its own epistemological commitments. Even though this paper walks some steps towards the clarification of these commitments, more work on the history, sociology and epistemology of ecology is necessary to build a richer and more complete image of the uses of function in the BEF and, generally speaking, in ecology as a whole.

An important contribution highlighted here is the distinction between the BEF and the BES research programs (Cardinale *et al.*, 2012), because it allows us to map in a more consistent manner the different objects of functional ascription. Although our focus here fell on the BEF, more metatheoretical work on the uses of function in the BES needs to be done.

Generally speaking, a philosophical point of view on the objects of ecology helps in showing the importance of establishing consensus over terms, concepts, and scopes involved in the construction of theories and models in a scientific field. In this manner, philosophy can contribute to the construction of a consistent ontology for ecology, to be reached through collective works, such as those developed by Schwarz and Jax (2011). As Thomas Kuhn ([1962], 1996) and many others after him showed, scientific consensus and progress under one paradigm is only possible when the scientists working inside a scientific community accept all the same basic concepts and vocabulary, among other features. Ecology, in general, and the BEF, in particular, could benefit from efforts to generate a more consistent conceptual framework. Loreau (2010) expressed well the prospects of the BEF to integrate older traditions of ecology, such as community and ecosystem ecology, into a unified and stronger trend of research, building general consensus in spite of the divergences among the participants. Although the BEF has already reached an impressive consensus, in order to build a more unified field or a Kuhnian paradigm for ecology, much work has to be done for building a consistent ontology for this science. In the avenue towards this ontology, function is one of the concepts that require more discussion and clarification. And given the variety of uses of function, this will entail the construction of typologies such as the one presented in this paper, which should discuss also the epistemological assumptions of the functional discourse.

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