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Function and "functioning" in ecology: what does it mean?

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Many investigations in current ecological research focus on ecological functions, the functions of biodiversity, or the functioning of ecological systems. However, within ecology "function" is used in several different meanings. The most important ones are those of function as denoting either processes, roles, services or the "functioning" of whole systems. Some of these meanings pose considerable problems in terms of their ability to apply them in empirical research. These problems together with the ambiguity of the term "function" constitute considerable impediments for generalizations of research results. In order to improve this situation, the current paper describes the different meanings of "function" and discusses the requirements necessary to unambiguously apply the concept(s) in practice. This is illustrated by the example of current discussions on the "functions of biodiversity".

"Function" has become a prominent concept in ecology. Current interest in functions especially relates to the role or function of biodiversity, the analysis of ecosystem functioning, the idea of functional redundancy of species and – closely related – functional classifications (functional groups) of species. But what does "function" mean? There are strongly differing meanings and uses of "function". How can we adequately distinguish and describe these different meanings? Is the use of function concepts in ecology perhaps more a problem than a solution as it implicitly refers to teleological and normative arguments, e.g. in the notion of the "functioning" of ecosystems? A clear understanding of what function means in each particular case is necessary both for avoiding misunderstandings and wrong generalizations, as well as for applying the concept in practice. In this paper, I will try to contribute to a clarification of the different meanings which "function" has in ecology. To do so I will first introduce four different meanings of "function" and then investigate the requirements and the obstacles for implementing different notions of "function".

Four meanings of "function" in ecology

Four major uses of "function" in ecology can be distinguished:

1. First of all, in many instances "functions" denote what happens between two objects (meaning both organisms and inanimate things): a fox eats a mouse, or nutrients are assimilated by a plant. As such "function" refers to state changes in time and is a synonym for "process", or sometimes more specific for "interactions" between the objects. This use of "function" is a purely descriptive one. In many cases it also refers to the cause–effect-relations underlying these processes. Dependent on the specific task, phenomena are, therefore, either simply described as temporal sequences (without considering the specific effective causes) or they are described as causal chains (see the distinction between "pathway" and "mechanism" in Pickett et al. 1987).

2. In broadening the perspective from a single process to several ones, the specific objects (e.g. organisms) now appear in a more complex context, namely the larger systems of which they are part. The questions may here refer descriptively to the different processes and are: "what happens?", "which processes occur?", "how do organisms interact which each other and with their environment? In other cases, however, the perspective may change from a primary focus on the parts to a focus on the whole system. This implies a completely different category of questions and a different meaning of "function". The questions now are: "how does the whole 'function'?", "how is the whole sustained?", "what do specific parts contribute to this?", "which parts fulfil a particular 'function'?" As a new meaning, the "functioning" of a complex system of interactions thus comes into focus here, referring to some state or trajectory of the system under consideration and to the sum of those processes that sustain the system.

3. In focusing on the relation between parts and wholes, the status of the objects themselves changes. They are not mere "protagonists" of processes, as in the first perspective, but they have become bearers of functions. That is: they are attributed a role within the system. For example a plant is seen not just as an object assimilating nutrients by the help of solar energy, but is now perceived in the role of a primary producer within the ecosystem. It is possible here to distinguish between a function as such (the role, e.g. primary producer) and the bearer of the function, which is said to fulfil a function. Like in a theatre, the same role (e.g. Hamlet) can be played by different actors.

This meaning of function is especially important within ecology in connection with the idea of functional types and functional groups (Smith et al. 1997, Wilson 1999). On the basis of process-relevant attributes, organisms (individuals or the species they belong to) are here divided into different groups. Two major approaches towards functional groups can be distinguished: one approach is to classify organisms by their roles within a system. Examples are the classical types of "producers", "consumers" and "decomposers", the feeding types of benthic stream organisms (Cummins 1974) or the Eltonian niche (Elton 1927, p. 63., likens the niche to the "profession" of a species). In the other approach, classifications are not based on the organism's role in building the ecological system and its maintenance but refer to the strategy by which the organisms care for their own survival in the system, or under specific environmental conditions, respectively. Examples are the classical life-form types of Raunkiaer (1934), characterizing the ways in which plants survive unfavourable seasons, or the CRS-strategies of Grime (1979). This perception of "functional types" is also connected to niche concept, namely that of G. E. Hutchinson (1957, 1978), who perceived the niche, so to speak, as the "clothes" of a species in the sense of a matrix of the organism's requirements. Distinctions of this kind have been proposed by different authors (Catovsky 1998, Hooper et al. 2002, Lavorel and Garnier 2002) who used the terms "functional effect groups" und "functional response groups" for these two different types of functional groups.

4. Finally, the system is frequently extended even more by taking the relations of an ecological system to humans into focus. Here, "function" is understood as something that is attributed to a system, depending on its practical use. These "functions" mostly relate to the whole system: "a function of the ecosystem is to provide oxygen" [for humans] or: "the stream has a function of eliminating sewage through its self-purification". The word "function" here in fact denotes a particular "service" of the system for human beings. This meaning is commonly implied in the context of "ecosystem services" (Costanza et al. 1997, Daily 1997, de Groot et al. 2002). In principle, of course, such "services" can likewise be described as relating to other living beings.

The four different meanings of "function" described: functions as processes, the function(ing) of a system, functions as roles, and functions as services, are the most important ones within ecology and the environmental sciences, but by no means exhaustive. As an obvious additional meaning, function as a "mathematical function" should be mentioned.

Distinguishing between these different meanings is of much more than academic or semantic interest. Two basic problems, which influence both research on functional issues in ecology and the application thereof, underlie these distinctions. They relate to problems of how to operationalize the different function concepts and to the normative assumptions and implications which some of them contain. By "operationalize" I mean to put the concept into practice by applying it to specific empirical situations. Concepts of "function" that are operationalizable should allow one to unambiguously distinguish between those phenomena which are to be called "functions" and those which are not.

Functions as means and ends: (how) can we measure functions?

A crucial distinction within the different notions of "function" in ecology is that between (a) a perspective focused on the "performance" of specific objects (mostly organisms) within temporal sequences and/or causal chains and (b) one which asks for the role, the importance of objects for something else, in particular for a complex system. The more narrow meaning of the term "function" is used only for (b) (Hesse 2000). Problems to operationalize and thus measure functions in ecology arise if these different perspectives are confused. Also, to operationalize functions as perceived under the perspective of (b) is more difficult than for those under perspective (a).

From the theoretical and philosophical side, the purely descriptive use of function in the sense of "processes" and causal chains (i.e. perspective a) is largely unproblematic. This kind of research on "functions" is a major field since the beginnings of ecology as a science. It describes, for example, how individuals of different species interact in a lake or a forest, which trends can be found in the long-term dynamics of the different populations, the overall biomass of the system, or the flow of particular substances within it. From the technical side, such a description and analysis of "structure and function" even of very complex systems, is still a challenging and often technically difficult task.

Some additional problems, however, are connected with the second perspective (b), focusing on the "whole". This relates to questions such as how ecosystem functioning is maintained and which roles particular species (or biodiversity; below) play for this functioning, or if there are species which may be considered "redundant". A major difficulty with the application of function in this narrow sense (b) is the following. While ecology, as a natural science, normally deals with questions of how things proceed or work, and thus with means and mechanisms, the questions here is also "what for?" and thus related to ends. But ends – purposes – are normally beyond the realm of the natural sciences. The critique that arises immediately is that we are posing a teleological question or even one of sense, of meaning. So, are questions about the role of a particular species within the ecosystem and about the "functioning" of whole systems unscientific?

The problem as such – concern about "what for?" or even "why?" questions, and thus about teleological assumptions within biology – is not new. Especially in connection with evolutionary theory and organismic biology, it has fostered a large number of publications (Rosenberg 1985, Mayr 1988, Ruse 1989). But as these authors also point out, such questions per se are not illegitimate for biology as a science and are even considered as a necessary means in describing and explaining biological objects. However, the way in which they are dealt with is crucial for the scientific rigor of biology.

To ask about the function (the role) of the heart or the kidneys within an organism makes sense. It is possible and important to describe the processes of the heart purely in terms of physiological and even hydrodynamic terms: how the heart works. But it is also important and even necessary to ask about the function (role) of the heart in the context of the whole organism. We could never really understand the physiological processes if we did not know the purpose of these processes, namely to provide the exchange of metabolically important substances for the whole body, the whole organism. We might also say that the heart has the function to inspire love poems, but that would not be what we mean regarding the function of the heart. It would be, in the words of Wright (1994), an accidental function, a "function as", in the same sense that I could use my laptop or a bone "as" a paperweight, even though nobody would claim that this was "the" function of these objects.

In the early days of ecology, communities or other ecological systems were sometimes identified with an organism (Clements 1916, Phillips 1935). The organism then was used and is also used today frequently as a metaphor for ecological systems, for example, in speaking about "ecosystem health" (Rapport 1989, Costanza et al. 1992). However, it is not the organism but human societies which can serve as an adequate model when it comes to describing functions (roles) within an ecological system and the functioning of the whole system. The philosophical problems described e.g. by Nagel (1961, pp. 520ff) for the application of function concepts to the social sciences mirror much closer those encountered in ecology than the way in which function concepts are used in organismic biology.

In contrast to parts of an organism, a particular species has no clearly defined role within an ecosystem: a bird may have the function of being prey to other animals – but only if these carnivorous animals are parts of the specific system. If there are no predators in the system, the same species or even individual will not have the role "prey". Even if we can say that the bird actually has the role of being prey, we can also find other roles, e.g. its role to distribute seeds and nutrients, to be predator for insects, etc. That is, like a person within a human society, who may be teacher, spouse, child, politician etc., either at the same time or at different times, it can have several roles. Roles can change and the same person as well as the same species can even take opposing roles in time (an extreme example is given by the reversal of predator–prey-relationships, Barkai and McQuaid 1988). "The" one and only role of a species does not exist. Roles are strongly context-dependent. Also, species (and even single individuals of a species) can live in different ecological systems (migrating birds, many ubiquitous species) like persons can change the society in which they live, e.g. by emigrating. In contrast, the heart can never take the role of the kidney and only by means of surgery can leave its original system.

An additional and crucial problem in describing the function of a species, or particular variables, (e.g. biodiversity) in or for the ecosystem is the definition of the system itself. This is even more important when the "functioning" of the whole system shall be described. While the system "organism" and its reference state ("healthy") are given and known rather well, this is the case neither for human societies nor for ecological systems. It also can easily be decided if an organism is alive or dead, while this is enormously difficult to decide for a human society (Nagel 1961, p. 527ff) or an ecological system (Jax et al. 1998).

In contrast to organisms, which set their own boundaries and reference states, ecological systems are strongly dependent on the specific perspectives of the observer. There are no generally accepted definitions of the "ecosystem" or the "community" which could be usefully applied for providing clear reference states, for describing ecological functions or for allowing statements about the "functioning" of the system. Such definitions have to be developed in each specific case (below).

The functions of biodiversity: an example

To illustrate the points made above, the current discussion about the function(s) of biodiversity is a good example. We may here distinguish among three questions to which specific meanings of "function" are related, all of them referring to some role of biodiversity within the realm of ecology and conservation:

- How does biodiversity relate to ecosystem processes (=ecosystem functions)?
- How does biodiversity relate to the functioning of ecosystems?
- How does biodiversity relate to ecosystem services (=ecosystem functions)

Most of the recent debate on the functions of biodiversity is in fact focused on the first issue. It is in part a revival of the old diversity–stability debate (Goodman 1975, Trepl 1995), but takes into account some critical points, which led to the failure of the former theories, namely insufficient data availability and a lack of clear distinctions in terms of the variables investigated (Pimm 1984). The new studies investigate the influence of changing biodiversity (mostly species numbers) on specific processes (or even properties) of ecosystems. Such processes ("functions") are, for example, biomass production, drought resistance, or decomposition of litter (overviews by Tilman 1996, 1999, Schläpfer and Schmid 1999, Loreau 2000, Giller et al. 2004). Generalizations regarding this kind of function (role) of biodiversity, however, are difficult to arrive at. The kind of correlation between biodiversity and ecosystem functions (processes) seems to depend very much on the specific processes, species groups, and systems considered (Martinez 1996, Cardinale et al. 2000, Schwartz et al. 2000, Bellwood et al. 2003), even if biodiversity is considered just in terms of species numbers (but see Bengtsson 1998). This is also one impediment for the ability to make statements about the consequences of changing biodiversity for the overall "functioning of ecosystems". The intensity of one process might be increased by higher species diversity, while another might not.

The expression "functioning of ecosystems" is sometimes used simply instead of "ecosystem functions" (in terms of ecosystem processes, which are implied here), although it mostly also alludes to some overall function (performance) of the whole ecosystem (Ruesink and Srivastava 2001, Naeem and Wright 2003, Giller et al. 2004, Hooper et al. 2005) or to those processes which are thought to be the "critical processes" of the system (Walker 1995, Griffiths et al. 2000). However, neither precise definitions of the ecosystems (the "whole") nor of their reference states are given. In most cases processes or states mentioned are perceived as a sort of "indicator" for the "functioning" of the whole system. This confusion, although with another problematic aspect, is also visible in a publication of the Ecological Society of America (ESA) on "Biodiversity and ecosystem functioning". The authors state:

"Ecosystem functioning reflects the collective life activities of plants, animals, and microbes and the effects these activities – feeding, growing, moving, excreting waste, etc. – have on the physical and chemical conditions of the environment. (Note that 'functioning' means 'showing activities' and does not imply that organisms perform purposeful roles in ecosystem-level processes.) A functioning ecosystem is one that exhibits biological and chemical activities characteristic for its type." (ESA 1999, p. 3).

Although it is emphasized that "functioning" is meant as a purely descriptive term (the sum of a number of processes, or activities), this meaning is changed in the last sentence of this quote. The aim of investigating "functioning" ecosystems here is clearly not to observe any activities of organisms in a particular area, but specific activities that sustain some "typical" ecosystem. Here "functioning" clearly receives a normative dimension in the sense that it refers to some pre-defined reference states of an ecosystem (those that "exhibit biological and chemical characteristics of its type"). The "functioning" of the ecosystem thus is a desirable state, and the organisms in fact are investigated (as) if they perform purposeful roles for its perpetuation. This is a legitimate aim of applied ecological research, but it goes beyond a pure description of processes that occur in some aspect of nature. In particular – and this is the case for any statements about the "functioning" of ecosystems – it presupposes that the ecosystem must be defined, as well as the reference state that has to be retained within a particular time-frame. In fact, this is almost never done, as the definition of the ecosystem is mostly taken for granted. But neither the definitions of the ecosystem nor of its reference state are trivial tasks.

Ecosystems cannot be identified or found in nature. Instead, they must be delimited by an observer. For one and the same chunk of nature this can be done in many different ways, depending on the specific perspectives of interest (Allen and Hoekstra 1992, Jax 2002, Sagoff 2003). Making statements about the functioning of an ecosystem also requires some criteria when it is "destroyed" or "dysfunctional" (Pickett et al. 1989, Schaeffer and Cox 1992, Jax et al. 1998). As there is a seemingly endless number of variables which might be described within an ecosystem, this means selecting the crucial variables to which "functioning" pertains and by which it can be measured.

In the debates on ecosystem functions and ecosystem functioning there is a plethora of variables named for this purpose (Woodward 1994, Schwartz et al. 2000, Giller et al. 2004). The same holds for the question as to whether and to what degree species are functionally redundant. The debate about the redundancy of species in ecosystems was initiated in particular by Walker (1992, 1995). Only if the "functions" to which redundancy refers are made explicit, is it possible to judge if a particular species is redundant with respect to this specific function, that is, for example, if the role it performs in the ecosystem process of decomposition can also be fulfilled by other species present in the system.

A discussion overlapping with the discussion about the redundancy of species is that of determining "functional diversity" instead of species diversity (Martinez 1996, Petchey and Gaston 2002). Determining functional diversity presupposes describing the functional groups which constitute an ecosystem and its functioning or which contribute to an ecosystem process (functional effect groups; above). These functional effect groups are the groups that also are discussed when the redundancy of species in ecosystems is considered. Determining them is done in many different ways (Lavorel et al. 2002, Naeem and Wright 2003), and is an ambitious task, especially if not only groups (or traits) relating to specific ecosystem processes ("functions") are sought, but those indicating the functioning of the whole system. The number of such groups (and thus the possible range of functional diversity) varies with the ecosystem processes ("functions") selected and with the specific classification schemes applied. Estimates of functional diversity can thus not easily be transferred and generalized between different systems and sites. Functional groups determined on the basis of response types by definition cannot contribute directly to statements about relations of functional biodiversity and ecosystem functioning (but see Hooper et al. 2002, Naeem and Wright 2003).

Walker (1992, 1995) lists a number of "functions" for describing ecosystem functioning, which he sees as "critical processes (functions) that determine and maintain it" (Walker 1995, p. 749). He also emphasizes that species which are redundant at one time might not be at another (the "insurance hypothesis" Yachi and Loreau 1999, being a corollary of this). However, it seems that there are still efforts to either ask questions regarding whether or not there are species which are redundant in an absolute way, or to ask "how many species are required for a functioning ecosystem?" (Woodward 1994). But neither ecological functions (be it processes or roles) nor ecosystems are given by nature as such nor is the ecosystem a natural end to its parts. Ecosystem, functions and the ends to which they serve are always (also) dependent on the observer and his or her specific questions and perspective of interest. These interests must not necessarily be societal in a strict sense (in the sense of biological conservation or social well-being), but can also be guided by scientific interests of researchers, or the theories which the scientific community embraces.

There are in fact different degrees of normativity, ranging from scientific goals and purposes which can legitimately be set by the researchers, to real societal goals. In a recent scientific report of the ESA on the ecosystem effects of biodiversity (Hooper et al. 2005), however, the meaning of the term "ecosystem functioning" is extended towards societal interests. Here it is defined to encompass ecosystem properties (including sizes of compartments, as organic matter, and processes), ecosystem goods and ecosystem services. That is, it extends beyond a scientific concept and includes value dimensions. In a similar way Giller et al. (2004, p. 426) characterize ecosystem functioning by three categories of "ecosystem functions", which are for them ecosystem processes, ecosystem properties and ecosystem values (composed of ecosystem goods and ecosystem services). The scientific idea of the "functioning" of a system in terms of processes and elements that sustain it, that is, the effort of a mechanistic explanation of natural processes, thus merges with the normative idea of ecosystem services. Travelling further along this way will increasingly require interdisciplinary approaches to biodiversity research, integrating not only economical considerations but also the social sciences (Machlis 1992, Endter-Wada et al. 1998, Jentsch et al. 2003).

The problem of a normative dimension in describing the functions of biodiversity is not as problematic in the case of describing the impact of biodiversity on ecosystem services as the major and explicit aim of research. The definition of "ecosystem services" consciously implies a normative setting of goals in terms of human needs (including even aesthetic, cultural or spiritual functions; de Groot et al. 2002). Within this framework (set by society and not by science), the question of how different levels of biodiversity contribute to the performance of these services can be investigated within a purely descriptive context, once the goals are set.

It should be noted, that within the literature on ecosystem services, there is sometimes a distinction between services, functions and processes, but also here, not in a consistent way. For Costanza et al. (1997, p. 253), the distinction between ecosystem services and ecosystem functions is such that "ecosystem functions refer variously to the habitat, biological or system properties or processes of ecosystems" while "ecosystem goods (such as food) and services (such as waste assimilation) represent the benefits human populations derive, directly or indirectly, from ecosystem functions". However, in the table they provide, this distinction between a descriptive concept ("functions" in the sense of processes) and a normative concept ("services") is blurred. Thus "functions" also include "soil formation processes'' as well as ''regulation of hydrological flows'' and even ''providing opportunities for recreational activities''. De Groot et al. (2002, Table 1, p. 396) even describe a kind of hierarchy of process, function and services: ''services'' referring in fact to something directly useful to humans (e.g. ''maintenance of productivity on arable land'' or ''pollination of crops''), while ''function'' and ''ecosystem processes and components'' are rather difficult to distinguish with several different categories mixed under either heading. Thus ''ecosystem processes and components'' are as well ''weathering of rock, accumulation of organic matter'' as ''role of biota in movement of floral gametes'', which would more pertain to ''function'' in the strict sense. What de Groot et al. describe as ''functions'' instead are ''pollination'', and ''food'' the first one of which might better be described as a process.

Conclusions

Questions about the functioning of ecosystems, the function(s) of biodiversity, or the functions of species within a system can be posed in a useful and scientifically sound way. This also pertains to a perspective that focuses on the whole system and the roles which particular objects play within it. But it presupposes that it is acknowledged that functions and ecosystems cannot as such be found or identified in nature, but to a high degree depend on defining the specific systems and reference states which are to be investigated. For a specifically defined system it can be investigated if and how much a specific species, and/or biodiversity, contributes, either for its maintenance as a whole or for a specific process within the system. Especially in the debate about biodiversity and ecosystem functions, empirical research is already focused rather clearly on specific single processes. Much less clear, however, is the relation of these findings to the ''overall functioning'' of the ecosystem and also what precisely is meant by ''functioning'' here. Within the discussion about ''ecosystem services'', most participants are aware of the clear purpose-related definition of the systems. The word ''service'' clearly refers to something which somebody (humans beings) desires and values as good. People expect something from nature and they select the things they need on the basis of value decisions. They thus are subject to societal decisions and not to scientific findings. Given this evaluative framework, particular processes and organisms can then be scrutinized with respect to the degree that they contribute to the performance of these services. This does not, and should not, imply that they have no other function (role) – either for themselves or for other beings – beyond that. Many discussions on ''ecosystem health'' in fact also refer to ''functions'' as services. The use of the word ''health'' in this context seems however unfortunate, as by alluding to the organism metaphor it conveys the impression of a norm, a reference state of ecosystems to be found in nature.

In conclusion, there are at least four important meanings of ''function'' in ecology, some of which might better be referred to by other terms. Function refers, in a descriptive sense, to processes and the causal relations that give rise to them, to the role of organisms within an ecological system, to the overall processes that sustain an ecological system (which together determine its ''functioning'') and finally to the services a system provides for humans or other organisms. If the use of the word ''function'' is to be retained for all these different notions, it should at least always be made explicit, in which specific meaning the term is used. 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.

To measure functions it is also essential to specify the system and the reference state considered. Although this is normally done with respect to the specific experimental system, the whole ecosystem, in particular, to which the conclusions about ''functions'' refer, is mostly defined only vaguely – if at all. Without these steps, generalizations regarding the functions of species and/or biodiversity will also remain elusive. 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.

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