Studies in History and Philosophy of Biol & Biomed Sci xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Studies in History and Philosophy of Biol & Biomed Sci

journal homepage: www.elsevier.com/locate/shpsc

Functional ecology's non-selectionist understanding of function

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ARTICLE INFO

Keywords:
Functional biodiversity
Function
Biodiversity
Ecosystem function
Biological individuality
Superorganism

ABSTRACT

This paper reinforces the current consensus against the applicability of the selected effect theory of function in ecology. It does so by presenting an argument which, in contrast with the usual argument invoked in support of this consensus, is not based on claims about whether ecosystems are customary units of natural selection. Instead, the argument developed here is based on observations about the use of the function concept in functional ecology, and more specifically, research into the relationship between biodiversity and ecosystem functioning. It is argued that a selected effect account of ecological functions is made implausible by the fact that it would conflict with important aspects of the understanding of function and ecosystem functional organization which underpins functional ecology's research program. Specifically, it would conflict with (1) Functional ecology's adoption of a context-based understanding of function and its aim to study the functional equivalence between phylogenetically-divergent organisms; (2) Functional ecology's attribution to ecosystems of a lower degree of part-whole integration than the one found in paradigm individual organisms; and (3) Functional ecology's adoption of a physiological or metabolic perspective on ecosystems rather than an evolutionary one.

1. Introduction

In the recent years, the notion of *functional biodiversity* has become increasingly important in ecology. This is particularly the case in the *biodiversity and ecosystem function research* program (or BEF research, for short), a field of ecological research which studies the effects of biodiversity on the functioning of ecosystems (Chapin et al., 2000, 1997; Hooper et al., 2005; Loreau, 2010a, 2010b; Naeem, 2002; Tilman, Isbell, & Cowles, 2014). BEF research aims to achieve a synthesis of the two traditionally isolated ecological subfields of *community* and *ecosystem* ecology, and of their respective concerns for the distribution and abundance of species interacting in particular environments (i.e. biodiversity) and for the ecosystem processes (e.g. biomass productivity, cycles of nutrients and flows of energy) which arise from those interactions (i.e. ecosystem functioning). To this aim, BEF researchers develop ways to classify organisms into *functional groups* or *types*, on the basis of similarities of potential contributions to ecosystem processes. Many BEF researchers claim that this synthesis, besides being a significant scientific achievement, is of critical societal importance given the many benefits that humans derive from well-functioning ecosystems (Laureto, Cianciaruso, & Samia, 2015; Loreau, 2010b, p. 51; Naeem, 2002, p. 1540, p. 113).

A key concept at the interface of these domains of inquiry, and which underlies the classification of organisms into *functional groups* or *types*, is that of *ecological function* (e.g. K. W. Cummins, 1974; Lavorel & Garnier, 2002; Hooper et al., 2002). In BEF research, the ascription of functions to organisms and other biodiversity items serves as a conceptual bridge between the traits of those biodiversity items and their contribution to ecosystem processes (Petchey & Gaston, 2006, pp. 750–752; Nunes-Neto, Do Carmo, & El-Hani, 2016, p. 299). BEF research thus looks at how the particular traits (structural, phenological, behavioral, etc.) of organisms explain their potential contributions to ecosystem processes, such as biomass productivity, nutrient cycling, energy flows, and so on (Loreau, 2010b; Naeem, 2002, p. 1539, p. 51). Such a linkage of traits to ecosystem processes aims to improve upon the more abstract "black box" approach characteristic of classical eco-

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https://doi.org/10.1016/j.shpsc.2018.05.001
Received 15 September 2017; Received in revised form 26 February 2018; Accepted 6 May 2018

system ecology, which tended to disregard the identity of the species involved in ecosystem processes on the assumption that most ecological functions could be performed by many different species (Hagen, 1992, pp. 90–98, 103–106; Cooper, 2003, pp. 48–49).[1]

While the concept of function has been widely discussed in the philosophy of biology (for reviews, see McLaughlin, 2001; Wouters, 2005; Garson, 2016), only a few recent discussions have been devoted to the concept as it is used in ecology (Maclaurin & Sterelny, 2008, sec. 6.2; Odenbaugh, 2010, sec. 3; Gayon, 2013, sec. 5; Nunes-Neto, Moreno, & El-Hani, 2014; Dussault & Bouchard, 2017; Cooper, El-Hani, & Nunes-Neto, 2016). Nonetheless, a consensus emerges in those discussions, according to which one of the most advocated philosophical theories of function, namely the *selected effect* theory, is poorly suited for accounting for the concept of function as it is used in ecology (see Nunes-Neto, Moreno, & El-Hani, 2013). The commonly invoked argument in support of this view is the following: insofar as, on the one hand, the selected effect theory of function can only apply to the traits or parts of entities which are targets of natural selection, and on the other hand, ecosystems are not customary units of natural selection, then the selected effect theory cannot account for the ascription of functions to organisms conceived as parts of ecosystems. This argument thus draws on the well-known criticism of group selection (Maynard-Smith, 1964; Williams, 1966) and contemporary biology's ensuing adoption of an individualistic take on natural selection.

The aim of this paper is to reinforce the current consensus by presenting an additional, and I think more fundamental, argument against the applicability of the selected effect theory of function in ecology. This argument is based on the theoretical practice of functional ecologists and more particularly on that of BEF researchers. I maintain that a selected effect account of ecological functions would be at odds with the very understanding of the function concept as it is used in ecology and BEF research.[2] While, as I will later highlight, the usual argument against the applicability of the selected effect theory of function in ecology is ultimately an empirical one which hinges upon the empirical question of whether natural selection customarily operates at the level of ecosystems, the argument I develop below is conceptual. What I argue is that the epistemic aims for which the function concept is used in ecology and the view of ecosystem functional organization associated with this use involve an understanding of function with which a selected effect account would conflict.

Thus, importantly, the argument developed below does not hinge on whether or not ecosystems are customary units of natural selection. This independence from issues regarding levels of natural selection is significant, given the fact that, as I will highlight, the view that natural selection can operate at supraorganismic levels has been partly rehabilitated in the last decades. This partial rehabilitation results mainly from Wilson and Sober's collaborative work on multilevel selection, which identifies environmental conditions under which natural selection can realistically occur at the level of groups and multispecies assemblages (see e.g. Sober & Wilson, 1998; Wilson & Sober, 1989). Thus, in contrast to the usual argument against the adoption of a selected effect account of ecological functions, the argument I develop below is independent of issues regarding levels of selection and would retain its cogency no matter how prevalent community and ecosystem selection may turn out to be.

My discussion will be organized as follows. In section 2, I will discuss the usual argument against the adoption of a selected effect account of ecological functions. I will contend that this argument is less straightforwardly compelling than has been assumed when one considers Wilson and Sober's partial rehabilitation of the idea that natural selection can operate at the level of multispecies assemblages. In section 3, I will develop an alternative argument against the adoption of a selected effect account of ecological functions, which is based on the practice of functional ecologists rather than on claims about levels of selection. First, I will argue (in section 3.1) that a selected effect account of ecological functions would conflict with the context-based understanding of function adopted in functional ecology and BEF research and with functional ecologists' aim of studying the functional equivalence between phylogenetically and taxonomically divergent organisms. Second, I will argue (in section 3.2) that a selected effect account of ecological functions would entail a view of ecosystems as exhibiting a degree of part-whole integration comparable to that found in paradigm individual organisms (i.e. a view of ecosystems as superorganisms), which conflicts with functional ecologists' more communitarian picture of ecosystem-level functional organization. Third, I will argue (in section 3.3) that a selected effect account of ecological functions would entail a view of ecosystems as evolutionary individuals (i.e. as units of natural selection), which conflicts with functional ecologists' more metabolic understanding of the individuality of ecosystems. In section 4, I will turn to the suggestion made by many proponents of the usual argument against the adoption of a selected effect account of ecological functions that the ecological function concept should instead be interpreted through the prism of Cummins's (1975) alternative *causal role* theory of function. The extent to which the observations made in section 3 reinforce this suggestion will be briefly discussed.

2. The usual argument against selected effect ecological function

As mentioned in the introduction, a consensus has emerged among philosophers of ecology to the effect that the selected effect theory of function cannot adequately account for ecological functions. The commonly invoked argument in support of this view is that insofar as the selected effect theory of function can only be applied to the parts or traits of biological entities which are units of natural selection, a selected effect account of ecological functions would require that some of the traits of organisms within ecosystems be shaped by natural selection operating at the level of ecosystems (Maclaurin & Sterelny, 2008, p. 114; Odenbaugh, 2010, pp. 250–251; Gayon, 2013, pp. 76–77; Cooper et al., 2016, pp. 111–112). A selected effect account of ecological functions would therefore rest on the assertion that ecosystems are customary units of natural selection. Yet, although many classical community and ecosystem ecologists explicitly committed to the view that natural selection commonly operates at community and ecosystem levels (e.g. Tansley, 1935; Allee, Emerson, Park, Park, & Schmidt, 1949, Chapter 35; Dunbar, 1960, 1972; Odum, 1971), this view has lost favor among contemporary biologists and ecologists (see e.g. Whittaker, 1975, Chapter 8; Harper, 1977; May, 1978). This loss of favor, partly results from Maynard-Smith (1964) and Williams's (1966) influential critiques of group selection, which have convinced many biologists and ecologists that natural selection primarily operates at the level of individual organisms (see Hagen, 1992, Chapter 8; DeLaplante & Picasso, 2011, p. 184). Accordingly, Maclaurin and Sterelny (2008, p. 114) observe:

> [L]ocal [ecological] assemblages do not have selective histories. They are not part of lineages. Communities are not elements of a

[1] In this paper, I will assume an understanding of the notions of ecological community and ecosystem as characterizing complementary perspectives on the same (multispecies) level of organization rather than as denoting distinct levels (see Hutchinson, 1978, pp. 214–215; Hagen, 1989; Callicott et al., 1999, pp. 23–25). As I will argue in section 3.3, the functional perspective which ascribes functions to organisms within multispecies assemblages is more characteristic of ecosystem ecology than of community ecology. Thus, in what follows, my primary focus will be on the ascription of functions to organisms within ecosystems.

[2] It should be noted that, in the present paper, I will focus on the notion of function underlying what functional ecologists refer to as *functional effect traits,* in contrast to *functional response traits* (Catovsky, 1998; Hooper et al., 2002; Jax, 2010, pp. 54–55). Insofar as the former are concerned with the *roles* that organisms fulfill within ecosystems, they are the ones most directly relevant to BEF research. The latter underlie classifications of organisms in terms of their ability to thrive in various environmental contexts and so are more directly relevant to community ecology's aim of explaining species distributions.