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THEMATIC ISSUE ARTICLE: ECOSYSTEMS OR ORGANISMS?

# Individuality as a Theoretical Scheme. II. About the Weak Individuality of Organisms and Ecosystems

**Philippe Huneman**

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**Abstract** Following a previous elaboration of the concept of weak individuality and some examples of its instances in ecology and biology, the article focuses on general features of the concept, arguing that in any ontological field individuals are understood on the basis of our knowledge of interactions, through the application of these general formulas for extracting individuals from interactions. Then, the specificities of the individuality in the sense of this weak concept are examined in ecology; I conclude by addressing the differences between ecosystems and organisms as they appear in the viewpoint of such concept.

**Keywords** Biological individual · Community ecology · Ecological communities · Evolution · Metaphysics of science · Organisms · Quasi-independence

In Huneman (2014, this issue) it has been argued that a weak concept of individuality can be defined in terms of a "formal concept," elaborating Simon's idea of quasi-independence, and a "material concept" that applies the formal concept within a specific theoretical domain by instantiating some of its variables in terms of magnitudes defined by the variables of the theory. In this article, I'll explore general features of this weak concept of individuality, before exploring the specificities of ecological individuality—in order to address issues about the ontological status of communities that have pervaded ecology from Clements to Sterelny (2006), then elaborating the kind of relations that can be made between ecosystems as weak ecological individuals and organisms.

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P. Huneman (✉)
Institut d'Histoire et de Philosophie des Sciences et des Techniques (IHPST), CNRS/Université Paris I Sorbonne, Paris, France
e-mail: philippe.huneman@gmail.com

## The Salient Features of Weak Individuality

Before turning to the relationships between organisms and ecological communities as organisms, let's review some of the features of the weak concept of individuality.

(1) In this approach "individual" is a theory-dependent name. What "individuals" are depends upon our knowledge of interactions, since it is related to the strength of interactions, but the notion of strength cannot be defined outside a theory. A theory provides the values of the variables in the scheme for individuality; individualities are singled out according to this scheme, on the basis of our knowledge of interactions. In this sense, "who are the individuals?" is answered via *resulting values of variables provided by* a theory. The "weak concept" is actually a scheme that allows, in a theory of interactions, a set of interactions to be singled out that will be definitional of the individuals in the domain.

This means, first, that as such the "weak concept" does not capture anything; it is only this concept as instantiated in a theory—the "material concept"—under which the individuals fall. Second, there is another kind of pluralism about individuality here: if something is known through two different theories, it is possible that the weak concept of individuality will pick out different individuals according to each of the theories (think, for example, of immunology and developmental theory; or functional ecology and community ecology). This is another type of pluralism than the one emphasized above, determined by the increasing values of threshold H. However, one could make an argument in favor of granting more reality to individuals that are picked up by several theories, in a way analogous to the claim made by tenants of "robustness analysis" (namely, theorems that are derived in models which differ according to their main parameters, called "robust theorems," are more likely to capture something real; Levins 1966; Weisberg 2006).

(2) It also follows that, philosophically speaking, this view is of Quinean inspiration. Quine famously said that what there is, is the values of variables of our best theories. Here, individuals in a domain are indeed defined by the linked variables of the theory of the domain. However, it is less straightforward than Quine's view, since individuals are defined by schemes using variables whose definitions are given by a theory of interactions. In other words, while for Quine to exist is something univocal (it can be read off the equations in the same way in all domains), here, to be an individual is not something univocal or domain-independent (as such, the equations in a theory cannot give us the individuals: we go through the weak concept as a scheme). This entails two important consequences.

(a) "Individuality" is not exactly a metaphysically universal concept like "natural kind" or "causation" (whatever the proper meaning of these concepts is). Since what "strength of interaction" means can be very different between domains and theories, what "individual" means, concretely, can be very heterogeneous (whereas for many authors—even though the range of views about causation/natural kinds is vast—to be a "cause" (e.g., Salmon 1984), or to be a "natural kind" (e.g., Khalidi 2013) is something robust across several domains). However, the main claim made here is that the formal weak concept captures the universal way each theory in general has resources to define individuals, build criteria to identify them, and tools to draw boundaries. As a concept *proprio sensu* (which is by nature likely to have an extension), "individual" designates the scheme within which the variable h has been instantiated, i.e., as a *material* concept, therefore it is intrinsic to a theory; but it can be used as a *general concept* only in the sense of the formal scheme for extracting individuals on the basis of interactions.

(b) Notice an apparent circularity here: I spoke of the weak concept scheme as something allowing us to pinpoint individuals in a set of interacting entities; but one could say that these "entities" are themselves individuals, so the "weak concept" concept is circular.

Granted, if it is not circular, I admit that it is at least hierarchical. Actually this is not really circular, or it is the same sense of circularity as the one Woodward (2003) displays when he defines causation in terms of manipulation (which, as intervention, assumes some meaning of causation). Woodward's analyses are intending to capture the way scientists ascribe causation (even though it is not at all describing what scientists do, since few of them actually do structural equations or causal modeling). Similarly, the weak concept of individuality[1] intends to capture how we can speak of individuals such as ecosystems, cells, organisms, assuming that we know a lot about ecological or physiological interactions. So in a sense, here there would be a sense of individuality that is supposed as a primitive. (Which also justifies talking of a *weak* concept here, exactly as in Woodward's analyses of causation.)

I won't directly argue with that; I would rather say that all our "individuals," theoretically, can be made up of individuals in the sense of another theory; but since the material concept is internal to a focal theory, it does not have to account for a concept of individual that is proper to theories already assumed by this focal theory (in the sense that biology assumes physics and chemistry, etc.). For instance, assuming that there are individual organisms and that they can be identified in a specific physiological, cellular, or immunological theory does not seem to be a fatal flaw for a theory of ecological individuals.[2]

(3) Many concepts of individuality (e.g., Sober and Wilson 1998) emphasize functional cohesion, which often means either division of labor, or just the existence of some causal role functions (sensu Cummins 1975). In the present view, the weak concept does not refer to any functions. What counts are only the interactions and their strengths.

This sort of deflationist move is exactly parallel to Brandon and McShea's (2011) recent theory of complexity in biology. Actually, they define complexity by the number of cell types (or part types); this is a very minimalist view of complexity since it leaves out any functionality. The rationale, quite convincing, is that no satisfying uncontroversial concept of complexity exists that would enable one

[1] Actually, I use "concept of weak individuality" and "weak concept of individuality" interchangeably. Even though one could object that they are two different things (e.g., "a communist concept of society" versus "a concept of communist society"), here the differences are not so important, especially because we are not assuming any concept of individuality; so I can just stipulate that "weak individual" is the object of a "weak concept of individuality."

[2] In the same way, if we use these schemes to individuate cultural entities, we may for example use Dawkinsian *memes* as entities, assuming many things regarding the entities likely to produce, encode, or transmit memes, but these assumptions as such would not entitle someone to question the fact that there are cultural individuals.

to deal with issues about the evolution of complexity through phylogenetic times. The price is, of course, the counterintuitive consequence that some broken devices would be more complex than some functioning devices. Anyway, an analogous rationale here holds: integrating functionality into the sort of absolutely general concept of individuality would make it impossible to remain at the same level of generality.

Yet, if "functionality" is left out of the formal weak concept of individuality (as a universal scheme), it can be recovered in material concepts of individuality in some domains—provided that functional interactions count as stronger, for example, than non-functional interactions. For instance, in functional ecology, trophic or mutualistic interactions are functional; they may allow for defining some functional types (in a specific sense of "functions," that may be Cummins' (1975) systemic sense) such as herbivore, etc. (Simpson 1988)—and may count more significantly for defining interaction strength than non-functional interactions (Poisot et al. 2013).

However, only the "systemic," causal role sense of function is used here—not the etiological, selected effect sense of function, defended by Wright (1973), Neander (1991), etc., according to which "the function of Y is X" means "Y has latter been selected for doing X" (see Huneman 2013 for an overview). For a consideration of this meaning of "function" we have to look at the connection between the weak and the strong concepts of individuality (sketched below).

## Ecological Concepts: Relation Between the Two Versions, Weak and Strong, and Circularity

Until now, I have defined a weak concept of individuality as a universal scheme for identifying individuals on the basis of interactions; and, in the context of ecology, I contrasted it with the strong concept, defined by natural selection. It is therefore natural to wonder about their articulation.

Actually, to be more precise we now have a strong concept of a *biological* individual, i.e., as unit of selection, and a weak concept of individuality *in general*. In many cases of biological individuals, the two concepts can be applied. Organisms and cells would be examples of that. Cells indeed have been units of selection in the past, and possibly are sometimes units of selection even when parts of larger individuals, as is visible in the case of cancer processes (i.e., Nagy 2004). Cells can also be seen as weak individuals—the membrane of the cell, by moderating exchanges of cell components with the outer space of the cell, is very likely to realize the kind of decoupling between intrinsic and external interactions that is formalized by the weak concept of individuality.

Things are quite complicated for organisms: they can be seen as units of selection and then fall under the strong concept. But what falls under the strong concept also instantiates the weak concept to the extent that evolutionary biology is a theory, and that it is possible to derive a material realization of the scheme (2) according to Huneman (2014, this volume) by considering natural selection as interactions, so that organisms, as well as genes or cells, are picked up as individuals. But organisms also fall under the realization of the weak concepts when the focal theory is, for example, physiology or immunology. This only reflects the fact that evolutionary biology is the most encompassing theory in biology—organisms as well as cells or genes are its objects. Therefore it is not surprising that for these objects individualizing can be done either through the latter theories, or through evolutionary biology itself. As indicated before, in the contrary, in ecology there can only be objects of the weak concept of individuals.

A consequence of this relation between concepts is that the same structure of nestedness is seen either when applying the strong concept of individuality—according to which we can find the degrees of organismality, as defended by authors such as Reeve and Hölldobler (2007), Queller and Strassmann (2009), or others abovementioned in Huneman (2014, this volume)—or when applying the weak concept of individuality, since it gives rise to nested kinds of individuality. However, the overlap will only be partial. In the latter case, an ecosystem such as the gut microbiome could be seen as an individual, which will be comprised within an individual that will be the organism (Huss 2014), and in turn it might be that the organism will be part of a community of species that will also be an individual for ecological theory. Hence the nestedness of individuality from the viewpoint of the weak concept of individuals applied to ecology (or: the material weak concept in an ecological framework) will only partially overlap with a set of nested organisms sensu the strong, evolutionary concept (i.e., cells, organisms, etc.), which does not recognize ecosystems or communities as individuals.

The important question, however, is how both concepts can be articulated. Here is an indication. Clearly, when individuals exist as units of selection, they also have many interactions with other individuals, and they emerge as individuals through selection processes acting on low-level individuals, as highlighted by the "evolutionary transitions" research program (Michod 1999). Therefore, they can be in turn seen as putative individuals with respect to the interaction-based, weak concept. But the articulation should also be conceived of in more dynamical terms. Actually, even though the weak concept of individual is more encompassing than the strong concept (since it does not require selection), it is plausible that what is a weak individual can be acted upon by selection since it is

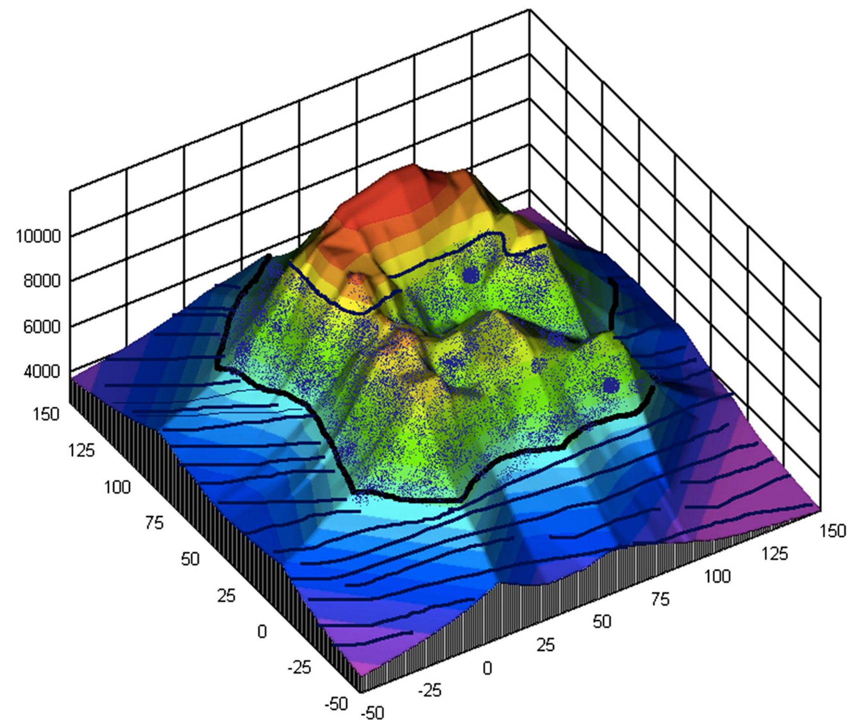


**Fig. 1** Simplified representation of the way individuals with their boundaries can emerge from interactions. The planar axes x and y represent the set of entities; z = f(x, y) represents the intensity of interaction between x and y. Depending on the value of "strong interaction" threshold H, the "individual" emerging from interaction will be the set of values (x, y) corresponding to either the shaded surface area marked with dots or the area crossed by lines. The steepness of this surface may vary, and this determines the degree of blurriness of the boundaries of this individual

individualized through interactions and displays properties of robustness. And conversely, one hardly sees how something that is not such a weak individual could be acted upon by selection (since by definition it does not have any self-cohesion and endurance in time).

Hence, to put it bluntly, weak individuality seems a precondition to be respondent to selection as a whole, or delineates candidates to be units of selection—and therefore logically and chronologically precedes strong individuality. But on the other hand selection stabilizes some weak individuals by maintaining the patterns of interaction. The overall picture of individuality thus should be one of a circular dependency between both states of individuality, strong and weak. And this circularity of course evolves in time—individuals ceasing to be units of selection can still be weak individuals, and other weak individuals can become units of selection, get stabilized, and so on. This dynamical perspective should be eventually adopted when it comes to deciding about the individuality of ecosystems and communities. We now turn to this topic, but focusing on the issues raised by ecological communities and ecosystems only as weak individuals.

## Ecological Individuals

According to the weak concept of individual, there might be ontological "ecological communities." These communities are not defined by some salient boundaries (Cadenasso et al. 2003); actually, they emerge from ecological interactions. Levins and Lewontin (1985) already said that "the question of the boundaries of communities is really secondary to the issues of interaction among species." The weak concept sketched here tried to make sense of this priority of interactions over boundaries. These just derive from the sets of interactions picked up by the weak individuality scheme (see Fig. 1).

Ricklefs (2008) famously called for "disintegrating the community"—in the sense of recognizing that communities may not be the most relevant level for understanding ecological functioning as well as the processes that yield biodiversity. The reason is that implicit processes that involve external communities at a regional scale are in fact intertwined with local processes in a community, so that focusing on the local community blinds us to the genuine ecological processes accounting for biodiversity patterns and ecosystem functioning even at the local scale. For him, regional scales and metacommunities would be more appropriate scales and units for ecological analysis. Applying the weak concept of individual will disentangle ecological units likely to be the seat of highly self-contained sets of processes, and possibly contribute to deciding to what extent ecological communities are a genuinely relevant scale for ecological understanding.

The problem therefore, in order to understand what ontological ecological communities can be, consists in understanding at a high enough level of generality the structure of ecological interactions, so that the weak concept's scheme can be applied. One related question will therefore be to assess the relative weights of various ecological interactions: if some kind of interaction has more potential for giving rise to a set of interactions, it will be more relevant for instantiating the scheme of weak individuality, and tracking these interactions could be a good proxy for discriminating individuals through this scheme. Given the typology of ecological interactions this can be a promising option, as I am arguing now.

Ecologists used to distinguish three interactions: predation, competition, and mutualism. In population ecology, the first one has for a long time been approached through the Lotka-Volterra equations (Kingsland 1995), which are also able to deal with competition. Mutualism has since three decades ago been the object of a thorough evolutionary investigation, based on game-theoretic approaches and tools (Noe and Hammerstein 1994; Herre et al. 1999; van Baalen and Jansen 2001; Bshari and Bronstein 2004). Among other features, it displays characteristic timescales that are different from those of the two others.

All of these interactions between two species contribute to the set of interactions likely to allow the definition and discrimination of ecological individuals. However, it has increasingly been shown in the last decade that another interaction pervades ecosystems, namely what Jones called "ecosystem engineering" (Jones et al. 1994; Wright and Jones 2004; etc.). Through it, an organism changes the ecosystems around it, and then, the environmental demands on itself and organisms of other species. Ecosystem engineering is labeled as "niche construction" (Odling-Smee et al. 2003) when it is viewed rather in the perspective of evolutionary biology. It raises some issues regarding the boundaries of its extension: while obviously chemical exchanges between a collection of earthworms and their surroundings, or the web of a spider, are cases of "ecosystem engineering," should all effects of the motions of earthworms disturbing sand, or chemical exchanges due to breathing birds, be classified as ecosystem engineering? However, a certain vagueness can be tolerated, and for our present purpose it is enough to consider that ecosystem engineering is a fourth class of ecological interactions.

This ecosystem-engineering interaction has an important particularity: it takes place between a large number of organisms (actually, all organisms are concerned with the changes due to earthworms in the pH of the soil), and between organisms and the biotic elements of ecosystems. Its timescale is also very large, since organisms affected by ecosystem engineering may be those occurring several generations after the first engineering effects. (See Lehmann 2007 for an interpretation of niche construction in terms of long-lasting inherited effects of phenotypes.)

Ecosystem engineering is indeed pervasive in all ecosystems, as has been made salient by Jones and colleagues in various papers. "Ecosystem engineering on many other species occur in virtually all ecosystems because the physical state changes directly create non food resources, directly control abiotic resources, and indirectly modulate abiotic forces that, in turn, affect resource use by other organisms" (Jones et al. 1994). It has been shown as well that even in hostile or low-diversity environments, such as microalgae, ecosystem engineers are also pervasive (Arrigo et al. 1991). And its impact on productivity is very high as compared to other interactions' impact (Wright and Jones 2004).

The fact that ecosystem engineering interactions involve many species is relevant for the way interactions actually constitute ecological communities and ecosystems. In effect, given this feature and the general pervasiveness of such interactions, taking two species randomly, there are many chances that one interaction between them is of the sort "ecosystem engineering." Hence, regarding the frequency of interactions—the kind of consideration crucial for the "counting" view of weak individuality sketched in Huneman (2014, this volume)—ecosystem engineering seems to be quite important.

Now, concerning ecosystems, when one considers an abiotic element and—through applying scheme (2) of Huneman (2014, this volume)—considers the elements with which it is in interaction, there are many chances that such interaction will be of the sort "ecosystem engineering," since ecosystem engineering is an ecological interaction that strongly involves the abiotic. Another way to argue in this sense is to consider that ecosystem engineering is the only *direct* interaction with the abiotic—since other ecological interactions impinge on abiotic elements through the modification of some species abundance and possibly habitat and behavior. Yet it is reasonable to think that indirect interactions are less intense on the average than direct interactions, at least at the timescales that concern biodiversity patterns and ecosystem functioning. Therefore many strong interactions (between the organisms and the abiotic) are indeed constituted by ecosystem engineering.

All these reasons support the claim that ecosystem engineering has a prominent role in constituting the strongest and most frequent interactions that occur in communities and ecosystems. Tracking ecosystem engineering could be a cue to finding out genuine ecosystems and communities.

More recently, ecologists have widened their considerations of interactions by adding another type of interaction, namely the "facilitating interactions" (Bruno et al. 2003). This is not exactly a fifth kind of interaction, since it overlaps with ecosystem engineering as well as with mutualisms, and may in a sense be seen as pertaining to another way of partitioning interactions in kinds. Cases where ecosystem engineering positively impinges on growth rate or abundance of some species are cases of facilitation interaction. But "facilitation" can be seen as a more general aspect of interactions: it embraces all interactions, whatever their ecological type, through which one species positively affects another one. Thus there is a pervasive range of facilitating interactions—"most species interactions are indirect and positive"(2003, p. 124)—and these provide couplings between species that are supportive of communities as integrated wholes. Therefore the degree of facilitation can enter as a major component in the sets of interactions that realize a high value of the variable h, measuring the strength of interactions and defined in Huneman (2014).

The above remarks about the weight of ecosystem engineering in constituting genuine ecological communities and ecosystems already imply that facilitation interactions play an important role in structuring these genuine communities and ecosystems. But a further point should be developed that relates to competition. Actually it could be seen as counterintuitive to include *all* interactions in what defines a community as an individual. Competition seems to be the contrary of an integrating interaction; and predation may be less integrating than mutualism, and would seem at first sight to negate the individuation of the set of species so interacting. This is true but has to be mitigated.

Competition above all seems to be tied to *facilitation*. While competing species compete, the best competitor $a$ is a facilitator regarding other species $b_1$, $b_2$, … competing with competitors $c_2$, $c_3$, … of lower competitive quality than $a$. This is even clearer with predation: as Bruno et al. (2003) put it, "although rarely recognized as such, a trophic cascade is simply an indirect facilitation" (p. 124). Especially, the effect of taking facilitation into account, as they argue, is the fact that the realized niche for a species can exceed the fundamental niche. Whereas competition indeed tends to competitive exclusion and therefore seems to decrease the number of species likely to coexist in a community, considering facilitation, through this process leading to an overlap of realized niches, enables one to understand that communities can encompass more species than what mere competition predicts. The often-overlooked solidarity between competition and facilitation, once taken into account, shows that competition in general may not be seen as a des-individualizing factor, so that the weak concept of individuality is allowed to include all kinds of interaction in the definition of the weak individuality scheme (2) defined in Huneman (2014). Especially, when competition interactions in a set of species occur in such a way that facilitation relations can be pinpointed whose impacts on growth rates of populations of various species do not average away when compared to the impact of direct competition, then competition may indeed be contributing to structuration of ecological individuals.

An issue analogous to the one just discussed about the role of competition can also be raised for organisms: there are actually many very strong interactions that are negative—think of the rejection reaction against antigens due to the immune system. This would count as an objection against the weak concept of individuality (the "strong exclusion objection," so to speak) since it seems that the strength of interaction does not contribute to defining individuality—strong interactions are excluding ones. However, thinking in terms parallel to the relation competition/facilitation in trophic cascades mentioned above, the answer consists in emphasizing the facilitation aspect of these reaction reactions—they facilitate persistence and replication of other components of the immune system and of the milieu. Ecosystem views of the microbiome have been articulated recently (Costello et al. 2012); in the perspective they define, one could sketch such the basics of an answer to the strong exclusion objection, to the extent that the physiology of the organism or a part of it is framed in terms of ecological interactions, including competition.

## Differences Between Ecosystems and Organisms?

As we started this investigation, in Huneman (2014, this volume) by enquiring about the status of ecosystems and the reliability of the analogy between ecosystems and organisms, it is natural for the closing section to go back to this question and develop the consequences the weak individuality view bears on it.

At first sight it seems that organisms are more self-contained and bounded than ecosystems. However, first there are non-metazoan organisms whose status is not so easy to define, and whose boundaries and self cohesion can be called into question: slime molds, aphids—but even butterflies (considering the breakup between adult and larval morphs across development) raise issues. So boundaries and self-containment are not proper ways to distinguish the ontological status of organisms and ecosystems/communities.

Relying on the interactions-first view of individuality that is instantiated by the weak concept of individuality, we have a criterion for finding out the genuine individuals in both domains of ecology and biology. As we have seen, in this perspective boundaries, in any case, come as a consequence of interactions. The interaction patterns proper to all entities supposedly making up organisms and ecosystems, respectively, indeed single out indeed single out weak individuals that may start and fade out more or less continuously or abruptly. In the case of a sharp fade-out, they will be well-bounded individuals; in the former case of a continuous and slow fade-out, they will be individuals with fuzzy boundaries, likely to overlap with other ones. So it cannot be a priori decided that some individuals—organisms—have sharp boundaries and others—ecosystems—have fuzzy boundaries. It is a priori possible that in some area of functional or community ecology one will empirically find ecosystems or communities that are more bounded, and possibly more contained, than some supposed organisms. This will hang upon their proper interactions patterns, that can only be empirically checked out.

Hence, using the weak individuals view leads to mitigating the idea that organisms are genuine individuals and that ecosystems are just indexical or nominal individuals; it may be like this as a result of the empirical enquiry, but it cannot be stated in advance, and actually much of what we know seems to support the idea that some tightly integrated ecosystems are more (weak) individuals than some organisms. This hypothesis provides a strong support for any approach that sees organisms as ecosystems and applies ecological concepts and methods to explain organismal features.

## Conclusion

In this article we designed a general scheme of individuality that could be equally applied to organisms, ecosystems, communities, and more generally to any ontological domain where a theory of interactions has been elaborated. Individuality seems therefore a very general concept, but only in the sense of the emergence from an already modeled set of interactions. This scheme of individuality is said to be a "weak" concept because of its already assuming a theory and some models. In this sense, "individual" is also a local concept, but the way individuals can be defined, identified, and bounded is something universal captured by the scheme (2) aforementioned, which is valid across all theories. In other words, no operational definition of what "individual" is could be given outside a theory, but only a formal scheme.

The universality of the concept "individual" relies on its being a universal scheme for using theories to determine individuals within the ontological domain addressed by the theory. Hence this formal concept of individuality can be said to be "meta-theoretical" (since it is instantiated into a "material concept," endowed with an extension, only when a theory allows to instantiate the variables); it is also of Quinean inspiration.

This is a philosophical concept: it does not describe the practices of the sciences, no more than Woodward's concept of causation, although quite sensitive to scientific practice, does describe real scientific models of causal inference but reconstructs them into structural equations. The present concept of individuality reconstructs operations through which individuals such as ecosystems or ecological communities can be pinpointed in the sciences, and generalizes this into a formal concept of individuality.

The contextual reason for elaborating such a concept is the inability of strong concepts of biological individuality to make sense of some communities as individuals, which goes against familiar uses and preconceptions in ecology. However, it aims at a metatheoretical generality that goes beyond ecology.

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## References

Arrigo KR, Sullivan CW, Kremer JN (1991) A bio-optical model of Antarctic sea ice. J Geophys Res 96:10581–10592
Brandon R, Mc Shea D (2011) Biology's first law. Oxford University Press, New York
Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. TREE 18:119–125
Bshari RS, Bronstein JL (2004) Game structures in mutualisms: what can the evidence tell us about the kinds of models we need? Adv Study Behav 34:59–104
Cadenasso ML, Pickett S, Weathers K, Jones C (2003) A framework for a theory of ecological boundaries. Bioscience 53:750–758
Costello E, Stagaman K, Dethlefsen L, et al (2012) The application of ecological theory toward an understanding of the human microbiome. Science 336:1255–1262
Cummins R (1975) Functional analysis. J Philos 72:741–764
Herre EA, Knowlton N, Mueller UG, Rehner S (1999) The evolution of mutualisms: exploring the paths between conflict and cooperation. Trends Ecol Evol 14:49–53
Huneman P (2013) Introduction. In: Huneman (ed) Functions: selected and mechanims. Springer, Dordrecht, pp 1–18
Huneman P (2014) Individuality as a theoretical scheme. I. Formal and material concept of individuality. Biol Theory. doi:10.1007/s13752-014-0192-9
Huss J (2014) Methodology and ontology in microbiome research. Biol Theory. doi:10.1007/s13752-014-0187-6
Jones C, Lawton J, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386
Khalidi MA (2013) Natural categories and human kinds: classification in the natural and human sciences. Oxford University Press, New York
Kingsland S (1995) Modeling nature. University of Chicago Press, Chicago
Lehmann L (2007) The evolution of trans-generational altruism: kin selection meets niche construction. J Evo Biol 20:181–189
Levins R (1966) The strategy of model building in population biology. Am Sci 54:421–431
Levins R, Lewontin R (1985) The dialectical biologist. Harvard University Press, Cambridge
Michod R (1999) Darwinian dynamics. Oxford University Press, New York
Nagy JD (2004) Competition and natural selection in a mathematical model of cancer. Bull Math Biol 66:663–687

Neander K (1991) Functions as selected effects: the conceptual analysts defense. Philos Sci 58:168–184

Noe R, Hammerstein P (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav Ecol Sociobiol 35:1–11

Odling-Smee J, Laland K, Feldman M (2003) Niche construction: the neglected process in evolution. Princeton University Press, Princeton

Poisot T, Mouquet N, Gravel D (2013) Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. Ecol Lett. doi:10.1111/ele.12118

Queller DC, Strassmann JE. (2009) Beyond society: The evolution of organismality. Philos Trans R Soc Lond B Biol Sci 364:3143–3155

Reeve HK, Hölldobler B. (2007) The emergence of a superorganism through intergroup competition. Proc Natl Acad Sci USA 104:9736–9740

Ricklefs RE (2008) Disintegration of the ecological community. Am Nat 172:741–750

Salmon W (1984) Scientific explanation and the causal structure of the world. Princeton University Press, Princeton

Simpson BB (ed) (1988) Biological diversity in the context of ecosystem structure and function: proposal for an IUBS (International Union of Biological Sciences). Biology International 124:15–17

Sober E, Wilson DS (1998) Unto others: the evolution and osychology of unselfish behavior. Harvard University Press, Cambridge

Sterelny K (2006) Local ecological communities. Philos Sci 73:215–231

van Baalen M (1998) Coevolution of recovery ability and virulence. Proc R Soc Lond B 265:317–325

van Baalen M, Jansen VA (2001) Dangerous liaisons: The ecology of private interest and common good. Oikos 95:211–224

Weisberg M (2006) Robustness analysis. Philos Sci 73:730–742

Woodward J (2003) Making things happen: a theory of causal explanation. Oxford University Press, Oxford

Wright JP, Jones CG (2004) Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. Ecology 85:2071–2081