Philosophy of Science (2026), **00**, 1–11
doi:10.1017/psa.2026.10242

PSA PHILOSOPHY OF SCIENCE ASSOCIATION
PHILOSOPHY OF SCIENCE

SYMPOSIA PAPER

Levels and Hierarchies in Evolution

Javier Suárez

Department of Philosophy, University of Oviedo, Oviedo, Spain
Email: javier.suarez@uniovi.es

(Received 04 January 2025 UTC; revised 09 June 2026 UTC; accepted 10 June 2026 UTC)

Abstract

I analyze the main characteristics of the hierarchy of levels of selection as manifestors of adaptation (i.e., hierarchy of levels of evolutionary organization) and show that, while ranked, this hierarchy is nonnested. Secondly, I consider a potential objection to my approach derived from Eronen and Ramsey's (2025) claim that *levels of organization* should be teased apart from *levels of selection*. I argue that their approach rests on a failure to distinguish between interactors and manifestors of adaptation, for while a hierarchy of interactors does not correspond to a hierarchy of levels of organization, a hierarchy of manifestors does.

1. Introduction

The notion of *level* is of wide application in contemporary philosophy and biology.[1] Oppenheim and Putnam (1958) suppose the classical locus of the so-called layer-cake model of reality, according to which levels are structured in a stepwise compositional fashion, where theories formulated in terms of higher-level components (e.g., social structures) could potentially be reduced to theories formulated in terms of lower-level components (e.g., atoms or subatomic particles). Oppenheim and Putnam's model was supposed to account for all the existing sciences, under the assumptions that the order of the sciences and how these could be theoretically reduced to one another reflected the ultimate order of nature. An underlying assumption in their model was that levels generated hierarchies, and these hierarchical ranks were essential for understanding nature.

Even while Oppenheim and Putnam's model is rejected in contemporary science because of its many incongruences (see Potochnik and McGill 2012), the concept of level still plays a key role in today's philosophy, particularly in its application to biology. In this case, its application is narrower than in Oppenheim and Putnam's, as

[1] Across the article, I will assume that the notion of level I am analyzing is ontological (Craver's levels of nature) and not merely epistemic (Craver's levels of science). This is important because it will lead me to ignore epistemic accounts of levels (e.g., Brooks 2021).

© The Author(s), 2026. Published by Cambridge University Press on behalf of Philosophy of Science Association. This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-ShareAlike licence (https://creativecommons.org/licenses/by-nc-sa/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the same Creative Commons licence is used to distribute the re-used or adapted article and the original article is properly cited. The written permission of Cambridge University Press or the rights holder(s) must be obtained prior to any commercial use.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

we are focusing not on how nature as a whole is structured but rather on how the different biological entities (cells, multicellular organisms, colonial organisms, etc.) are hierarchically structured. In fact, the notion of level is pervasive in several fields of biology. For example, in physiology, it is customary to distinguish systems, organs, tissues, and cells; in ecology, one often distinguishes between ecosystems, regional ecosystems, local ecosystems, avatars, and organisms; in taxonomy, between kingdoms, phyla, classes, orders, families, genus, and species; and so forth. Levels can be established based on several criteria: scale levels (arranged according to scale properties such as size or tempo), causal levels (arranged according to the action of causality), or compositional levels (part–whole relations) (Craver 2007, 171). In general, the different biological levels are established in hierarchies of compositional inclusion, where entities at a higher level are supposed to include, as *components*, only entities from the lower level, in a way that creates the appearance of a *nested* order (sec. 3).

The reason why we tend to order the biological world into levels partially rests on their heuristic value in understanding the complexity of nature. As Eldredge (1985), doing pioneering work on the notion of levels and on biological hierarchies, once put it: "[H]ierarchies actually deal with complexity by teasing it apart; it is as if hierarchies are more honest in their simple recognition that a system is complex than is an approach that seeks unity in characterizing the system in simple terms" (Eldredge 1985, 11).

Similarly, Wimsatt characterizes levels "as local maxima of regularity and predictability in the phase space of alternative modes of organization of matter" (2007, 209); Brooks et al. (2021) open their *Levels of Organization in the Biological Sciences* by claiming that "levels demarcate quasi-independent channels of causal interactions and are sites of *scale-specific dynamics* and *causal generalizations*" (Brooks et al. 2021, 7, emphasis added). All these are ways of claiming that levels are structures of reality that both allow understanding its complexity and, I would claim, reflect the very structure of nature.

In this article, I focus on one of the uses of the notions of hierarchy and levels as they are applied in evolutionary biology, concretely in the debate on levels of selection, where it has been especially useful to tease apart biological complexity. I specifically argue that this view of levels of organization as levels of selection generates a nonnested evolutionary hierarchy, highlighting the necessity of rethinking our metaphysical assumptions on hierarchy construction, at least in evolutionary biology. Secondly, I consider a potential objection to my approach derived from a recent work by Eronen and Ramsey (2025), where they claim that the notion of "levels" used in the debates on units of selection should be distinguished from the notion of "level" that is used in the debate on levels of organization. I will argue that Eronen and Ramsey (2022) miss an important distinction between two types of units of selection: *interactors* and *manifestors of adaptation* (*manifestors*, in what follows) (Lloyd 1992, 2024; Suárez and Lloyd 2023). If we take this distinction into account, then levels of selection correspond to levels of organization because manifestors are the result of organizational processes in their focal level.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

2. The levels of evolutionary organization are nonnested

The nested hierarchy of the evolutionary hierarchy is generally accepted in biological research. For example, in his *Unfinished Synthesis*, Eldredge claims, "Many recent discussions of hierarchy in evolution seem almost to synonymize hierarchy with selection at different levels. A fundamental premise of this book is that the biological entities that participate in the evolutionary process are themselves hierarchically arranged *in a nested fashion*. Thus, *ontology* [i.e., how selection operates] virtually forces our evolutionary theory to be structured hierarchically" (1985, 104, emphasis added).

Echoing this, Tëmkin and Eldredge (2015, 184) have recently claimed: "Biological evolutionary theory is ontologically committed to the existence of nested hierarchies in nature," restating Eldredge's commitment to the nestedness of the evolutionary hierarchy.[2]

The assumption about nestedness is also present in most discussions about evolutionary transitions in individuality (Maynard-Smith and Szathmáry 1995). For instance, Michod's (1999) model, according to which a transition entails a fitness transfer from the lower-level entities to the higher-level entities, involves an assumption about nestedness: If the lower level loses its direct visibility to natural selection because its fitness gets transferred to the higher level, then the higher level must contain, as components, all and only the lower-level units. Similar considerations apply to Godfrey-Smith's (2009) model of Darwinian individuality. The evolution of a Darwinian individual at the higher level entails the de-Darwinization of the lower-level units, which become nested within the newly emerged Darwinian individual.

The assumption is also present in earlier works on units of selection. For instance, Lewontin's (1970) founding article presupposed that the biological world was nested in a hierarchy that included molecules, organelles, cells, gametes, (multicellular) organisms, some groups of organisms, populations, and higher levels. Hull's (1980) abstract approach to natural selection, distinguishing between interactors and replicators, generated a dual hierarchy of both interactors and replicators, as illustrated in Brandon's (1988) work. In all these cases, nested evolutionary hierarchies were presumed (for a helpful analysis, see Griesemer 2005).

Similarly, the assumption is present in most philosophical accounts about levels, including Craver's (2007) mechanistic model, in which mechanisms are composed of parts that can also be mechanisms, and this generates a nested rank. This equally applies to Wimsatt's (2007) model: "By level of organization, I mean here compositional levels—hierarchical divisions of stuff ... organized by part-whole relations, in which *wholes at one level function as parts at the next (and at all higher) levels*" (Wimsatt 2007, 201, emphasis added).[3]

[2] For those unfamiliar, Eldredge (1985) makes a distinction between a genealogical (focusing on levels exemplifying reproductive traits, i.e., modification and retention of information) and an ecological (focusing on levels exemplifying traits related to ecological survival, i.e., reflecting the economic organization of living beings) hierarchy and contends that there is no interaction between them (except for organisms that belong to both) and that each of them is nested. I have no space here to discuss these ideas, but my argument for nonnestedness relies on how these two hierarchies interact.

[3] Wimsatt's approach includes a tripartite distinction between *levels*, *perspectives*, and *causal thickets*, and only the former would be nested. My claim here will be that levels of organization in biology, which necessarily result from evolution, are nonnested. Thus, I do not think Wimsatt could reply that what I describe are mere perspectives or thickets.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

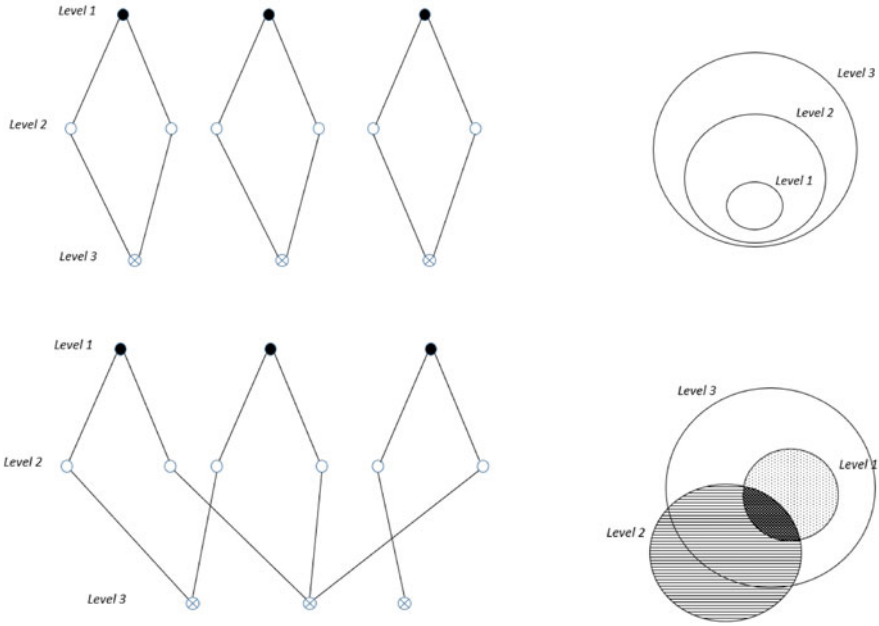


Figure 1. *Upper*, Two ways of representing nested hierarchies (graph; Venn diagram). Level 2 would be the focal level. *Lower*, Two ways of representing nonnested hierarchies (graph; Venn diagram).

This general view concerning the nested nature of levels of organization can be summarized by citing a passage from Eronen and Brooks (2023, sec. 1, emphasis added; see also Potochnik and McGill 2012, 121): "This idea that levels of organization of organization form 'nested' compositional hierarchies where there are wholes at higher levels and their components at lower levels, and the components themselves can be further decomposed into parts, *remains one of the core features of the notion of levels of organization up to this day*."[4]

To argue that a hierarchy is nested means that the entities in the hierarchy are related based on inclusiveness. In a nested hierarchy, the level where a phenomenon occurs is the focal level, and entities below (less inclusive) and above (more inclusive) are the lower and higher levels, respectively. Semiformally, nestedness can be defined as follows: Take three levels, *Ln*, *Ln**, and *Ln***, and assume that *Ln*** is higher than *Ln**, which is in turn higher than *Ln*. Then, when one generates a rank of these three levels, for example, a rank of sets and subsets, it is assumed that the rank constitutes a nested hierarchy if all the entities belonging to *Ln* belong to *Ln**, and hence they also belong to *Ln***. The nestedness assumption derives from the idea that levels include a relation of composition, and composition is ordered in a nested way. Figure 1 shows two ways of representing nested and nonnested hierarchies.

[4] One important exception to this general trend is Simpson (1984), who conceived evolutionary theory as an inter-nested hierarchy between the three modes of evolution he distinguishes: quantum evolution, phyletic evolution, and speciation.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

If the assumption about the nested nature of the evolutionary hierarchy is so pervasive,[5] then one may think there is something correct in it. Unfortunately, the assumption is simply an ideal that does not correspond to the real structure of levels of evolutionary organization and, hence, the type of ideal that a pragmatist should reject. I have two reasons to assert this.

Firstly, the mechanism that produces levels of evolutionary organization does not require a nested biological hierarchy. To introduce this argument properly, I must first introduce a distinction between two meanings of levels of evolutionary organization or, also, levels of selection (Lloyd 1992, 2024; Suárez and Lloyd 2023).[6] The term *levels of selection* can be ambiguously used to refer to two types of entities: interactors and manifestors. A unit of selection is an *interactor* when, in effect, it engages (as a cohesive whole) in fitness-affecting interactions with its environment in a way that reproduction is differential. For example, for all we know, and assuming that sexual selection is going on, humans are interactors for traits such as their eye colors because different variants of the trait within the population are expected to lead to differential reproduction of their bearers. On the other hand, a unit of selection is a manifestor when it is the result of selection reputedly acting at its focal level so that one or some of its traits are engineered (or to put it differently, are a product of transtemporal accumulation) to carry out the function(s) they perform. In this sense, manifestors are the result of optimization at their focal level, at least for one trait and often for more than one trait, as occurs with the type of entities Okasha (2018) calls *type 1 agents* (a specific type of manifestor). For instance, humans are manifestors for organs such as the eye because the organ has been optimized through the constant action of natural selection to perform its function. Manifestors are thus products of selection, whereas interactors exist because there is a process of selection currently going on at that level.

Given their nature as *products* of selection, I consider manifestors to be the best candidates to play the role of levels of evolutionary organization. Thus, we must analyze the mechanism that produces manifestors to see whether nestedness is theoretically required to interpret their evolution. Manifestors are generated through the persistent action of selection on a trait (or traits) on a specific focal level. The mechanism often used to analyze how this process occurs is multilevel selection, or kin selection, but note that this approach requires the action of multilevel selection as well, is reducible to the latter, or even is epistemically parasitic on multilevel selection (see Lloyd 2024). Although most multilevel selection models presume a nested hierarchy, in which particles are nested within collectives, this requirement is not necessary. As Okasha explains, "The underlying causal mechanism [of evolution by natural selection] does not require nesting; it could work equally well with overlapping groups of lower-level units" (Okasha 2006, 44). That is, the main process triggering evolution by natural selection (multilevel selection) is often theoretically conceived as if it acted on a nested hierarchy of levels of selection. But the presupposition is not needed for the theory to work and be applicable to the evolution of the biological world.

[5] Eronen (2021) has already questioned the nestedness assumption. Yet he has not done so from an evolutionary perspective or developed the consequences for evolution.

[6] Lloyd (2024) distinguishes two more meanings (replicators, beneficiaries of adaptation), but since these other two are not relevant for the point I will make, I will not use them in my discussion.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

My argument could be contested by arguing that multilevel selection explains evolution acting on/generating interactors, but not generating manifestors, which are the units I claim generate levels of organization. This is correct. But note that multilevel selection can also generate manifestors, and if it describes the way natural selection acts, it must be the force generating manifestors too—whenever these are produced. There is a more serious objection to this argument, though. One could argue that my position is merely *theoretical*: Theoretically, multilevel selection could act on a nonnested world and even produce different levels of organization in a nonnested fashion. But the biological world is in fact nested: Empirically, different levels of evolutionary organization only arise in a nested fashion.

I, however, claim that this objection is incorrect because there is evidence of natural selection producing manifestors across a nonnested hierarchy, exactly in the nonnested way I think the evolutionary hierarchy is organized. Some holobionts constitute a canonical example of this (Suárez 2020). Holobionts are symbiotic assemblages that result from the association between an animal or plant host plus its symbiotic microbiome. Most holobionts contain parts that reproduce independently from one another; in most circumstances, this could prevent the evolution of a manifestor at the level of the holobiont, as many researchers have argued (Skillings 2016; Douglas and Werren 2016). Yet some evidence suggests that some holobionts are manifestors of adaptation in a very specific way, as shown for the case of vampire bats (Suárez 2020). In these cases, certain traits of the microbiome would be responsible for generating the nonnestedness of the evolutionary hierarchy. These traits will be such that they will depend on the microbiome for their phenotypic expression because the animal host (bat) cannot integrate them into their genome and transcribe them by itself. Yet the long-term persistence of these specific traits historically/evolutionarily depends on their phenotypic expression within the context of a vampire bat. Otherwise, these traits would likely be lost by the bacteria bearing them. The main prediction would be that these traits, which have also been called *hologenomic traits* (Suárez and Triviño 2020), will engage in higher horizontal gene transfer within the context of the microbiome, will be easily acquired and expressed by several bacterial phyla, and will also be easily lost outside the host environment.

These traits, which constitute the basis for holobionts to be manifestors, are the ones generating a nonnested evolutionary hierarchy. They would entail the existence of a manifestor at the level of the bacterial phyla of the microbiome, at the level of the host, and finally, at the level of the biological composite formed by the host plus these specific microbiome traits. Note that in this hierarchical organization, the levels of manifestors will be nonnested because only parts of a lower level (the hologenomic traits) will belong to the higher level, but the lower level as a whole would not belong to the higher level, despite its necessity for the expression of lower-level traits. Holobionts thus constitute an empirical example of the nonnestedness of the biological hierarchy.

3. Levels of selection and levels of organization

The account I have presented is prone to one objection, though. In a recent article, Eronen and Ramsey (2025, 503) ask about the notion of "levels" underlying the debate on units of selection. Their main claim is that there are at least two concepts of

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

hierarchy and *level* that are usually conflated in the debates on units of selection: a hierarchy of levels of organization (e.g., molecules, cells, organisms, populations, species) and a hierarchy of levels of fitness-affecting interactions (Eronen and Ramsey's preferred deflationary account of levels of selection), where entities are entangled together because they engage in fitness-affecting interactions with one another. Eronen and Ramsey believe that both hierarchies require the existence of particles (lower level) and collectives or groups of a certain sort (higher level) in a nested relationship.

Eronen and Ramsey believe that these two conceptions of "level" must be distinguished for two reasons. First, ontologically, they claim that "although the parts and collectives in levels of organization *can* engage in fitness-affecting interactions, they do not have to" (Eronen and Ramsey 2022); additionally, they claim that their criterion for defining levels of selection needs to be liberal enough to accommodate many different processes, and in this sense, it will not have a neat correspondence to levels of organization as these are traditionally defined. Second, epistemically, they argue that each notion of *level* plays a different role in the debates on organization, the former (levels of selection) being important for analyzing how specific examples of multilevel selection work and the latter for asking more general questions (e.g., the role of multilevel selection in the emergence of new levels of organization, or the relationship between both concepts).

I think Eronen and Ramsey (2025) are pointing to something partially correct concerning levels of selection, but they fail to use the conceptual tools that would allow them to characterize the problem correctly. Particularly, they fail to distinguish between the two meanings of *level of selection* I introduced earlier: interactor and manifestor. Distinguishing these two concepts illuminates where their argument fails and why at least a specific meaning of *level of selection* (manifestor) has a neat correspondence with traditional levels of organization.

If by *level of selection*, Eronen and Ramsey (2025) mean interactors, then they are correct: Taking fitness-affecting interactions, which is the defining feature of interactors, as the criterion to determine levels of organization is way too liberal. In fact, a common mistake in part of the recent literature on units is to think that because interactors need to form "a cohesive whole," they must already possess evolved properties for being visible to natural selection (Suárez and Lloyd 2023, 44). But interactors are simply empirically and "statistically" cohesive; that is, they are cohesive enough so that it is possible to tell apart cases when natural selection is acting on them from cases when the effects perceived at their level are merely a cross-product of selection acting at a different level. In other words, it is easy for interactors to appear. They simply require the existence of a trait at their focal level that leads to differential reproduction either to their own level or to a lower level. That's why species, almost every holobiont, and groups are often interactors. Interactors lead to product-of-selection adaptations, but they do not necessarily lead to the evolution of engineering adaptations[7] at their focal level because they do not

[7] See Lloyd (1992, 2024) and Suárez and Lloyd (2023) for the notions of "engineering adaptation" and "product-of-selection adaptation."

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

necessarily reproduce themselves in a way that is consistent enough to generate those traits. In this sense, as Eronen and Ramsey (2025) correctly claim, interactors cannot equate traditional levels of organization, even though they also form their own biological hierarchy.

Manifestors are also a level of selection and, I claim, the one that most neatly corresponds to traditional levels of organization, at least as these are seen in biology.[8] This is because manifestors, because of their own origin as the result of a persistent selection process acting at their focal level, exemplify the typical features of levels of organization as these are conceived in biology. Firstly, manifestors correspond to real structures of the world that can be identified through a robust analysis (Wimsatt 2007), their existence is established based on part–whole relationships (i.e., their existence is compositional), and their existence at one focal level imposes constraints on their lower-level component parts (Moreno and Mossio 2015). For example, because humans are manifestors for the eye organ, the existence of the organ imposes constraints on how cone and rod cells should be disposed and interact. Or when manifestors become type 1 agents, they reduce the internal conflict between their parts, to a point at which they lose their own autonomy. This latter notion of *constraint* is important because it is the key element of the organizational account of individuality elaborated by Moreno and collaborators. An advantage of the concept of manifestor is that it allows explaining where these constraints come from (i.e., their origins), what norms they impose in their component parts, and how they operate. Additionally, the type of constraints imposed by the manifestor on the lower-level parts is not a necessary characteristic of the interactor, as Eronen and Ramsey (2025) also notice. However, it seems to be a defining feature of levels of organization because it allows creating a certain sense of "order" at the focal level, which seems a reasonable criterion for referring to a level as a level of "organization."

Secondly, all the usual lists of levels of organization include units that are classical manifestors. For instance, Eronen and Ramsey (2025) provide a list that includes molecules, cells, individuals, populations, and species. But all these have been shown to be manifestors, in certain cases (for a summary, see Lloyd 2024). Other lists may include colonial organisms (e.g., some species of ants, termites, bees), holobionts, or some other types of groups. My claim is that the elements of these lists are typically included because they have been shown to be, at least in certain circumstances, manifestors as the concept has been defined for the debates on units of selection.

Thirdly, most of the properties that have been used to define biological individuality, which could ultimately be taken as conditions to elaborate a hierarchy of levels of organization, correspond to features that have been selected for at the specific level where there is a manifestor. This has been shown in Clarke's (2013) work on the concept of individuality, where she argues that different properties (division of labor, germ–soma separation, immunological recognition, etc.) correspond to either a demarcating or a policing mechanism, preventing selection from a lower level and

[8] I do not think the concept applies beyond biology, but I guess those friendly to the generalized Darwinism project would be sympathetic to finding manifestors in social structures—or any other traditional nonbiological levels of organization.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

hence ensuring that the focal level acts as a manifestor. Thus, a hierarchy of manifestors would be ontologically prior or even equivalent to any other hierarchy of levels of organization.[9]

If my arguments about the relationship between the manifestor and the debate on levels of organization are correct, they show, contra Eronen and Ramsey's approach, that the debates on levels of selection provide an adequate platform to evaluate the notion of level of organization. Hence, my conclusion about the nonnestedness of the biological hierarchy is still supported by the evidence.

4. Conclusion

In this article, I have carved out one of the metaphysical characteristics of the evolutionary hierarchy (as a hierarchy of levels of selection), arguing that it must be a hierarchy of nonnested levels. My argument has been based on two observations: firstly, that theoretically, there are no grounds to assume that the evolutionary hierarchy needs to be nested, as the mechanism used to study it (multilevel selection) does not require such assumption; secondly, that there are some good empirical examples of levels of evolutionary of organization existing at cross-levels, hence empirically supporting the existence of a nonnested hierarchy. Secondly, I have considered a potential objection by Eronen and Ramsey's (2025), who claim that the notion of "level" at play in the debates on levels of selection is different from the notion of "level" that appears in levels of organization. I argued that their position is mistaken because it rests on failing to appropriately distinguish between interactors and manifestors of adaptations as two meanings of the term *level of selection*. Once this distinction is cleared up, it becomes patent that the hierarchy of interactors does not correspond to the hierarchy of levels of organization, whereas the hierarchy of manifestors (which is the one where I grounded my arguments for the nonnestedness of the biological hierarchy) does.

Acknowledgments. This article was presented at the 2024 Biennial Meeting of the Philosophy of Science Association, as part of the symposium "Pragmatist or Merely Pragmatic? Using Pragmatism in Biological Practice." I thank all my co-panelists, as well as the participants, for their comments. I also thank Gui Sanches de Oliveira for reading and commenting on a previous draft. Finally, I formally thank the Ministry of Science, Innovativeness and Universities, project PID2022-137993NA-I00, "An Exploration of the Philosophy of Lineages in the Light of Contemporary Biology" for financial support.

Funding Statement. Ministry of Science, Innovativeness and Universities, project PID2022-137993NA-I00, "An Exploration of the Philosophy of Lineages in the Light of Contemporary Biology."

Declarations. None to declare.

References

Brandon, Robert N. 1988. "Levels of Selection: A Hierarchy of Interactors." In *The Role of Behavior in Evolution*, edited by Henry C. Plotkin, 51–71. Cambridge, MA: MIT Press.

[9] This does not mean I am committed to a reduction of all concepts of individuality to the manifestor, or to any other concept of evolutionary individuality. My claim is simply that the properties used to classify other types of individuality result from processes of selection on specific traits (or properties) generating the product that we call *manifestor*.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

Brooks, Daniel J., James DiFrisco, and William C. Wimsatt, eds.(2021) *Levels of Organization in the Biological Sciences*. Cambridge, MA: MIT Press.

Brooks, Daniel S. 2021. "A New Look at 'Levels of Organization' in Biology." *Erkenntnis* 86 (6):1483–508. https://doi.org/10.1007/s10670-019-00166-7.

Clarke, Ellen. 2013. "The multiple realizability of biological individuals." *The Journal of Philosophy* 110(8):413–435.

Craver, Carl F. 2007. *Explaining the Brain: Mechanisms and the Mosaic Unity of Neuroscience*. Oxford, UK: Clarendon Press.

Douglas, Angela E., and John H. Werren. 2016. "Holes in the Hologenome: Why Host-Microbe Symbioses Are Not Holobionts." *mBio* 7 (2):e02099–15. https://doi.org/10.1128/mbio.02099-15.

Eldredge, Niles. 1985. *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*. New York: Oxford University Press.

Eronen, Markus I. 2021. "Levels, Nests, and Branches: Compositional Organization and Downward Causation in Biology." In *Levels of Organization in the Biological Sciences*, edited by Daniel J. Brooks, James DiFrisco, and William C. Wimsatt, 77–88. Cambridge, MA: MIT Press.

Eronen, Markus I., and Brooks, Daniel S. 2023. "Levels of Organization in Biology." In *The Stanford Encyclopedia of Philosophy*, edited by Edward N. Zalta & Uri Nodelman. Stanford: Metaphysics Research Lab, Stanford University. https://plato.stanford.edu/archives/sum2024/entries/levels-org-biology/ (accessed 2 July 2026).

Eronen, Markus I., and Grant Ramsey. 2025. "What Are the 'Levels' in Levels of Selection?" *The British Journal for the Philosophy of Science* 76 (2):495–518. https://doi.org/10.1086/718990.

Godfrey-Smith, P. 2009. *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

Griesemer, James R. 2005. "The Informational Gene and the Substantial Body: On the Generalization of Evolutionary Theory by Abstraction." In *Idealization XII: Correcting the Model. Idealization and Abstraction in the Sciences*, edited by Nancy Cartwright and Martin R. Jones, 59–115. Amsterdam: Rodopi.

Hull, David L. 1980. "Individuality and Selection." *Annual Review of Ecology and Systematics* 11:311–32.

Lewontin, Richard C. 1970. "The Units of Selection." *Annual Review of Ecology and Systematics* 1:1–18. https://doi.org/10.1146/annurev.es.01.110170.000245.

Lloyd, Elisabeth A. 1992. "Unit of Selection." In *Keywords in Evolutionary Biology*, edited by Evelyn F. Keller and Elisabeth A. Lloyd, 334–40. Cambridge, MA: Harvard University Press.

Lloyd, Elisabeth A. 2024. "Units and Levels of Selection." In *The Stanford Encyclopaedia of Philosophy*, edited by Edward N. Zalta. Stanford: Stanford University Press. https://plato.stanford.edu/entries/selection-units/.

Maynard Smith, John, and Eörs Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford: W. H. Freeman Spektrum.

Michod, Richard E. 1999. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.

Moreno, Alvaro, and Matteo Mossio. 2015. *Biological Autonomy*. Dordrecht: Springer.

Okasha, Samir. 2006. *Evolution and the Levels of Selection*. Oxford: Oxford University Press.

Okasha, Samir. 2018. *Agents and Goals in Evolution*. Oxford: Oxford University Press.

Oppenheim, Paul, and Hilary Putnam. 1958. "Unity of Science as a Working Hypothesis." In *Concepts, Theories, and the Mind-Body Problem*, edited by Herbert Feigl, Michael Scriven, and Griver Maxwell, 3–36. Minneapolis: University of Minnesota Press.

Potochnik, Angela, and Brian McGill. 2012. "The Limitations of Hierarchical Organization." *Philosophy of Science* 79 (1):120–40. https://doi.org/10.1086/663237.

Simpson, George G. 1984. *Tempo and Mode in Evolution*. New York: Columbia University Press.

Skillings, Derek. 2016. "Holobionts and the Ecology of Organisms: Multi-Species Communities or Integrated Individuals?" *Biology & Philosophy* 31:875–92. https://doi.org/10.1007/s10539-016-9544-0.

Suárez, Javier, 2020. "The Stability of Traits Conception of the Hologenome: An Evolutionary Account of Holobiont Individuality." *History and Philosophy of the Life Sciences* 42 (1):11. https://doi.org/10.1007/s40656-020-00305-2.

Suárez, Javier, and Elisabeth A. Lloyd, 2023. *Units of Selection*. Cambridge: Cambridge University Press.

Suárez, Javier, and Vanessa Triviño, 2020. "What Is a Hologenomic Adaptation? Emergent Individuality and Interidentity in Multispecies Systems." *Frontiers in Psychology* 11:187. https://doi.org/10.3389/fpsyg.2020.00187.

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press

Tëmkin, Ilya, and Niles Eldredge. 2015. "Networks and Hierarchies: Approaching Complexity in Evolutionary Theory." In *Macroevolution*, edited by Emanuele Serrelli and Nathalie Gontierr, 183–226. Dordrecht: Springer. https://doi.org/10.1007/978-3-319-15045-1_6.

Wimsatt, William C. 2007. *Re-Engineering Philosophy for Limited Beings: Piecewise Approximations to Reality*. Cambridge, MA: Harvard University Press.

Cite this article: Suárez, Javier. 2026. "Levels and Hierarchies in Evolution." *Philosophy of Science*. https://doi.org/10.1017/psa.2026.10242

https://doi.org/10.1017/psa.2026.10242 Published online by Cambridge University Press