

# Species as natural entities, instrumental units and ranked taxa: new perspectives on the grouping and ranking problems

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This paper addresses the two problems that together constitute the species problem: the grouping problem (the question: on what basis should organisms be allocated to groups that are candidate species?) and the ranking problem (the question: on what basis should such groups be ranked as species?). We inquire what it means to say that species are real or that species are natural units, and argue for solutions to the grouping and ranking problems that allow us to be realists about species while at the same time avoiding the problems of a naive realism about species. In the account presented here, theoretical relevance is what constitutes the reality of species.

**ADDITIONAL KEYWORDS:** DNA barcoding – grouping problem – integrative taxonomy – philosophy of biology – pluralism – ranking problem – realism – species problem.

## INTRODUCTION

The long-standing debate on the concept of species hinges on a number of questions that remain unanswered. For instance, are species merely instrumental units, i.e. tools constructed for specific purposes in biological research without having reality in nature, or do species exist as real entities in nature? If species are mere tools without existing as entities in nature, what makes those groupings of organisms that are identified as species into useful tools for research, and on what basis should organisms be grouped into species to obtain the best tools? If species are natural entities, what kind of entities are they, and which natural factors bind organisms together into species? Either way, the next question is, what makes a particular grouping of organisms (be it a tool or a real entity) into a species, rather than, say, a genus or variety? Do the groups that biologists identify as species and give binomial names have anything in common with each other that other groups lack? If so, what?

If not, then why do we consider the various species of birds, insects, flowering plants, fungi, microbes, etc. to be species? These two clusters of questions have become known as the grouping problem and the ranking problem, respectively (Mayr, 1981; Mishler & Brandon, 1987; Baum, 2009). Together, they constitute the species problem (e.g. Wilson, 1999; Reydon, 2004, 2005; Richards, 2010; Kunz, 2012; Zachos, 2016; Wilkins, 2018).

Next to these clusters of questions, the numerous species concepts that have been advanced over the years as part of the debate give rise the question of which (if any) of the available concepts is the correct one, both theoretically and for practical purposes, and whether, instead of searching for the correct species concept, perhaps a plurality of concepts should be adopted to serve different purposes. The literature on the topic is vast, and it is not clear how many distinct species concepts have been proposed. A commonly mentioned count is 22 (Mayden, 1997, 1999), but other counts range from seven (with 27 variations and combinations; Wilkins, 2011) to 92 (Lherminier & Solignac, 2000) or > 100 (Wilkins, 2009). Most of the available concepts,

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however, are variations on one or more fundamental ones, such that the number of genuinely distinct species concepts probably is comparatively low. Still, the multiplicity of available species concepts, the absence of any clear criteria to single out the one concept that specifies what species really are or the one that constitutes the best guideline for practical purposes, and the grouping and ranking problems constitute persistent problems for biological science. Species are the ‘currency’ of biological science (Agapow *et al.*, 2004: 162) and play crucial roles in research, the formulation of knowledge statements and scientific communication, and the problems thus need to be addressed.

In the present paper, we advocate solutions to the grouping and ranking problems that involve a view of species as natural entities that are ranked as species on the basis of instrumental grounds. The view we defend combines realism about individual species with anti-realism about the species category. As a general solution to the grouping and ranking problems, this view is not new; as Ereshefsky (2010, 2011, 2014) pointed out, Darwin’s writings can be interpreted as encompassing the same view of species. More recently, Baum’s (2009; Wright & Baum, 2018: 10) view of species as ‘ranked taxa’ also resolves the grouping and ranking problems along these lines. Our contribution does not consist of proposing new solutions to the grouping and ranking problems, but in fleshing out some of the details in existing solutions and presenting new arguments for them. More precisely, what is new in our account is: (1) our explication of what kind of natural entities species are; (2) our explication of the grounds on which such entities should be ranked as species; (3) our argument for species pluralism that shows how species pluralism follows from causal pluralism in the living world; and (4) our explication of the consequences of species pluralism for integrative taxonomy and DNA barcoding.

In what follows, we first discuss the species problem in more detail, focusing on the question of whether species are real entities, and then present our solutions to the grouping and ranking problems. We conclude by examining some consequences of our account for taxonomic practice, addressing integrative taxonomy and DNA barcoding.

### ARE SPECIES REAL ENTITIES IN NATURE?

That species are real entities in nature is a fundamental assumption in many contexts. Everyday practices in which references to species are made, for example in field guides, zoos, natural history museums, the IUCN Red List of Threatened Species, and so on, all presume that species are real entities that exist in nature and can be discovered, described, protected, counted, etc. (Kunz, 2012; Reydon, 2013a; Reydon, 2019). In

addition, the central role that species play in the biological sciences is difficult to understand if species were not to be real entities in nature (Wilson, 1992: 38; Cracraft, 1997: 327–328; Mace, 2004: 711; Schlick-Steiner, 2010: 422). After all, what would biologists be talking about if species are not real and they publish new findings about the species they have studied?

In particular, an important (though unachievable) aim of biological research is to establish an inventory of all species that exist, establish species counts of the various regions of the world and provide concise species descriptions (May, 1988, 1990, 1992, 2010; Dayrat, 2005; Mora *et al.*, 2011). May (1992, 2010), for example, asked us to imagine what an extraterrestrial explorer visiting the Earth would want to know and suggested that the explorer would first inquire about the number and variety of kinds of organisms inhabiting our planet. May called it a sad truth and embarrassment that, notwithstanding the long history of biological research, we still would not be able to answer that question even approximately. In a similar spirit, Wheeler *et al.* (2012: 2) recently called for ‘a comprehensive inventory of species and detailed map of the biosphere’. Underlying such appeals is the problem that taxonomy and exploration of biodiversity are taking place at increasingly slower paces. But a deeper problem relates to the assumption that species counts have definite answers. The assumption is that species are real entities in nature, such that at any point in time there is a fact of the matter regarding the question of how many such entities genuinely exist (even though that number is constantly changing as a consequence of speciation and extinction events). As the literature on the philosophy of biology of the past decades has shown, however, straightforward realism about species is difficult to uphold.

Note, first, that from a philosophical perspective the question which of the available species concepts might be the correct one is interpreted as a question of how to define the scientific term ‘species’. Notwithstanding common references to ‘species concepts’ in the literature, strictly speaking the controversy is about the meaning of a technical term in a specific area of science and not about concepts. In philosophy, concepts are conceived of as pieces of mental content (e.g. my concept of cats, based on my personal experiences and knowledge about cats) or abstractions represented in the minds of cognitive agents (Margolis & Laurence, 2014). This is not what is at stake in the debate; what is at stake is the question of what the term ‘species’ as used in biological science means, and the various species concepts that are available in the literature are definitions of that term that specify its meaning (Wilkins, 2009: xi; Wilkins, 2011). Definitions do not all give the meaning of a term in the same way, however, but can perform various functions: they can tell us

what the entities falling under a particular term are, tell us how in practice to individuate and identify the entities falling under the term, prescribe how a term should be used, describe how a term is used in real practices, tell us how a variable should be measured, and so on. Accordingly, philosophers distinguish between different kinds of definitions (Gupta, 2015).

In the debate on species concepts, two kinds of definitions are central: theoretical definitions and operational definitions (also called theoretical and operational concepts; see Hull, 1997; Mayden, 1997, 1999). Theoretical definitions specify what species are in accordance with the relevant scientific theories in which the term features, whereas operational definitions or concepts tell us how to deal with species in practice (how to individuate and delimit them, how to allocate organisms to species, on what basis to rank groups as species, etc.). The philosophical debate revolves around the following two pairs of contrasting positions (for more detailed discussions, see Dupré, 1999; Kunz, 2012; Reydon, 2005, 2013a; Richards, 2010):

1. *Monism vs. pluralism*: Monists hold that there is one correct theoretical definition of the term 'species.' Accordingly, the problem is to find the correct one among the available definitions, eliminating all others. Pluralists, in contrast, hold that there may be multiple acceptable theoretical definitions. For example, it may be the case that we need different definitions for application in different parts of biodiversity (e.g. one for birds, another for flowering plants, and so on), or that we need different definitions for different contexts of investigation (e.g. one for evolutionary studies, another for developmental genetics, etc.), or both in conjunction.
2. *Instrumentalism vs. realism*: Instrumentalists hold that species groupings are nothing more than tools devised by us to serve particular purposes without representing groups of organisms that really exist in nature, i.e. we group organisms into species, but the resulting groupings do not represent aspects of reality and do not exist as parts of reality. Realists, in contrast, hold that species groupings represent groups of organisms that really exist as groups in nature, or at least that species represent real aspects of the natural world, independently of our interests and grouping practices. Note that the issue here is the reality of individual species, such as *Drosophila melanogaster* and *Arabidopsis thaliana*, not the reality of the species category.

These two pairs of positions yield four combinations. Which of these are feasible ways of thinking about species?

## MONISM

Let us first examine monism. The most straightforward position would be monistic realism: species are real groups of organisms, and there is one correct theoretical definition of the term 'species' that picks out these groups. However, the large number of definitions and the persistent failure to achieve agreement on which of these, if any, pick out real groups that are good candidates for being ranked as species suggests that this option is unlikely to be feasible. Likewise, for monistic instrumentalism, even if we think of species groupings as mere tools for research, the persistent lack of agreement on which of the available definitions yields the correct tool and the fact that using different species definitions in practice can yield diverging results make it unlikely that there is only one right tool for the job. Moreover, instrumentalist views of species generally clash with the view that in some sense species must be real, and fail to provide a theoretical definition of 'species'. Although this suggests that monism is not a feasible position, this is still a matter of controversy. Several authors have argued that the various available species concepts can all be subsumed under a single overarching concept that specifies the nature of species, yielding a monistic view of species. We examine three such accounts to achieve more clarity on the feasibility of a monistic view of species.

Mayden (1997, 1999) suggested that the species problem was attributable to, among other things, a conflation of theoretical and operational species concepts (Mayden, 1997: 414–415; Mayden uses 'concept' and 'definition' interchangeably) and that a monistic view is 'fundamental to the whole of biological sciences' (Mayden, 1997: 418). Descent and speciation are processes that occur only in lineages, and only lineages with at least a minimum of integrity participate in speciation processes, Mayden argued, such that a theoretical understanding of species as lineages should be central in evolutionary theory to connect species as the products of evolution (i.e. branches on the tree of life) with the processes that produce them. As he put it: 'Without a primary concept as a working hypothesis and to serve as a bridge between pattern and process, it is untenable that we can advance on many fronts' (Mayden, 1997: 418). Mayden examined 22 definitions and concluded that a monistic account is possible with the evolutionary species concept (that defines species as lineages with their own independent evolutionary trajectory) as the theoretical concept that explicates what species are. This primary concept (as Mayden calls it) subsumes all other available (secondary) concepts as merely operational tools that further explicate how the primary concept applies in various

contexts of investigation (Mayden, 1997: 383, 1999: 97).

Although Mayden's monism was largely driven by the practical need for a clear explicative definition of the species category, De Queiroz (1998, 1999, 2007) proposed a similar view on the basis of an ontological assessment of available definitions. According to De Queiroz, all available species concepts share a common ontological element, suggesting that there is a single, general concept under which they can all be subsumed. As he put it: 'As it turns out, all contemporary species concepts share a common element [that] is fundamental to the way in which species are conceptualized. The general concept [...] equates species with separately evolving metapopulation lineages, or more specifically, with segments of such lineages' (De Queiroz, 2007: 880–881). Both authors thus hold that there is one explicative definition of the species category that specifies what species are: independently evolving lineages. Their views on the relationship between this primary concept and the other available definitions differ, however: Mayden argued that all other concepts are merely operationalizations of the primary concept, whereas De Queiroz claimed that all other concepts share the same ontological element.

A core element in both accounts is the distinction between explicative work that definitions and concepts can perform (stating what species are) and operational work (providing guidelines for various practical purposes). Richards (2010: chapter 5) followed Mayden's and De Queiroz' approach and highlighted this 'division of conceptual labor' to formulate a solution to the species problem that, similar to Mayden's solution, is 'theoretically monistic and operationally pluralistic' (Richards, 2010: 142). Although Richards advocates this view, he remains cautious when it comes to fully committing to theoretical monism. He pointed out: 'Whether or not this solution turns out to really solve the species problem remains to be seen. We need to determine how universal the theoretical concept based on the idea of segments of a population lineage can be.' (Richards, 2010: 142). Richards pointed out that for sexually reproducing vertebrates the lineage concept will adequately explicate what species are, whereas for asexually reproducing invertebrates (where every parent–offspring line is a separate lineage), plants (in which much hybridization occurs) and bacteria (which reproduce asexually and where much horizontal gene transfer occurs) the theoretical concept does not seem to fit well. Richards thus leaves the options open to recognize multiple different kinds of species-level lineages (yielding theoretical pluralism rather than monism) or to deny that all organisms form species.

We suggest that Richards' caution is well taken. Any explicative definition that conceives of species as branches on the tree of life presupposes that evolutionary

history is adequately depicted as a dichotomously branching tree. However, the adequacy of this representation of evolutionary history is increasingly doubted for much the same reasons as those that underpin Richards' caution (Doolittle & Baptiste, 2007; Doolittle, 2010; O'Malley & Koonin, 2011; Baptiste *et al.*, 2013). In large domains of biodiversity, organisms simply do not form clear-cut population-level lineages that can be delimited as species.

Moreover, not all available theoretical concepts, in fact, involve an ontology of species as lineages. Mayr's biological species concept, for instance, does not define species as spatiotemporally extended lineages, but as populations of organisms that are reproductively isolated from each other (Mayr, 1942: 120; Reydon, 2005: 141, 2008). Mayr (1987, 1988, 2004: chapter 10) emphasized that his definition was 'non-dimensional' and comparative: under this definition, a population is a species only in relationship to other populations existing at the same time and from which it is reproductively isolated. It does not involve any view of species as lineages and, as a widely used theoretical definition that continues to be the standard view of species in biology textbooks, constitutes an important counterexample to the view that all species definitions can be subsumed under a lineage definition. Several other counterexamples exist: the morphological species concept, the phenetic species concept, the ecological species concept and the recognition species concept all are theoretical (not operational) definitions that do not conceive of species as lineages, but as spatiotemporally localized populations or as sets of similar organisms (Reydon, 2005: 141 ff., 2008, 2013b). The solution advocated by Mayden, De Queiroz and Richards, then, fails: some prominent theoretical definitions do not conceive of species as lineages or lineage segments, and these authors erroneously subsume these under an overarching theoretical concept that states that all species are lineages (Reydon, 2013b: 386).

It is thus doubtful whether monism is a feasible position in the species debate. In any case, proponents of monistic positions, such as Mayden, De Queiroz and Richards, have failed to show that their views fit the spectrum of available species definitions (Reydon, 2004, 2005, 2008; for further critical discussions of species monism, see Dupré, 1993, 1999; Hull, 1997, 1999).

#### PLURALISM

We now turn to pluralism, which is left as the more plausible option. For the same reasons as monistic instrumentalism, pluralistic instrumentalism is not a feasible option, and we will not consider it further. Of the four possible positions, then, pluralistic realism seems the only option. But this position, too, has problems. For instance, although philosophers

of biology have long argued that a realist view of species is compatible with pluralism (Kitcher, 1984; Ereshefsky, 1998, 2010; Dupré, 1993, 1999, 2001; Wilkins, 2003), they have defended different versions of pluralistic realism. All share the view that multiple theoretical definitions of ‘species’ are acceptable, all of which yield groupings of organisms that are real or at least represent real features of nature, even though the different groupings do not map onto each other. Although it is not problematic to assume that there are multiple ways of grouping organisms that all represent real features of nature, it remains unclear why all the resulting groups should be counted as species. The various available versions of pluralistic realism provide different perspectives on this matter, but none provides an answer that could settle the matter once and for all (Reydon, 2005: 150–154).

We want to suggest a pluralistic realist position that aims to avoid this problem, starting from the observation that species are not entities that can be observed directly. In the field, we can directly observe individual organisms and (to some extent) populations, but not species. Thus, species cannot be thought of as things that exist ‘out there’ in a straightforward manner, in the way organisms or pieces of furniture exist. Instead, species are theoretical entities, the existence of which is inferred on the basis of theoretical considerations. ‘Species’ is a theoretical term, similar to ‘electron’ or ‘gene’, that, like other theoretical terms in science, is intended to represent aspects of nature that are highlighted in the scientific theory in which it features (i.e. evolutionary theory). Various such aspects are connected to the concept of species, including reproductive (in)compatibility of organisms, trait similarity and shared ancestry.

As an alternative to straightforward species realism, we thus suggest that the reality of species is better understood as consisting of what species represent (we explain this in more detail below). That is, species should be thought of as groups of organisms grouped together by us with the aim of representing biologically important aspects of nature. Given that they latch onto aspects of the natural world, species are not purely conventional groups (groups made by us on the basis of whatever interests we might have), but they do not simply exist ‘out there’ in the world either. This view is a weak form of realism about species (but for reasons of space, we cannot elaborate in detail how this form of realism maps onto the spectrum of positions that have been put forward in the philosophical debate on scientific realism).

Note that we do not suggest that simply any group that represents some aspect of reality should automatically be thought of as real in the above sense. Although the groups of all things larger than

a breadbox (an anonymous reviewer’s example) or all cars made in Germany (Bird & Tobin, 2018: section 1.1.1) represent something about the world, they cannot be seen as real groupings because their membership criteria are determined essentially by us on arbitrary grounds. Some things are larger than a breadbox whereas others are not, and some cars are made in Germany whereas others are not, but taking the size of a breadbox or the borders of a country as membership criteria is a matter of choice. Neither of these properties is of any particular theoretical or explanatory importance, nor do they tell us much about what the world is like. The membership conditions of these two categories are set by us on the basis of idiosyncratic interests, and we might as well have chosen different conditions. In the case of species, in contrast, the membership conditions are set more by nature than by us, and we have much less leeway when it comes to grouping organisms into species. The point is that the aspects of nature that evolutionary theory highlights and that species are intended to represent are causal factors that play important explanatory roles with respect to the origin of biodiversity, adaptation, organismal form, etc. Latching onto these factors is what lends reality to the groupings we identify and name as species.

To develop this idea further, we now turn to the central issues in the debate between monists and pluralists, the grouping and ranking problems.

### GROUPING AND RANKING: WHAT IS NATURAL ABOUT SPECIES?

In the preceding section, the grouping problem surfaced as the question: how can there be multiple, mutually incompatible ways of carving up biodiversity into groups that are all real and seem to occupy the same taxonomic level? The ranking problem is the question: why would all these groups be species? The solution for which we argue in what follows is the view that there are many different ways of grouping organisms, and many (but certainly not all) of these yield real groups in nature, but there is no reason to single out one or several ways as grouping organisms into species. This is realism about individual groups, but not about the species category; in the same way as the taxonomic ranks below and above the species rank are usually thought of as conventional, ranking a group as a species should be seen as a matter of convention. To flesh out this suggestion (which, again, is not new; see Ereshefsky, 2010, 2011, 2014) in more detail, we will consider seven different ways of grouping organisms, asking which of these yield real groups in nature and which might be good candidates to be ranked as species.

## SEVEN WAYS OF GROUPING ORGANISMS

The grouping problem can be tackled by examining the main reasons for which the species problem continues to be unresolved. Basically, species are groups of organisms held together as a group and distinguished from the members of other groups by various causal factors that underlie the patterns of organismal diversity observed in nature. The problem is attributable to the fact that there are many such causal factors, and focusing on different factors often yields different groupings that do not map onto each other.

To define the notion of species theoretically, criteria are required that: (1) identify relevant causal factors in nature (i.e. factors that play a role in speciation processes and in maintaining species in existence); and (2) provide a basis on which these factors can be prioritized. The factors under consideration can be factors that cause populations to evolve independently of each other (reproductive barriers, changes in mate recognition, and other factors) and causal factors that hold organisms together as a group and distinguish the organisms in one group from the members of other such groups (e.g. recency of common descent or trait similarities). In addition, the criteria are supposed to represent the theoretical role of species in biological research; they should represent how species feature in evolutionary theory, ecological theorizing, developmental genetics, and so on, and how species function in biological explanations, inferences, etc. This is because species are theoretical entities, both in the sense that our best scientific theories are about species (as the main products of evolution, entities that undergo evolution, ancestor–descendant lineages and, as such, elements of natural history and the basic types of organisms that exist in nature) and in the sense that species are groups that play various epistemic roles in research practice (as counting units of biodiversity, units of information storage and retrieval, units of scientific communication, types over which generalized statements can be made, the fundamental units of taxonomy, etc.).

Here, a principal reason for the persistence of the species problem is clearly visible: too much is subsumed under a single biological concept. Philosophers of biology and biologists have long pointed out that it is unlikely that all the different aspects of nature and of biological research practice that species are supposed to represent can indeed be represented by a single unit. Thus, a plurality of definitions is probably required to cover them all (e.g. [Mishler & Donoghue, 1982](#); [Ereshefsky, 1992](#); [Dupré, 1993](#); [Reydon, 2004, 2005](#)). However, different views have been advocated of what such a plurality of definitions should look like. To achieve more clarity on this matter, consider

some of the various factors in nature that species are supposed to represent.

Every theoretical definition of the term ‘species’ refers to one or more causal factors to explain what species are. The various available definitions use different criteria to highlight different biological factors that underwrite the grouping of organisms into species. The three most prominent such factors are as follows: (a) organismic traits (as in the morphological species concept or the phenetic species concept); (b) prezygotic and/or postzygotic reproductive (in)compatibility of organisms (as in the biological species concept); and (c) common descent (as in the various versions of the phylogenetic species concept). Other factors include occupying the same niche (as in the ecological species concept), following the same evolutionary trajectory (as in the evolutionary species concept), and others. Different definitions yield different, often incompatible groupings, all of which are called ‘species’ and given binomial proper names, although grounds are lacking on which it could be decided which groupings represent the species that exist in nature. One can understand this situation by thinking of the term ‘species’ as it is used in biological science and related contexts (such as conservation efforts, biotechnology, etc.), as a homonymic term that covers a considerable diversity of ways of grouping organisms in different contexts of work ([Reydon, 2004, 2005](#)).

The extent to which different definitions of the species concept yield incompatible groupings can be seen in recent studies that have shown that species counts are strongly dependent on the definition used. The number of endemic bird species in Mexico, for example, was found to vary between 101 when using the biological species concept and 249 when using a version of the phylogenetic species concept ([Peterson & Navarro-Sigüenza, 1999](#)). Likewise, [Barrowclough et al. \(2016\)](#) found that the use of the phylogenetic species concept yielded approximately twice the number of bird species as would be obtained when using the biological species concept. Using the morphological species concept, the whitefly species complex *Bemisia tabaci* counts as a single species, but when species are identified according to reproductive isolation and phylogeny it emerges as a complex of 24–28 species ([Liu et al., 2012](#)). In a meta-analysis of 89 studies, [Agapow et al. \(2004\)](#) found that using versions of the phylogenetic species concept led to an average increase of > 48% in species counts compared with counts based on non-phylogenetic definitions. Such examples clearly show that the various factors underwriting groupings of organisms into species yield groupings that are not always compatible. As a consequence, many species definitions that try to incorporate multiple biological factors (such as integrative definitions, discussed

in the section below on integrative taxonomy) are problematic because they may incorporate factors that underwrite incompatible groupings.

To explore this problem in more detail, by way of example we briefly examine the possible combinations of the three principal biological factors that can underpin species, mentioned above [(a), (b) and (c)]. We do not aim for an exhaustive analysis of all possible combinations of all biologically relevant factors. Considering these three factors yields seven possible combinations of factors (three involving only one factor, three involving two, and one involving all three), yielding seven possible species definitions (see [Table 1](#)). All three factors are biologically important and have been highlighted as fundamental when it comes to defining what species are. But, as we will argue in what follows, only three of the possible combinations are biologically meaningful. By ‘biologically meaningful’, we mean to express that some combinations of factors yield definitions that fit the framework of evolutionary theory (as the fundamental framework of thought in biology), whereas other combinations yield definitions that conflict with this framework.

#### GROUPINGS USING ONE FACTOR

Consider the possible combinations shown in [Table 1](#). Definition 1 [using only factor (a)] yields the morphological species concept, the phenetic species concept and the typological species concept, according to which organisms are grouped into species on the basis of sameness in selected traits. On all three definitions, trait similarity is what holds organisms together in species, and trait differences determine distinctions between such groups. The definitions differ, however, with respect to which traits are counted as relevant for species membership. The traits are not weighed, because in order to weigh traits differentially (e.g. with respect to their evolutionary significance) one would need to invoke additional factors as grounds for weighing, and when factors are added, the definition would cease to be definition 1. Therefore, on definition 1 male and female organisms would often

need to be allocated to different species on the basis of trait differences, because reproduction cannot be considered. This is particularly problematic in cases of extreme sexual dimorphism, such as Krøyer’s deep sea angler fish (*Ceratias holboelli*) or the scarce vapourer (*Orygia recens*). Clearly, then, definition 1 is not biologically meaningful, because it does not allow for a distinction between evolutionarily important and unimportant traits.

Definition 2 [using only factor (b)] yields the biological species concept and conceives of species as reproductive communities. On this definition, reproductive compatibility of organisms holds them together in a group, and prezygotic and/or postzygotic reproductive incompatibility distinguishes between organisms of different groups. Reproductive compatibility is taken here to mean the capability of creating fertile offspring, such that the production of sterile hybrids is discounted. However, not all reproductive communities should be counted as species: demes, populations and metapopulations, for example, are parts of species but not themselves species, except when a species is present only in the form of a single (meta)population. Thus, although definition 2 is biologically meaningful and answers the grouping problem, it still needs to be clarified which of the reproductive communities on various levels of organization count as species. This is the ranking problem, and we will return to this later.

Definition 3 [involving only factor (c)] yields genealogy-based species concepts, according to which organisms are held together in groups because of shared ancestry. But common descent does not underpin distinctions between groups. On the assumption of a single origin of life on Earth, all organisms share a common origin, such that for any two organisms the question of whether they are related by common ancestry *simpliciter* is not particularly meaningful. Distinctions between groups rest on how far back in time the common ancestor is located, such that the question is whether their common ancestor is more or less recent in comparison with the common ancestor they share with other organisms. To delimit groups of organisms that could count as species under

**Table 1.** Possible definitions of the concept of species following from all possible combinations of three main relevant biological factors

Factor	Definition						
	1	2	3	4	5	6	7
(a) Trait (dis)similarities	+	–	–	+	+	–	+
(b) Reproductive (in)compatibility	–	+	–	+	–	+	+
(c) Common descent	–	–	+	–	+	+	+
Biologically meaningful?	No	Yes	No	No	Yes	No	Yes

definition 3, cuts must be made in the continuum of ancestor–descendant relationships, because there are no natural boundaries in the continuum that would allow for the identification of natural groups. Although the making of cuts in the tree of life is, of course, possible, this will not yield species that represent something in nature without invoking additional factors to determine where the cuts in the tree are to be placed. Definition 3, then, is not biologically meaningful.

Note that for brevity we ignore the current debates on the adequacy of the tree of life as a representation of evolutionary history (Doolittle & Baptiste, 2007; Doolittle, 2010; O'Malley & Koonin, 2011; Baptiste *et al.*, 2013). Note, too, that we are considering the tree of life diachronically and not synchronically. When looking at only currently living organisms (a synchronic perspective), numerous software packages enable researchers to use molecular data to partition a group of organisms into monophyletic groups that constitute candidates for being attributed species rank, including SpedeSTEM (Ence & Carstens, 2011), BPP (Yang, 2015), DISSECT and STACEY (Jones, 2017). Such packages, however, partition already available groups that have been delimited using other criteria, without tracing candidate species back through time to the branching events in which they originated. That is, common descent is not the only factor involved. Rather, on synchronic perspectives common descent comes into play after organisms have been grouped on the basis of other factors, such as reproductive compatibility (see definitions 5 and 7). Software packages such as the ones mentioned above, then, rely implicitly on combinations of factors and cannot be seen as tools for delimiting species under definition 3.

#### GROUPINGS USING TWO FACTORS

Now consider definitions involving two factors. Definition 4, involving factors (a) and (b), does not constitute a traditional view of species. This is for good reason, because groupings of organisms on the basis of trait (dis)similarities are often incompatible with groupings of organisms on the basis of reproductive (in)compatibility. Using trait (dis)similarities in combination with reproductive (in)compatibility thus leads to a question of prioritization: when trait (dis)similarities suggest one way of grouping and reproductive (in)compatibility suggests another, incompatible way of grouping, which factor trumps the other? Lacking additional criteria, prioritizing either way would be an arbitrary choice.

Definition 5, involving factors (a) and (c), attempts to solve the problem that definitions 1 and 3 face by adding a second factor. This allows us to define boundaries between groups in the continuum of the

ancestor–descendant history of life by defining cuts in the continuum, represented as splits in the tree of life. Given that descent constitutes a continuum, using trait (dis)similarities as an additional grouping factor supplements factor (c) without any incompatibility, provided that traits are selected for which similarities are attributable to common descent (i.e. homologies). The main issue when using this definition is therefore to distinguish homologies from similarities based on convergent and parallel evolution (homoplasies) and to use only homologies as the basis for grouping organisms (Laubichler, 2014: 73; Schmitt, 2016). The ensuing definition, the phylogenetic species concept (Hennig, 1950, 1965, 1966), is a mixture of two grouping factors that are weighed equally. The two factors are not independent, however, because relevant trait similarities are supposed to indicate common descent, and the selection of traits is made dependent upon common descent. Traits thus have a diagnostic role as indications of which naturally occurring populations have a common ancestor, such that they should be grouped together into a species. But traits also have a defining role, because many homologies originate in distant ancestors, and only shared recent ancestry is relevant for delimiting species.

Although definition 5 enables us to delimit groups of organisms in the genealogical continuum, it does not lead to an unequivocal delimitation of such groups, because it leaves us with a choice regarding the treatment of ancestral and sister groups. A new trait can originate in a population that has split off from an ancestral population and go to fixation there, distinguishing it from its ancestor population. This can be represented as a dichotomous split in the tree of life, where one descendant branch is characterized by the presence of the trait (apomorphy), whereas the other descendant branch and the ancestral branch lack the apomorphy (but are characterized by a plesiomorphic character state). Hennig (1950, 1965, 1966) suggested that the ancestral branch and both descendant branches should be thought of as distinct species, leading to the extinction of the ancestral species in a split, and the origin of two new species. But clearly another option exists: to count the ancestral branch and the descendant branch lacking the apomorphy as the same species that continues to exist, identify the branch defined by the apomorphy as a new species that has branched off from its ancestor (Reydon, 2006: 243–237), and recognize the ancestral species as a paraphyletic species. Note that in definition 5 no distinction is made between morphological and genetic traits. Even though genetic traits indicate ancestry, they do not intrinsically have priority over evolutionarily significant morphological traits. Both are weighed equally. Therefore, definition 5 allows paraphyletic species, which are normally rejected by conventional taxonomy. As Schmitt (2014:

53–54) pointed out, Hennig saw his suggestion as a convention based on practical considerations regarding the needs of taxonomists to delimit species clearly, rather than as a view of how species as real entities are to be delimited. Note that the questions of what exactly Hennig's own views were, and how much present-day approaches in phylogenetic systematics incorporate Hennig's own views, are topics of ongoing debate, and different interpretations exist of Hennig's views (e.g. [Rieppel, 2011](#); [Schmitt, 2016](#)). In either option, however, traits play a role as defining groups in addition to indicating common descent (and here, too, the question of which groups are given species status is the ranking problem, which we discuss later).

A second definition involving two factors to define groups in the genealogical continuum is definition 6, which combines factors (b) and (c). According to this definition, species originate when an ancestral group, defined by reproductive compatibility of its member organisms, splits up into two new groups between which a reproductive barrier arises. Although such a barrier can either be external or internal to the organisms in question, only internal barriers are what count for species membership, because the relevant criterion is whether two organisms would be reproductively compatible when brought into contact. But any reproductive barrier that is internal to the organisms must be based on genetic changes, and thus must constitute an apomorphy at the genetic level. Definition 6, then, as such is not biologically meaningful; it is a theoretical construct without counterparts in nature. Organisms cannot be grouped on the basis of common descent plus reproductive (in)compatibility alone, because reproductive (in)compatibility constitutes an apomorphy, thus automatically involving factor (a) in addition to (b) and (c).

#### GROUPINGS USING THREE FACTORS

This brings us to definition 7, which combines factors (a), (b) and (c) and yields the cladistic species concept. Here, reproductive (in)compatibility is placed on an equal level with the factors of trait (dis)similarities and common descent, and none has priority. This leads to groupings in accordance with Hennig's suggestion, taking every split in the tree of life as a rupture in the reproductive connections between both descendant branches and the ancestor branch, such that both descendant branches are to be conceived of as new species. This view of species is widespread but has been criticized. Most importantly, it has been pointed out that Hennig's species have too short a lifespan to yield a meaningful taxonomic system, such that traits should be given more weight in the definition of species ([Kornet & McAllister, 2005](#)). Note that in this case (in contrast to definition 5), no paraphyletic species are recognized.

#### ANSWERS TO THE GROUPING AND RANKING PROBLEMS

What do we learn from this combinatorial exercise? First, even when taking only three of the natural factors that underpin species, we are faced with multiple options for grouping organisms. Of the seven possibilities discussed above, only three are biologically meaningful. If more than three natural factors were to be taken into consideration, the number of options would increase, but that does not imply that the number of biologically meaningful definitions must increase too. Still, it is clear from the preceding discussion that there is more than one biologically meaningful way to group organisms, whereas a basis for choosing between them is lacking. Note that the problem is not that there would be no ways of delimiting species. Powerful software tools are available to delimit candidate species within a given group of organisms, but applying such tools constitutes merely one way of delimiting candidate species next to other ways that involve other combinations of factors. That is, we do not suggest that available tools for species delimitation are useless, but that each is useful for delimiting candidate species under the explicit assumption of one particular definition of species, while allowing for other possible definitions that yield different groupings.

Second, note that of the three biologically meaningful definitions, one involves a single factor (species as reproductive communities), one involves two (species as branches on the tree of life individuated by an apomorphy), and one involves three (species as groups of branches on the tree of life, some of which are individuated by an apomorphy, whereas others are individuated only in relationship to the former branches on the basis of reproductive connections). The first definition is meaningful in the context of the study of speciation processes, whereas the second and third are meaningful in the context of systematic biology (from the perspective of different schools of thought, with the second fitting general approaches to phylogenetic systematics and the third fitting a strictly cladistic perspective). All three definitions pick out natural groups, where the reality of species consists in their representing causal factors in nature that hold organisms together in groups. Given that the various factors feature in different natural processes, they do not necessarily yield the same groupings. Singling out one factor or combination of factors as the definition of species would amount to an arbitrary choice of one process as more relevant in the production of natural groups of organisms than all others. Hence, we suggest that none of the definitions can be interpreted as picking out 'the only real' species in nature; different combinations of factors yield different groupings, all of which can be viewed as real entities and candidates for being ranked as species.

This brings us to the ranking problem. From the preceding discussion, we have three candidates for real groups that could be ranked as species. Which criteria could be used to single out one way of grouping as yielding species, leaving the others as yielding real groups that do not constitute species? Two types of criteria can be relevant here: the reality of groups as representing important causal factors in nature, and theoretical relevance. Given that all three definitions yield real groups, the reality criterion alone will not be useful to answer the ranking problem. The second criterion is connected to the first. When the reality of groups is conceived of as consisting in representation of causal factors in nature, the reality of groups becomes theory dependent, because it is our best scientific theories that identify causal factors in nature. That is, as highlighted above, species are theoretical entities, and the biological theories and research programmes in which ‘species’ features as a technical term tell us what the biological basis of species is. The overarching theoretical framework of biology is evolutionary theory. But as multiple definitions fit this framework (i.e. are biologically meaningful, as we argued above), theoretical relevance will not be a useful criterion either.

We suggest that the only way to single out one factor or combination of factors as defining the species rank is by way of convention. That is, although there are multiple ways of grouping organisms into natural groups, the only way to single out one of these as grouping organisms into species is on the basis of a convention that is endorsed widely in the relevant academic community. This view is a combination of realism about grouping and conventionalism (or instrumentalism) about ranking (cf. Baum, 2009; Ereshefsky, 2010, 2011, 2014; Mishler, 2010; Wright & Baum, 2018). As Baum put it: ‘the species rank should be assigned by practitioners based on the semisubjective application of a set of species-ranking criteria’ (Baum, 2009: 74). Recently, Wright & Baum (2018) elaborated this view to show how it can be used to delimit bacterial species using conventional similarity thresholds. In the next section, we examine two consequences of this view for biological research practice.

#### DO INTEGRATIVE TAXONOMY AND DNA BARCODING INDIVIDUATE REAL SPECIES?

We begin with integrative taxonomy (Dayrat, 2005; Will *et al.*, 2005; Padial *et al.*, 2010; Schlick-Steiner *et al.*, 2010). Integrative taxonomy is based on the assumption that a rigorous delimitation of species can be achieved by combining different research contexts and using the combination as a basis for the delimitation of species: ‘Rigor in species delimitation can [...] be increased when several disciplines chosen

for complementarity are used’ (Schlick-Steiner, 2010: 421). The underlying thought is as follows. Different research contexts perform with different degrees of adequacy when it comes to delimiting species, but no context can be said to perform well. This is because different research contexts use different theoretical ideas of what species are; they have different biases regarding how species are to be delimited. By combining these different background theories, the hope is that such biases can be reduced, and species delimitations might converge onto the species that exist in nature independently of us. The required combination can be achieved in practice, it is assumed, by iteratively revisiting the same taxonomic problem from different perspectives until a stable delimitation is achieved.

Integrative taxonomy is enjoying increased popularity as a means to avoid having to use multiple species definitions in parallel. Integrative species, however, cannot be thought of as representing natural units in the sense discussed above, because they integrate multiple, often mutually incompatible grouping factors that are taken from different research contexts. They are artificial units, created for practical purposes. To see this, consider the three natural factors discussed in the previous section. These factors constitute aspects of distinct biological processes that occur at different levels of organization and that may or may not be connected in concrete cases. For that reason, in some cases they may yield coinciding groups, but it is to be expected that the number of cases in which this occurs is comparatively small, and in most cases, the three factors will yield incompatible groupings. A group of organisms that descend from a common ancestor is not necessarily also united by reproductive compatibility and/or trait similarity. There is no theoretical foundation for the assumption that the integration of different factors into one definition of ‘species’ will always yield concise groupings of organisms, nor is there empirical evidence that in practice these factors always (or even in many cases) support the same groupings, in contrast to what some philosophers of biology have claimed (e.g. Ruse, 1987: 238). As we have argued above, some combinations of factors are biologically meaningful and can yield concise groupings of organisms. The problem, however, is that this is not the case for all possible combinations. Although the pragmatic advantages of an integrative species definition are clear, the integration of incompatible factors into a single definition that is used to delimit species leads to internal conflicts in the definition. These can be resolved only by weighing some factors more strongly than others, on the basis of subjective decisions. Using an integrative species definition, then, necessarily involves subjective judgments about the question of which factors are more important in a given case.

Integrative taxonomy, then, is unable to minimize the biases that are connected to the various theoretical perspectives of what species are; if anything, it introduces additional biases.

We now turn to another popular approach to species delimitation, DNA barcoding. DNA barcoding is often presented as a method for the discovery of species as real entities in nature. [Hebert \*et al.\* \(2004a\)](#), for example, claimed that barcoding revealed the existence of ten species in butterfly group *Astraptes fulgerator*, where it had so far been thought that only one species existed. Barcoding rapidly advanced to a prominent method in taxonomy ([Hebert \*et al.\*, 2003, 2004a, b](#)). The identification of species by means of barcoding builds on common descent and on sequence divergences (i.e. trait differences at a genetic level) and, as such, is an instance of definition 5, discussed above. It is based on the comparison of mitochondrial cytochrome *c* oxidase I profiles of groups within established species. The criterion used, the Hebert 10× divergence criterion ([Hebert \*et al.\*, 2004b](#)), recognizes a new species when the sequence difference (the ‘barcode gap’) between two groups within an established species is larger than ten times the average divergence within that species. Two individual organisms are counted as members of different species when their genetic difference at the locus under consideration is 10% or larger. This clearly shows that traits (in this case one trait, the cytochrome *c* oxidase I sequence) are not used merely in a diagnostic manner but serve to define species. We recognize the importance of barcoding as a diagnostic tool but want to cast doubt on its use as a definitional criterion for species (see also [Kunz, 2018](#)).

In comparison to phenotypic traits, the use of genetic traits has clear advantages. Phenotypic traits are complex structures, such that the individuation of traits and trait differences is usually more difficult than for genetic traits. Using mitochondrial rather than nuclear DNA has the advantage that there is no recombination, such that the gene tree will be strictly dichotomous. Establishing relatedness on the basis of mitochondrial genetic traits is much less difficult than using phenotypic traits, which are usually determined by multiple loci that can each have a different ancestry. The vertebrate eye, for example, is homologous to cephalopod eyes with respect to some of its parts, but analogous (a product of convergent evolution) with respect to other parts. Carving up biodiversity into ‘barcode species’ yields a taxonomy that is free of inconsistencies, stable, and useful for a variety of practical purposes. In addition, the existence of a barcode gap is an empirical matter.

Problems arise, however, in relationship to the biological meaningfulness of the barcode gap as a criterion for the delimitation of species. The cytochrome *c* oxidase I gene is a protein-coding

gene that is subject to natural selection. Sequence differences between two individual organisms, however, are in most cases attributable to selectively neutral mutations and are therefore indicative of the time that has passed since their last common ancestor. That is, the sequence differences used to determine whether two organisms are conspecific are linked to the molecular clock: the older the separation between two organisms, the more their cytochrome *c* oxidase I sequences differ, and the more likely it is that they will be allocated to different species. This means that barcoding will not recognize evolutionarily young groups ([Hickerson \*et al.\*, 2006](#); [Kunz, 2018](#)). Groups that have split up very recently often have not had sufficient time to develop a barcode gap, such that the similarities and differences at the genetic level do not always trace the pattern of descent. Consider, for example, the Cichlid species radiations in East African lakes, in which new species are recognized on the basis of reproductive incompatibilities and with origins in very recent speciation events ([Seehausen \*et al.\*, 1999](#); [Seehausen, 2002](#)). Such species would not be recognized on the basis of barcoding ([Moran & Kornfield, 1993](#)). A similar example is found in the butterfly family Lycaenidae, where the 133 species in the genus *Agrodiaetus* that are recognized on the basis of reproductive incompatibility would constitute a single barcode species ([Wiemers & Fiedler, 2007](#)). Conversely (as an anonymous reviewer pointed out), given that only a finite number of mutations is possible at a given locus, loci can reach saturation and not mutate further. This means that very old taxa may exhibit more genetic similarity than younger taxa, and for very old splits the mitochondrial DNA may not be a reliable indicator of species status.

This connects to the widely recognized discrepancy between gene trees and species trees in phylogenetics ([Pamilo & Nei, 1988](#); [Nichols, 2001](#)). Splits between mitochondrial genome lineages do not necessarily coincide with splits between reproductive communities, such that the two criteria do not necessarily delimit species in the same way ([Hickerson \*et al.\*, 2006](#); [Kunz, 2018](#)). When, for young groups, organisms are grouped based on barcode differences, one may obtain different groupings than when the same organisms are grouped on the basis of reproductive (in)compatibilities. Barcoding uses the existence of genetic gaps to define species, such that splits are counted as speciation events only once a genetic gap has emerged between the groups. Such a choice is arbitrary, however, because proponents of barcoding do not provide theoretical grounds in its support, and other options (such as using reproductive incompatibility) are equally plausible. This makes it doubtful whether barcoding can be seen as a means to the discovery of real species.

## CONCLUSION

In this paper, we have presented perspectives on the grouping and ranking problems that involved realism about some of the groups of organisms delimited using various combinations of causal factors. This realism is based on the connection of species to a variety of causal factors in nature. We have argued that these causal factors often support incompatible groupings of organisms, such that a single definition of the term ‘species’ that integrates all biologically meaningful groupings will not be achievable. We have thus presented an abstract argument for species pluralism, built on the causal structure of the living world. The argument starts from the plurality of biological causes that hold organisms together in groups that could be attributed species status and shows how species pluralism follows from causal pluralism. This, in turn, implies instrumentalism about the ranking of groups as species. Singling out any of the possible real groups as species will have to take place on the basis of widely shared conventions. Our view thus entails anti-realism about the species category.

A central element of our solution to the species problem is a clarification of the meaning of claims that species are real. We have argued that a straightforward realism about species is not an option. Instead, realism about species should be seen as the view that the groupings of organisms that are identified and named as species represent important causal factors in nature highlighted in evolutionary theory, where different research contexts emphasize different causal factors. This ‘weak realism’ about species, we suggest, is both sufficiently realist to make sense of the role of species as the ‘currency’ of biology and sufficiently anti-realist to avoid such questions as what the one, true species concept might be. Some may see the context dependence of species as impracticable, but practical problems can be avoided by always making explicit which definition is used. With respect to the theoretical question, our view resolves the tension between pluralism and realism by highlighting that the question of whether species are real in an absolute sense is not a meaningful question to ask and should be reformulated as the question of what factors in nature species represent in the particular theoretical context in which they feature.

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