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# Chapter 1. We Are Nearly Ready to Begin the Species Problem

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## Abstract

This paper isolates a hard, long-standing species problem: developing a comprehensive and exacting theory about the constitutive conditions of the species category, one that is accurate for most of the living world, and which vindicates the widespread view that the species category is of more theoretical import than categories such as genus, sub-species, paradiagnosis, and stirp. The paper then uncovers flaws in several views that imply we have either already solved that hard species problem or dissolved it altogether – so-called We Are Done views. In doing so the paper offers new criticisms of the general lineage species concept (GLSC), evolutionary species concept (EvSC), biological species concept (BSC), other similar concepts, Ereshefsky's eliminative pluralism about the species category, and both Mishler's pessimism and Wilkins' phenomenalism about that category. Opposed to We Are Done views, the paper argues for a Revving Up view, on which we are nearly ready to begin the hard species problem in earnest. To help work towards these conclusions, the paper begins with an outline of a new kind of view of species (Barker 2019a), which proposes they are feedback systems of a mathematically specifiable and empirically testable sort.

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# 1 Introduction

What are species? More exactly, what are separately evolving species lineages?

They might be *feedback systems*, displaying a distinctive degree or grade of metapopulation level cohesion, which manifests and varies dynamically with the magnitude and frequency of feedback relations between several causal variable at population levels.

The next section briefly outlines that recent proposal (see Barker 2019a) – not to try to convince you it is true, but rather to provide just one example of a new *kind* of species theory. This will set the stage for the paper’s main aims, which involve next isolating a hard, long-standing problem for providing a theory of the species category (Section 3), and sorting species concepts that address that problem (Section 4). The paper then uncovers instructive flaws in several views that imply we have either already *solved* that hard species problem or *dissolved* it altogether – so-called We Are Done views. The flaws are found in cause-focused species concepts, such as the biological species concept (BSC) (Section 5), and in non-cause-focused species concepts, such as the general lineage species concept (GLSC) and evolutionary species concept (EvSC). Other We Are Done views challenged include those stemming from Ereshefsky’s eliminative pluralism about the species category (Section 7), Mishler’s pessimism about the category (Section 8) and Wilkins’ phenomenalism about it (Section 9). More constructively, the paper argues for a Revving Up view: rather than being done with the hard species problem, we are nearly ready to *begin* in earnest, as the feedback model will help exemplify.

## 2 Exemplifying a new kind of species theory: feedback species

In a feedback system, processes loop or cycle. The values taken by variables over one time period feed back into the system, influencing the values taken by those *same* variables at later times. Put differently, output conditions turn around and serve as input conditions in further iterations of the same or similar pattern, as exhaust air produced from combustion in a turbo engine is fed back into the system to help (via interactions with other variables) amplify further

combustion, thus increasing exhaust, and on and on until there is intervention, or a dampening feedback mechanism is engaged. How about in an evolving species lineage? It is widely agreed that any species is a group of populations, a metapopulation (de Queiroz 2005). But authors argue about which among a variety of processes or variables are *most important* for connecting and “holding together” the populations in the group. Nearly everyone acknowledges many variables often *interact*. But those variables deemed most important are privileged over those with which they interact and are then referenced in differing definitions of species concepts to the exclusion of the other variables. Many have privileged gene flow processes in this way (e.g., Mayr 1942; 1963; Morjan and Rieseberg 2004; Bobay and Ochman 2017), others the sharing of selection regimes and adaptive zones (e.g., Van Valen 1976; Cohan 2002), and so on. **Table 1** provides a partial list of variables that have been discussed. But fortunately, in recent years – including for both sexual and asexual populations – some experts have taken steps away from the privileging of just this or that small set of variables, making interactions between them central to their accounts of the nature of species (e.g., Templeton 1989; Boyd 1999; R. A. Wilson, Barker, and Brigandt 2007; Barker and Wilson 2010; Ellstrand 2014; Shapiro and Polz 2015; Novick and Doolittle 2021). The feedback model incorporates this but goes further, suggesting a long view on which interacting variables over one time period influence the values of these same and other variables at later time periods, which influences still later values of these variables at later time periods, and on and on over many periods, forming an evolving species system as the cycling feedback relations set it apart from other metapopulations.

Variable label	Name of variable	Example works appealing to variables
<i>g</i>	Gene flow	(Mayr 1963, Brooks and Wiley 1988, Morjan and Rieseberg 2004, Bobay and Ochman 2017)
<i>s</i>	Shared selection regimes	(Ehrlich and Raven 1969, Van Valen 1976, Lande 1980, Mishler and Donoghue 1982, Templeton 1989, Cohan 2011, Shapiro and Polz 2015)
<i>h</i>	Homeostatic developmental systems	(Ehrlich and Raven 1969, Mayr 1970, Wiley 1981)
<i>c</i>	Colonisation	(Hellberg et al. 2002, 275–77)

$m$	Mutation	(Mayr 1970, Hellberg et al. 2002, 275–77, Morjan and Rieseberg 2004)
$r$	Genetic recombination	(Carson 1957; Mayr 1970)
$t$	Trait similarities	(Barker 2019a)

Table 1. Provisional running list of causal variables entering feedback relations. Modified from Barker (2019a)

For instance, gene flow between populations in a group over some time period,  $t_1$ , distributes alleles between populations. That results at  $t_2$  in the populations having population level trait frequencies closer to each other than to out-group populations. Subsequently this helps ensure the populations participate, over  $t_3$ , in selection regimes in ways more like each other than out-group populations (e.g., Morjan and Rieseberg 2004). And in turn that may help cause further gene flow at  $t_4$ , and trait sharing at  $t_5$ , and selection regime sharing at  $t_6$ , and...The exact sequence needn't and surely won't continue on with the same degree of regularity as in a turbo engine; a suite of variables may feed back into the system in diverse and changing ways over time, with varying degrees of influence or importance across cases. This suggests a relatively inclusive account of the species category (e.g., Ellstrand 2014; Novick and Doolittle 2021), on which diverse variables and relationships between them can be recognised as important across species groups.

However, the feedback model needn't be so inclusive as to imply anything goes, or that species groups can't be distinguished from others. Part of the proposal is that *relative to many non-species metapopulations*, species groups feature distinguishing kinds of complex feedback regularity, even if this regularity is loose and liberal when compared instead to turbo engines. And the model doesn't purchase inclusivity at the cost of vagueness, as we'll later see some other views of species do when they discuss the cohesion produced by species-forming and species-maintaining processes without comprehensively detailing the nature of such cohesion (e.g., Mayr 1963; Hull 1976; de Queiroz 1998; Wiley and Mayden 2000a; see Barker and Wilson 2010). On the feedback model, evolutionary cohesion is something that species but also other types of metapopulations can exhibit in different degrees or ways, and it can be given exacting

but flexible mathematical descriptions that enable testable predictions. A basic central idea is that as feedback relations play out at the level of populations (within a group of them), this manifests *metapopulation feedback cohesion*, or  $M$ , at high level of the whole metapopulation (Barker 2019a). The values taken by recurring causal variables in the metapopulation feedback system can vary either in magnitude, frequency, or both. When magnitude and frequency are both high across many variables, that manifests a high value for  $M$  at the level of the whole metapopulation system, perhaps indicating a species or even sub-species. Low magnitudes and frequencies across many variables manifest low  $M$ , perhaps a genus or family. Intermediate values are of course possible. So,  $M$  at the metapopulation level varies dynamically with the magnitude and frequency of feedback relations between causal variables at population levels; evolving metapopulations lineages of many sorts may just *be* these dynamic feedback systems; lineages of the *species* type in particular may be those within a species distinguishing range of  $M$  values.

Now regarding prediction, consider a traditional view that has been widespread since the Modern Synthesis and will be part of this paper's focus. It proposes that within a variety of biological theories, the species category plays a more important or fundamental role than both more inclusive metapopulation categories (e.g., genus, family, or class) and less inclusive ones (e.g., sub-species, variety, or stirp) (see Wilkins 2018). As biologist Frank Zachos summarises it, "Species are the fundamental unit in many branches of biology" (Zachos 2015, 180). In combination with the feedback model this could be developed to predict that we'll find a metapopulation level – the species level, presumably – at which the involved metapopulations clump in feedback variable space in a more distinctive or patterned *and* theoretically important way than at other metapopulation levels. Call this variable space  $M$  space (Barker 2019a). In it, each axis depicts the intensity (some combination of feedback and magnitude) of a particular variable's feedback relations, a value whose measure is scaled between 0 and 1. For illustrative purposes, **Figure 1** borrows from Peter-Godfrey Smith's (2009) way of depicting such variable spaces (in a different, non-species context where feedback isn't central) and uses just three

example variables as axes: gene flow ( $g$ ), trait similarities between populations ( $t$ ) and sharing of selection regimes ( $s$ ). Suppose we plot a wide variety of metapopulations, from those hypothesised to be at or around the species level of inclusivity, to many of those thought to be much more inclusive metapopulations. (The example and figure set aside less inclusive metapopulations.) The traditional view would then predict that we get a distinctive clustering of a small proportion of the metapopulations in some non-zero patch of the variable space, one of distinctive importance to biological theories. That would be the “species category patch”, and may well have fuzzy boundaries, but stand out to some quantifiable degree, with the involvement of some variables in feedback relations reinforcing the involvement of others in such relations. Along with this, the traditional view could predict that most of the remainder of the metapopulations (more inclusive ones, such as those associated with genera or families<sup>2</sup>) feature significantly less intense feedback relations, perhaps “layering out” in a portion of variable space between the species category patch and point-zero, or even just clustering near point-zero in  $M$  space. Figure 1 represents the latter of these, in the case where the species category patch is in the top+back+right (though a few other interesting metapopulation, cases scattered in regions of  $M$  space intermediate between point zero and the species category patch, are also described below the figure).

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<sup>2</sup> This will sound strange to biologists who think any metapopulation is *by definition* less inclusive than, say, a whole genus or family. But the usual way that such inclusion is definitionally ruled out is by requiring that only members of the same *species* can form a metapopulation. We cannot accept that here, at least not without vicious circularity, because the very point is that we are seeking rather than presuming an account of the species category.

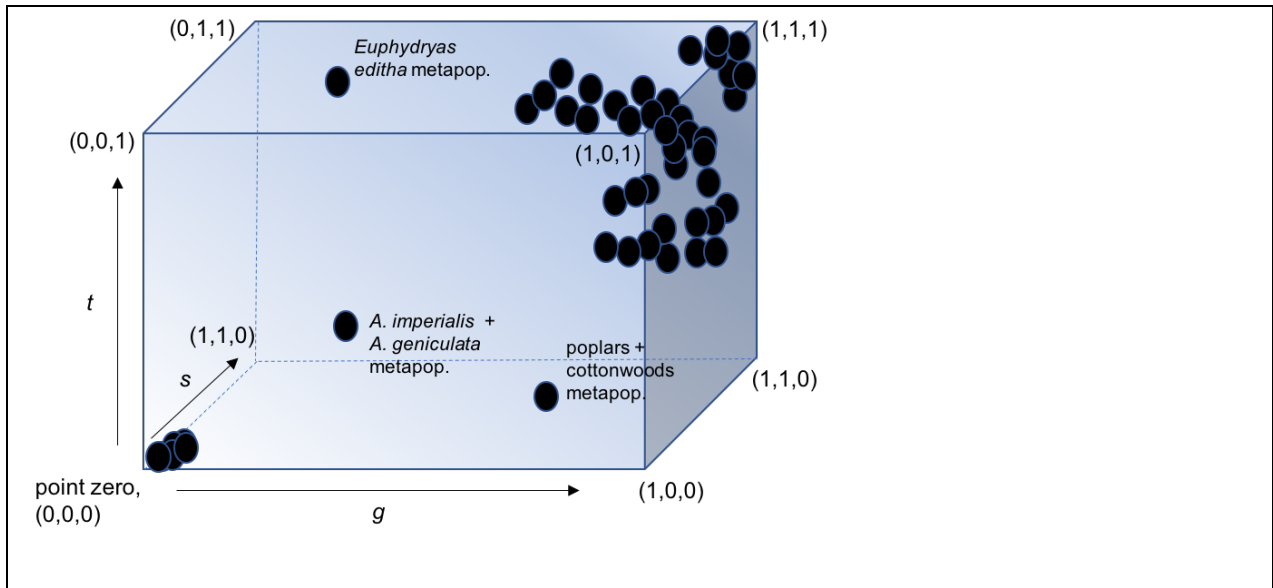


Figure 1. Plotting  $M$  values for metapopulations in  $M$  space.

Black ovals represent metapopulations. On the prediction described in the text, many will form a dense cluster near point zero, while others form a specie category patch in the back+top+right region. Outliers include the *Euphydryas editha* metapopulation, exemplifying the 1969 claim of Ehrlich and Raven that a California metapopulation within this butterfly group features very little gene flow between populations, but seemingly high  $t$  and  $s$ . The *A. imperialis* + *A. geniculata* example reflects the implication in Barbará et al. (2007, 1990) that sympatric groups from these two named *Alcantarea* species (bromeliads) feature low but non-zero  $g$ ,  $s$ , and  $t$ . The poplars + cottonwoods example is from Templeton (1989), who claimed low levels of  $t$  and  $s$  for this inter-specific group, despite significant levels of gene flow between the involved poplars and cottonwoods. (Design aspects of this figure are taken directly from Figure 3.1 and Figure 5.1 in Godfrey-Smith (2009), and the figure here is reused from my Barker 2019a paper.)

In sum, a theory about the nature of the species category could then gradually be developed in terms of species-specific patterns in  $M$  space, in an exacting and comprehensive manner that is

at once inclusive and flexible, but also detailed and clear enough about causal variables and cohesion to explicate ways in which the species category is distinctive and important.

Now having such an example of a new kind of view of species, we are ready to zero in on the hard species theory problem and argue that rather than being done with it as several views have implied, we are nearly ready to begin.

### 3 A theoretical species problem about constitutive conditions – are we done with it, or just revving up?

There are species *questions*, then there are species *problems* that evolve out of recalcitrant questions. Start with questions.

Above we asked “what are species?”. But we oughtn’t be so simplistic. People often instead put the question in terms of definition, saying “How should ‘species’ be defined?” But that is both simplistic *and* misleading, as it suggests the question is primarily about how we concisely summarise complex theories within pieces of language (definitions), when really we are interested in the theories themselves – in discovering the very nature of a putatively important category in the living world.<sup>3</sup> So “what is the *nature* of the species category, understood as a category of separately evolving lineage?” is better. Yet “nature” is both vague and ambiguous. So, best to say “what are the *constitutive conditions* of the species category?”, where we’re agreed on the minimal starting point that this is a category of separately evolving metapopulation lineage.

A category’s constitutive conditions are those *in virtue of which* things belong to that category – conditions that *make* things (under usual circumstance) belong to the category, independently of our abilities to *tell* whether those things in fact satisfy the conditions and thereby belong to the category (Mayden 1997; de Queiroz 1998). That is a distinction between what a category’s

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<sup>3</sup> See Cleland (2012) on this, with respect to the category *life*.



constitutive conditions *are* across cases, and when those conditions are *satisfied* in particular cases. For instance, according to the IUPAC (2019), what makes something a chemical element is being a type of atom in which all instances have the same number of protons in the atomic nucleus. That theory about the chemical element category's constitutive conditions was developed and widely deemed accurate over a period of approximately 25 years (1910 – 1930s) (Scerri 2019), before our abilities to tell the proton counts of atoms were as sophisticated as now, and when practitioners would often tell elements apart from, say, compounds without looking for protons at all.

In seeking the species category's constitutive conditions, we aren't seeking the conditions that make certain organisms belong to certain species groups, but rather the conditions that set all species metapopulations apart from other categories such as the genus, paradivision, sub-species, and stirp categories. The theories that propose such conditions are found in so-called *species concepts*. Each of these is a construct hoped to accurately correspond to the species category in nature. Although they are typically offered and interpreted as involving respective definitions of 'species', we are focusing on the constitutive conditions they propose. The (in)famous biological species concept (BSC), for instance, proposes that each species is a group of populations satisfying two constitutive conditions (Dobzhansky 1935; Mayr 1942; 1963; 2000b; Coyne and Orr 2004). One, the interbreeding condition, is there being gene flow between populations in the group. The other, the reproductive isolation condition, is there being a lack of gene flow between populations within the group and those outside it. Ernst Mayr urged these as constitutive because (or at least partly because) he thought each was *such an important cause* of conspecific populations becoming or remaining relatively homogenised in their traits – causes of holding the conspecific populations together, separated from other evolving lineages, and explaining why the living world is clumped into these lineages rather than, say, being "continuous" (Mayr 2000a, 161; 1963).

The BSC also helps illustrate how our species question about constitutive conditions eventually grew into the hard theoretical species problem on which we're zeroing in, because it is widely

agreed that the BSC's theory isn't *accurate in a general way* (Ereshefsky 2017). Many groups of populations appear to be species in virtue of satisfying conditions other than the two picked out as constitutive by the BSC. Indeed, these groups seem to be species despite failing to satisfy either the interbreeding condition (e.g., there isn't gene flow between all their populations) or the reproductive isolation condition (e.g., there is gene flow between some of their populations and others) or both. The BSC suffers these problem even though full elaborations of it seem to provide a relatively comprehensive and exacting theory that helps vindicate the traditional idea that the species category is of distinctive importance to several biological theories (e.g., Coyne and Orr 2004).

Many species experts (not all, as we'll see) now think that *every* species concept that has attempted to answer our species question has failed in one way or another. We can thus label and formulate the hard theoretical species problem that has emerged:

*The species category theory problem:* Despite laborious efforts, we lack a theory of the species category's constitutive conditions that meets, to high degrees, the following four desiderata:

- (i) comprehensive,
- (ii) exacting,
- (iii) accurate in a quite general way,
- (iv) helps vindicate the traditional idea that the species category is more important in a variety of biological theories than other categories of evolving metapopulation lineages.

The We Are Done views and Revving Up view discussed in this paper take very different stands on that problem.

According to one set of We Are Done views, we have already *solved* the problem via this or that particular species concept. This implies I was (and many others are) mistaken to say we lack a theory of constitutive conditions meeting the four desiderata (e.g., Mayden 1997; de Queiroz

1998; 2005; 2007; Coyne and Orr 2004; Bond and Stockman 2008; Camargo and Sites 2013). These are *Done by Solution* variants of We Are Done views.

According to a second type of We Are Done view, we are done for a very different reason: even if each individual species group is a real biological entity, there is no general species category to which all and only they belong *and* which could do the presumed important work in biological theories (e.g., Ereshefsky 1992; Mishler 1999; Pleijel 1999; Mishler and Wilkins 2018). These are *Done by Dissolution* varieties of We Are Done views.

I will argue both sorts of We Are Done views are off the mark, each for different reasons. But I won't argue that *no* people working on the species problem should bother further developing these views. We are fortunate that species problems are addressed by a large *community* of diverse researchers. At that more inclusive level it is best, given our humble state of knowledge about species, that both types of We Are Done view, and my alternative Revving Up view, continue to be developed. So, my negative or critical thesis is this:

*We Are Done views have not yet succeeded; currently there is no We Are Done view that everyone should endorse.*

My positive or constructive thesis is:

*Revving Up is plausible; some proportion of researchers working on species should endorse and further develop it, while others work on We Are Done views.*

More specifically, the Revving Up view that I will defend via examples and lessons drawn, says we have now learned enough from conceptual clarifications and past failures that we are well positioned to develop promising and testable new kinds of theories of the species category's constitutive conditions, theories that integrate strengths of prior ones while avoiding their weaknesses. The feedback model is an example of such a theory, and the time is ripe for developing other such theories as well. Nonetheless I maintain we haven't yet begun in earnest,

and rather are nearly ready to do so, because we haven't directly empirically tested such a theory, except via interpretations of past data. We are at a promising "about to start" stage.

The next step in supporting my critical and constructive theses is to distinguish the types of species concepts that attempt to solve the species category theory problem.

## 4 Setting aside taxonomy to focus on two kinds of functional species concepts

We Are Done views must take firm stances on species concepts, because these are where we find proposed theories that attempt to solve the species category theory problem. One widely endorsed distinction will help us focus on the relevant species concepts, and a less familiar distinction will then help us differentiate between varieties of We Are Done views.

### 4.1 Taxonomic vs. functional species concepts.

Many species experts have urged this distinction in one way or another (e.g., Cracraft 1989a; Endler 1989; Kimbel and Rak 1993; de Queiroz 1998; 2005; 2011; Ghiselin 2001; Zachos 2016). With minor tweaks, I will follow David Baum's (2009) way of characterising the distinction. What I am calling *taxonomic species concepts*, he calls species-as-taxa concept, and says these "are ones that emphasise the similarities between species and taxa at other ranks and mainly reflect a desire to guide taxonomists in the practice of assigning groups of organisms to species taxa" (2009, 74).

What I call functional species concepts, he calls species-as-functional-units concepts, which "are ones that emphasise the functional cohesion or causal efficacy of species and generally emphasise the role of the term "species" in evolutionary and ecological theory" (2009, 74).

And about applying the distinction, he says:

The clearest way to distinguish these 2 kinds of concepts is by asking the question: what is it about a group of organisms living at one moment that would make them one

species as opposed [*sic.*] to 2, or many, or a subset of a single species? If the answer is something about their functional integrity (e.g., interbreeding potential) or ecological cohesion, then the concept is “functional”... If the answer to the question stresses the same kinds of attributes that are used to delimit higher taxa, then the species concept is taxic in outlook. (2009, 74)

More generally, authors have characterised the functional concepts as understanding each denoted species to be an “evolutionary unit” (Ereshefsky 1991), a dynamic or “active” group of populations that partake in evolutionary processes connecting them (Ereshefsky 1992a, xiii; Eldredge and Cracraft 1980; Wiley 1981).

Clearly, it is functional species concepts that interest us here.<sup>4</sup> Those who attempt to solve the species category theory problem understand species to be metapopulations that *function* as active, separately evolving lineages (e.g., de Queiroz 1998). Their theories attempt to uncover the nature of these functional units by specifying the constitutive conditions of the species category. Taxonomic species concepts, on the other hand, offer views about how to taxonomise species in relation to other types of groups within a taxonomic system. As such they are typically more operational than functional species concepts.<sup>5</sup> This shouldn’t be taken to imply

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<sup>4</sup> Without further refining Baum’s distinction, some species concepts may count as both taxonomic and functional, e.g., Seifert’s (2014) *pragmatic species concept* refers to both a) the lineage divergence and evolutionary explanations typical of species-as-functional-units concepts, and b) the operational diagnostic criteria typical of species-as-taxa concepts. So let’s understand the class of taxonomic species concepts as excluding any concepts that refer additionally to the functional features that his other notion references. Then, the class of functional species concepts includes those that refer exclusively to functional considerations *and* those that refer to a mix of functional and taxonomic considerations.

<sup>5</sup> In setting aside taxonomic species concepts we set aside those that identify the species category exclusively in terms of genealogical exclusivity, or monophyly, or morphology, or diagnostic characters, or phenotype, or genotype, or some combination of those. See Baum (2009) for reasoning about this, and Zachos (2016) and Wilkins (2018) for species concepts that identify the species category by those criteria just listed.

there are no relations between them that, in other contexts, are very interesting and worth investigating.

#### 4.2 Cause-focused vs. Non-cause-focused functional species concepts.

The less familiar distinction to apply is between functional concepts that are cause-focused, and those that are non-cause-focused (Barker 2019a).<sup>6</sup> First consider the following points on which all functional species concepts seem to agree (Ereshefsky 1992b; de Queiroz 1998):

(A) *Metapopulations*: Each species is a *group* of populations, that is, a metapopulation.<sup>7</sup>

(B) *Differentiating process participation*: The populations in each species group participate in the same or similar *evolutionary processes* – e.g., gene flow, niche sharing, selection regimes, and so on – and do so to degrees or in ways that are different from how they interact with populations outside the group.

(C) *Evolutionary cohesion*: Through their differentiating participation in evolutionary processes, the populations in a species jointly manifest and maintain a special kind of evolutionary unity or *cohesion*, i.e., the shared participation connects them into evolving lineages of the species type, diverged from other groups.

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<sup>6</sup> In the 2019a paper just cited, I referred to functional species concepts as ‘ontological species concepts’, which now seems to me a less informative and potentially misleading term.

<sup>7</sup> If a group of, say, 3 populations is reduced to 1, is it still a group, still a metapopulation? I am not sure. But if not, then (A) will for some biologists be a merely contingent or typical feature of species, and for others a necessary one. The former type of biologist will allow that a species reduced to 1 population can still count as a species. The latter may be exemplified by Mayr. He was quite clear in his view that to be a species is partly to have a relational property—a group can only be a species if it is reproductively isolated from other groups, so that “[i]f only a single population existed in the entire world, it would be meaningless to call it a species” (1970, 14). He also insisted that to be a species is partly to be a *group of interbreeding* populations. If he was similarly strict about that property, then a species reduced from 3 populations to 1 would thereby cease to be a species, even were it reproductively isolated from other groups. The feedback model helps bring out what is sensible in this view, as it highlights the importance, to evolutionary phenomena, of feedback relations *between* populations, relations that are lost when just one population—a mere population—remains.

So (B) is thought to lead to or otherwise generate (C): the shared and differentiating participation in processes *result in* evolutionary cohesion distinctive of species. When outlining the feedback model above, I proposed further, more exacting specifications of these ideas. But that was going beyond what is so far widely agreed upon. We can say that in the relationship between (B) and (C), experts are collectively picking out a *species category pattern*. But among functional species concepts there is much disagreement, and collectively much vagueness and ambiguity, about that pattern.

What is clear is that when focusing on this pattern, some functional species concepts pick out causal processes referenced in (B) as constitutive of the species category, e.g., gene flow, niche sharing, participation in selection regimes. Others abstract from causes and instead focus on the cohesion or lineagehood cited in (C). Hence the distinction exemplified in **Table 2**, by two lists of functional species concepts. Bear in mind that the concepts listed as non-cause-focused do not imply that causes are irrelevant or unimportant to species. But they deliberately refrain from stating any particular involved causes among the conditions deemed constitutive. Their theories of category constitution focus on (C) rather than (B), as will further clarify below.

Cause-focused species concepts	Non-cause-focused species concepts
Biological species concept (BSC) (Dobzhansky 1935; Mayr 1942; 2000b, 200; Coyne and Orr 2004)	Evolutionary species concept (EvSC) (Simpson 1951; 1961; Wiley 1978; Mayden 1997; Wiley and Mayden 2000b)
Ecological species concept (EcSC) (Van Valen 1976)	General Lineage Species Concept (GLSC) / Unified Species Concept (USC) (de Queiroz 1998; 2005; 2007)
Cohesion species concept (CSC) (Templeton 1989)	Internodal and/or Hennigian species concept (ISC/HSC) <sup>8</sup> (Willmann, n.d.; Ridley 1989; Kornet 1993; Meier and Willmann 2000)

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<sup>8</sup> To some, listing the ISC/HSC in the right-hand column may seem unintuitive. But consider Baum (2009, 74) on this issue: “The internodal or Hennigian species concept argues that species are lineages (Ridley 1989). At first sight, this concept might seem to align with the species-as-taxa class because modern views of taxa assume that they

Recognition species concept (RSC) (Paterson 1985)	
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Table 2. Cause-focused vs. non-cause-focused species concepts, both types of functional species concept.

In now turning to Done by Solution variants of We Are Done views, we'll see there is a commonality among them. Each seizes on a particular functional species concept and claims or implies that it meets the four desiderata identified in our statement of the species category theory problem. "Mine wins!" has been a durable idea, especially for the BSC, and for the EvSC and GLSC,<sup>9</sup> which probably continue to have the most champions among functional species concepts despite their many vocal critics. But there are important differences too, between Done by Solution views that build on cause-focused species concepts, and those instead building on non-cause-focused counterparts. We start with the former.

## 5 Done by solution via cause-focused species concepts?

Empirical counterexamples are among the most widely proclaimed criticisms of cause-focused species concepts: for any one of these concepts there are apparently many kinds of living thing said to violate its proposals about constitutive conditions.<sup>10</sup> Challenges to the BSC that were briefly introduced above best illustrate this, as they have been representative, most thoroughly explored, and relentless. So, focus on them in more detail now.

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are, like lineages, natural chunks of the tree of life. However, internodal concepts are usually species-as-functional-units concept because the limits of a 'lineage' at a moment in time are not governed by history, morphology, or similarity, but by functional features. Indeed, internodal concepts are best viewed as versions of the evolutionary species concept (Simpson 1951, 1961; Wiley 1978)... the same can be said of the unified (or general lineage) species concept (de Queiroz 2005, 2007)."

<sup>9</sup> Both Naomi (2011) and Mayden (2013) discuss perceived similarities between the EvSC and GLSC.

<sup>10</sup> For reasons that can be inferred from our discussion above, we set aside criticisms based in operational considerations.



Critics of the BSC have often interpreted it as though the interbreeding and reproductive isolation conditions it proposes as constitutive are also *each necessary* and *jointly sufficient* for a group to be a species. Counterexamples then take one of three forms:

- Challenging the necessity of the interbreeding condition by appealing to groups of populations that seem to be species even though not all the populations within them are connected by gene flow.
- Challenging the necessity of the reproductive isolation condition by documenting groups of populations that apparently are species despite gene flow processes stretching beyond them to include out-group populations.
- Challenging the sufficiency of the combination of the two conditions for specieshood by documenting groups that do *not* seem to be species even though they satisfy the interbreeding and reproductive isolation conditions that make something a species according to the BSC.

For counterexamples of the first two sorts, critics have often appealed to non-animals, including algae and fungi and especially plants and bacteria. Many botanists, for instance, have argued that often there is little to no gene flow between populations *within* what certainly seems to be a species group – *Zea mays* (corn), or *Beta vulgaris* (beet), or what have you – thus violating the necessity of the interbreeding condition (e.g., Ehrlich and Raven 1969; Endler 1973; Levin and Kerster 1974; Lande 1980; Grant 1981; Futuyma 1998, 317). Conspecific populations often seem too geographically dispersed for processes of pollination (by wind or insects) to connect them. Botanists have also cited many putative cases of hybridisation and introgression *between* apparently distinct species groups, violating the necessity of the reproductive isolation condition (e.g., Anderson 1949; Eckenwalder 1984; Templeton 1989; L. H. Rieseberg and Soltis 1991).

Bacterial groups have seemed an even tougher case for the BSC's interbreeding condition, as their uniparental reproduction has suggested little gene flow between apparently conspecific

populations – or at least, gene flow of a different sort than seems important to uniting sexual populations into species (Dupré 1993; Cohan 2002; Franklin 2007; Doolittle 2019).

And to make matters seem unbearable for the reproductive isolation condition, many authors have argued that disagreeable phenomena found in plants and bacteria are also much more common in *animals* than previously supposed (e.g., Chesser 1983; Templeton 1989; Dawley and Bogart 1989; Whittemore 1993; Mallet, Besansky, and Hahn 2016).

Finally, the most familiar proposed counterexamples to the sufficiency of the BSC's two constitutive conditions are cases of sympatric or clinal speciation, wherein a group splits into two or more species despite its populations being connected by gene flow and together reproductively isolated from out-groups. This has been urged, for instance, in some insects (e.g., G. L. Bush et al. 1989), birds (e.g., Sorenson, Sefc, and Payne 2003), fish (e.g., Barluenga et al. 2006), and palms (e.g., Savolainen et al. 2006)

While I too think the BSC, and indeed all extant cause-focused species concepts, have so far failed the general accuracy desideratum of the species category theory problem, I think the underlying reasons for this are often misunderstood in misleading ways. It is all too easy to overestimate the force of, or misinterpret, the sorts of counterexamples just summarised,<sup>11</sup> which sometimes motivates species experts to become unduly pessimistic about solving the species category theory problem at all. A more nuanced interpretation of the counterexamples yields lessons that should motivate some experts to see us as now well positioned, in light of them, to develop new kinds of theories about the species category's constitutive conditions.

First and most obviously, a biologist working on one of the sorts of group cited in counterexamples wouldn't want to say, "you see, this shows that the \_\_\_\_\_ [BSC, EcSC, whatever] is a bad choice for *detecting or delimiting the species boundaries of groups I study.*"

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<sup>11</sup> As a graduate student I sometimes tripped in these ways – see Barker (2007).

This would be to put an operational spin on a challenge whose theoretical relevance, rather than operational relevance, we are assessing.

That distinction remains crucial when, for instance, interpreting Alan Whittmore's (1993) scathing presentation of plant counterexamples against the BSC. In it, he notes that when botanists are trying to detect species boundaries, they typically use taxonomic species concepts that employ similarity or character-based criteria, rather than the gene flow based criteria of the BSC. But his point isn't the much older and tangential one that the BSC is operationally inadequate for many plants. Rather it is that once the taxonomic species concepts have uncovered species groups, then *further investigation* of those, including investigation of population structure important to inferences about gene flow, suggests those groups violate the BSC's proposed theory about constitutive conditions. Merely using a taxonomic species concept instead of the BSC, and seeming to uncover many "good species" that way, is no problem in itself for the BSC; after all, it is possible in principle that the groups picked out by the taxonomic species concepts coincide with those the BSC *would* pick out. This is clearest when Whittmore notes that the most influential BSC champion – Ernst Mayr himself – used a taxonomic species concept for his own operational matters, then often argued that the groups thereby picked out agreed with the BSC. So, the counterexamples aren't about "what works operationally for my kinds of groups". They are about a theoretical problem: many good bets for species groups appear to violate the BSC's proposed constitutive conditions.

Once counterexamples are properly framed as theoretical, there are two general ways for a proponent of a cause-focused species concept to try defending against them.

One, *rejection*, is to give reason for rejecting some of the details of the supposed counterexample, e.g., to contest empirical claims or interpretations, implying that the conditions in question aren't violated after all.

The other, *revision*, is to grant the violation but then accordingly revise or clarify the initial proposal about constitutive conditions, so that going forward the violation is evaded.

There have been principled reasons for revising, in particular softening, the BSC. Both its proposed constitutive conditions are, of course, matters of degree. So how much gene flow *within* a group does the interbreeding condition require? How little gene flow *out of or into* the group does the reproductive isolation condition require? What Coyne and Orr (2004) describe as “hard line” versions of the BSC (Coyne and Orr 2004, 33–35) give an answer of *zero* to that second question. But other BSC advocates, including themselves, have justified switching to softer, more flexible versions of the BSC, upon growing appreciation that it is not just the amount of gene flow that matters but also the *kind*. In helpful historical work, Anya Plutynski (2019) documents how advances in molecular biology and genetics gradually overturned Mayr’s view of “the unity of the genotype”, showing how species experts interpreted the continuous finding that not all genes in the genome are interdependent and co-adapted. Rather, key distinctions between species groups can sometimes depend on a relatively small number of genes. BSC softening could then reason that gene flow *into or out of* a candidate species needn’t be zero for that group to retain its species candidacy, since small amounts of gene flow may not be enough to implicate the relevant genes (e.g., Coyne and Orr 2004). On the flip side, gene flow *within* a candidate group (between its populations) may be barely a trickle, even ten times less than the traditionally demanded equivalent of >1 migrants per generation,<sup>12</sup> yet still enough under the right conditions to spread the relevant genes for holding the group together (e.g., Morjan and Rieseberg 2004, 1341-1342).

With principled softenings of the BSC’s proposed constitutive conditions, it has in turn been easier to deploy rejection responses to the supposed counterexamples. BSC-friendly botanists have recently shown that many of the previous counterexamples were marshalled with what are now comparatively poor methods and outdated assumptions, and that newer and much more reliable and penetrating methods (especially genomic methods in the last ~15 years)

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<sup>12</sup> For the basis of this tradition see Wright (1931).

suggest the counterexamples are not nearly as wide-spread or clear cut as claimed.<sup>13</sup> For the first time, Loren Rieseberg and colleagues quantitatively tested some of the assumptions packed into presentations of plant counterexamples, and found much greater correspondence than supposed between the BSC and “good species” picked out by taxonomic species concepts, e.g., “75% of phenotypic clusters in plants correspond to reproductively independent lineages...and thus represent biologically real entities. Contrary to conventional wisdom, plant species are more likely than animal species to represent reproductively independent lineages” (Loren H. Rieseberg, Wood, and Baack 2006, 524).

Regarding uniparental groups, there has been a widely discussed resurgence in attempts to apply the BSC to bacteria, given growing appreciation of relationships between lateral gene flow, introgression, and homologous recombination (e.g., Dykhuizen and Green 1991; Fontaneto et al. 2007; Bobay and Ochman 2017). A study of 105 prokaryotic species found that “only a minor fraction (<15%) undergoes too little gene flow to be assigned to species based on the BSC” (Bobay and Ochman 2017, 499–500).

And although there has long been healthy debate about how often sympatric and clinal speciation occur in nature, genomic methods have now afforded new appreciation of how complex these issues are, and how simplistic associated past criticisms of the BSC were (e.g., Martin et al. 2015; E. J. Richards, Poelstra, and Martin 2018).

Such defenses often succeed in showing that many past criticisms were off the mark. But they fall short of the loftier aim of showing the BSC is generally accurate. A superficial reason is that although some of the cited percentages – 75% correspondence between BSC conditions and certain “good” plant species, 85% in the case of some bacteria – are higher than past criticisms suggested, they are still far from establishing *general* accuracy (even short of having a precise

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<sup>13</sup> See Ellstrand (2014) for a comprehensive review.

percentage threshold to point to). A deeper reason, far more instructive, is that time and again when gene flow has been important as the BSC would predict, this has been partly *because* of how it works in concert with *other* variables emphasised by apparently competing cause-focused species concepts (see Barker and Wilson 2010).

In his review that defends the relevance of gene flow to plant species, Ellstrand (2014) is up front about this, emphasising the importance of interactions between various types of gene flow and various types of selection. He notes this importance of interaction “simply was not recognised” from the 1960s through the 1990s (2014, 745).

In bacteria, Doolittle (2019) likewise points out that often when gene flow is important it is partly because other variables such as selection are too, and vice versa. In more technical terms, it is rare in clear cases of bacterial species that there isn't distinctive interaction between:

- the frequency of clonal or periodic selection (labelled  $s$  by Shapiro and Polz (2015)),
- the frequency of homologous recombination (labelled  $r$  by Shapiro and Polz (2015)),
- the frequency of lateral gene transfer.

In the majority of cases, they interact importantly (Novick and Doolittle 2021).

The key empirical finding to clarify in the past 20 years is that, often, *many or all* the disputed variables in given cases explain species coherence and distinctions by how they work *together* in complex ways.

But old views die hard. Even when authors document the importance of variable interactions, they sometimes contort for ways of privileging their preferred variable. Morjan and Rieseberg (2004), for instance, uncover the variables of selective sweeps and small amounts of gene flow working together to help connect populations as evolutionary units, but then imply the gene

flow variables are more important than the selection variables for evolutionary coherence because the role of the gene flow variables is distinctly “creative”. Barker and Wilson (2010) showed how such asymmetrical interpretations cannot be generally sustained, because often when one attempts to privilege any one variable among interacting others in such conceptual ways, they ironically leave it open for the other variables to be similarly privileged.

However, it’s not that all variables are important in the same ways at all times. Hardly. Sometimes gene flow is especially important, perhaps in some creative sense and with the help of mutation, selection, a background of frequently shared related traits, and...; in other cases, one or more of these other variables plays some critical role and gene flow is among the mere enablers (e.g., Ellstrand 2014, 245-247, and Table 1 above). So, there are three lessons to draw from shortcomings of Done by Solution views that proceed via cause-focused species concepts.

First, we seek a theory of the species category’s constitutive conditions – a functional species concept – that is more *inclusive* than these, i.e., that heeds the empirical finding of importance for many, not just a small set, of interacting variables. (See Table 1 again for example variables.)<sup>14</sup>

But second, we need the inclusivity to be *flexible*: sensitive to variation in the roles of variables across cases. This would be a theory that recognises distributed importance without demanding uniformity in importance. Proposing necessity for each causal variable is not going to work. We need flexible, even dynamic, inclusivity.

Third, whatever more flexible and inclusive approach we develop should be one that helps reconcile an ambiguity within these views, about what the relevant *effects* of the causes are. A number of philosophers and biologists have discussed this in terms of ‘species cohesion’ or ‘evolutionary cohesion’, and these discussions deserve to be better known amongst species

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<sup>14</sup> Templeton’s CSC was an early attempt at this, though not nearly as inclusive as is here being suggested.

experts in general (e.g., Mishler and Brandon 1987; Ereshefsky 1991; 2001; de Queiroz 1998; J. Wilson 1999; Brooks and McLennan 2002; Barker and Wilson 2010). At least two notions of ‘cohesion’ have been uncovered in the literature. One is more akin to similarity or uniformity or homogenisation of traits, within species groups – something Barker and Wilson 2010 elaborated as *response cohesion*. The other is a type of integration or organisation, which we explicated as *integrative cohesion*.<sup>15</sup> Proponents of cause-focused species concepts have collectively vacillated between both, as they see processes like gene flow as *homogenising* conspecific populations, but also talk of these processes as *integrating* those populations into separately evolving lineages.

In sum, we can and should aim for a species concept that is more inclusive and flexible while adequately resolving confusion about and relationships between types of cohesion. The feedback model presented at the outset of this paper was just one example that this can be done. It is far more inclusive than the typical cause-focused species concepts, allowing that many important causal variables not only interact, but do so in the unappreciated way of feedback relations, which help constitute species. This also provided flexibility, as the feedback relations needn’t be of the exact same frequencies and magnitudes across cases; there are many ways in which the relations can result in an  $M$  value within a species category patch of  $M$  space. And clarification of cohesion is proposed: the effects of cited causal variables are further implementations of those same variables, including similarity variables, and these feedback relations dynamically manifest  $M$ , a type of cohesion at the metapopulation level. Aside from the feedback model, there are numerous other ways one could develop a more inclusive and flexible concept that addresses cohesion considerations.<sup>16</sup>

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<sup>15</sup> My more recent 2019a paper shows how I think we didn’t fully explore and develop the consequences and applications of that distinction, and supplement it in crucial ways as the feedback model now does.

<sup>16</sup> For example, see Sterner (2019).



## 6 Done by Solution via non-cause-focused species concepts?

Turning now to attempts at Done by Solution via non-cause-focused species concepts, we find authors drawing much more radical lessons than I have advised, from the failures of species concepts discussed above. They have agreed that each cause-focused species concept is too exclusive when it tries to elevate just this or that cause (or small set of causes) to the status of being constitutive. But they have then banished all the usually cited causal conditions from having this status.

This is clearest from Kevin de Queiroz, who has repeatedly stressed with his GLSC/USC that *none* of the causal conditions deemed constitutive by others are constitutive for speciation on his view (de Queiroz 1998; 1999; 2005; 2007). Keeping in mind that he doesn't free constitutive conditions from having to each be necessary, and that he then uses the term 'necessary property' instead of 'constitutive condition', he says "A unified species concept can be achieved by treating existence as a separately evolving metapopulation lineage as the only necessary property of species" (2007, 879). Causal conditions such as differentiating gene flow processes, sharing of selection regimes, adaptive zones, etc., are then not constitutive or necessary and rather have a "secondary" status as "lines of evidence (operational criteria)" (2007, 879).

The EvSC of Simpson (1951, 1961), and that of Wiley and Mayden (2000), also expel the individual causal conditions from those that are constitutive, and they likewise appeal instead to how species lineages are separately evolving entities. Simpson elaborates that this involves the lineage having "its own unitary role and tendencies" (1961, 153), while Wiley and Mayden underscore a long view of such tendencies – they extend from history to future fates (2000, 73).

I agree these views avoid many of the counterexamples that haunt cause-focused species concepts. Counterexamples to necessity, in particular, are easier to avoid when you don't propose stringent necessity conditions in the first place.

But there is more than one way to free us from the offending necessity claims, as the feedback model exemplified (also see Boyd 1999; Griffiths 1999; R. A. Wilson 1999; Pigliucci 2003; R. A. Wilson, Barker, and Brigandt 2007; Slater 2014). And the way provided by these non-cause-focused species concepts is extreme, facing its own dilemma.

Either the banishing leaves us with so sparse a theory about the species category's constitutive conditions that it fails to be exacting and comprehensive, and we also aren't able to assess the extent of its accuracy; or, there is enough theory to allow some assessment of its accuracy, but the assessment shows we so far have insufficient reason to accept it as accurate: its lone extremely inclusive constitutive condition recognises far more kinds of groups as species than we are given reason to do.

In other words, non-cause-focused species concepts either don't provide a clear theory of the species category's constitutive conditions, or they hint at a wildly unfamiliar one without the justification this demands.

The first horn of that dilemma amounts to *vagueness* about evolutionary cohesion, rather than the cohesion *ambiguity* that plagued cause-focused species concepts. These species concepts are relatively clear that the lineage-identifying cohesion is of the integrative sort, rather than similarity based response cohesion. But so little about this integrative cohesion is unpacked that the notion is nearly vapid. Criticisms by others have suggested Simpson (1951, 1961) and Wiley and Mayden (2000) may be stuck on this horn of the dilemma, as it doesn't help much to be told that the evolutionary unity of a species consists in being a lineage with independent evolutionary fate and historical tendencies (e.g., Ghiselin 1987; Stamos 2003; cf. R. A. Richards 2010). This recalls Molière's quip, in *The Imaginary Invalid*, that we don't learn much about the

“dormitive virtue” of opium when a physician tells us this consists in “the power to put one to sleep”.

I tend to think, however, that a more charitable read of non-cause-focused species concepts pushes them from the first to the second horn of the dilemma, where they at least get a little farther along. Proponents of these concepts stress the senses in which species are evolutionary *lineages* of a certain sort. They don’t give elaborate theories about this, but enough to appreciate the dramatic consequences they then go on to infer from this.<sup>17</sup> What they don’t give is sufficient principled reason to accept these consequences, and thereby the accuracy of their views.

Again, this is clearest with de Queiroz:

When I use the term lineage, I am not talking about a clade or a monophyletic group (see de Queiroz 1998, 1999), and thus, I am not advocating a version of the phylogenetic species concept. A lineage, in the sense that I am using the term...*is a line of direct ancestry and descent*...Lineages are formed by biological entities at several different levels of organization. For example, every person can trace his or her ancestry back along an organism lineage that passes through a series of ancestral organisms. (de Queiroz 2005, 200, my emphasis).

Because he also specifies that he is talking about certain sorts of lineages – separately evolving metapopulation lineages – he *does* rule out some lineages from counting as species. Sensibly, a lone lineage of organisms, such as one tracing back from you to a parent, then a grandparent, then a great grandparent, and so on, will not count as a species because it is not a *metapopulation* lineage. Likewise, mere cell lineages, gene lineages, etc., will rightly be ruled

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<sup>17</sup> So to be clear, we should of course be on board with the idea that species are lineages! It’s the inferences they build from this that are questionable.

out from specieshood. But many other lineages are peculiarly let in, because groups of populations (that is, metapopulations) are found at a staggering number of levels of biological organisation. Within many groups of populations that are widely deemed species, there are sub-groups, of just some of the populations, which are themselves lineages too; most readers may recognise these lineages as sub-species or varieties or otherwise mere samples of species, etc. But de Queiroz's view implies they are instead themselves also whole species, calling them "species within species" (2005, 208).

He notes we also find metapopulation lineages above the typically recognised species level, each of which comprises multiple species and would normally be deemed a higher taxon (more inclusive than species taxon). But on his view, these very inclusive groups will likewise themselves be single species (while also subsuming others). And we cannot avoid recognizing very inclusive groups as species by stepping back to the concept of a metapopulation, and claiming that populations form a metapopulation in the first place only if they belong to the same species. In the present context that would be viciously circular, helping ourselves to the very species category we are at pains to uncover.

We need to be clear about the sense in which the dramatic consequences are extreme enough to demand more justification. It is familiar by now to claim that there are evolutionary metapopulation lineages at many "levels" of inclusivity, or that there are many degrees or grades of inclusivity. This is something for which I too have argued (Barker 2019a, Barker and Wilson 2010, 76). It has also been a basis for rank-free taxonomy proposals. So that idea is well-known. What is instead radical is the further implication that *all* of these putatively many levels are *species* levels (or degrees or grades). That abandons the widespread idea that the more traditionally recognised species level is especially important or fundamental within biological theories, and thus abandons the fourth desideratum listed in our statement of the species category theory problem. Experts have thought there are many reasons to believe that a level or grade of lineagehood corresponding to a more traditional conception of the species category species is of more theoretical import than, say, the grade corresponding to our conception of

stirps or paradivisions. The latter may well have some import – that, I think, is a valuable insight from appreciating there are many levels or degrees or grades of evolutionary metapopulation lineages. But it is a marked departure from our starting point to propose such import is roughly *equal* to that of a level or degree or grade more traditionally associated with the species category. Is there really nothing of theoretical importance that distinguishes between a species lineage and paradivision lineage? Even most rank-free taxonomy proponents would (whatever their misgivings about treating ‘paradivisions’ as a formal rank) demand further justification for this, as most have insisted on the distinct importance of lineages that are species in a more traditional and much less expansive sense than de Queiroz’s (Mishler 1999, 311).

So, the sharp departure from prevailing views may well turn out correct, but we should think so only upon good reason. Thus far we are short on this. De Queiroz points to analogous and now well-known departures from familiarity, e.g., some *taxonomic* species concepts (especially phylogenetic ones) also imply that what were once regarded as sub-species are instead species, and some concepts in *conservation* do something similar (de Queiroz 2005, 206-7). But the reasons experts give for those very different departures from familiarity won’t be of the sort needed when addressing the theoretical problem about functional species concepts on which we are working. In the taxonomic case the reasons will be taxonomic, and in the conservation case they will be based on the conservation value of various evolutionary groups. We are instead looking for a theory about units traditionally regarded as species that play distinguishing functional roles in evolution, roles *unlike* and more fundamental in many biological theories than those played by categories of variety, genus, stirp, paradivision, and the like. No surprise then, that those departures from familiarity in more applied fields have already become familiar, but researchers have yet to depart nearly as much with respect to theories of the species category.

De Queiroz also stresses that all proponents of other functional species concepts agree that species are separately evolving metapopulations. Some of his sympathetic readers (e.g., Camargo and Sites 2013) then infer that if we stop our theory about the species category’s

constitutive conditions *right there*, we will preclude the disagreement that comes when those proponents move on to fill in their respective theories with more comprehensive and exacting details, e.g., about gene flow processes, niche sharing, selection regimes, etc.

We can agree that preclusion of disagreement would have some advantages. But we would want such preclusion to be based at least partly on an accurate, comprehensive, exacting, and general theory that helps vindicate the importance of the species category, rather than on just the practical gains or relief we would get from less disagreement. Why think we now have such a theory, especially when all the usual causal processes studied and discussed have been banished from the status of being constitutive (relegated to lines of evidence)?

Notice how thinking through de Queiroz's view in this way can lead back to the first horn of the dilemma for non-cause-focused species concepts. At first, we moved these concepts away from that horn by appreciating some of their clear consequences as theories. But consideration of those consequences raised further questions. Why accept a theory with such consequences? What are the good reasons to do so? It is very hard to imagine someone adequately answering those questions in favor of the non-cause-focused species concepts without further clarifying *what it is to be a separately evolving metapopulation lineage*. When the concepts have such dramatic consequences, we should not accept them as accurate until hearing more from their proponents about the proposed conditions in which *separate metapopulation evolution* consist – what *makes* a metapopulation exactly *one* separately evolving lineage instead of *two*, for instance? – so that we are positioned to tell whether these are plausible enough that we should overthrow deep and familiar views (for related concerns see Haber 2013, 341; R. A. Richards 2010, 142; Pigliucci 2003, 598).

This helps address a view of Frank Zachos', which likely appeals to many biologists with pressing practical interests, or species problem fatigue. On his view, the absent details, about what separate evolution consists in, are of operational rather theoretical relevance (2016, 107-109). He cedes that we face hard operational challenges of *telling when*, for instance, a

metapopulation is two or instead a single separately evolving lineage. But he thinks these are not theoretical challenges – the theory is already comprehensive and exacting enough about what *makes* a metapopulation one, or instead two, or instead some other number, of separately evolving lineages. He also adds a nuance: what counts as comprehensive and exacting *enough* is relative to research discipline. Relative to philosophy standards, Zachos quickly grants that de Queiroz-type theories may in fact not be comprehensive and exacting enough. But relative to biology standards, he proposes they are.

I am sympathetic to ecumenical suggestions like Zachos'. And what counts as comprehensive and exacting "enough" is very probably relative to disciplines, projects, interests, resources, abilities, and other things. But the dilemma presented above suggests this doesn't help the non-cause-focused theories about the species category's constitutive conditions. It is hard to see how the consequences of what little theory we do get from these views are any less dramatic in *biological terms* than in *philosophical terms*. I am not exactly sure, however, how to apply the biology-vs-philosophy distinction here, so let me instead recount what seems the case.

There is a long-standing view *in biology* about the species level of organisation, and about this having fundamental theoretical importance. This has prompted searches *in biology*, as in many analogous cases in the history of science, for an exacting, comprehensive, and generally accurate theory about the species category's constitutive conditions, like analogous theories that sciences has worked hard to attain for *chemical element, electron, tectonic plate, cancerous tumor, cell*, and so on. Then some very thin non-cause-focused theories are proposed, ones that do not remotely approach how comprehensive and exacting our theories are for the other categories just mentioned. And these thin theories imply the long-standing *biological views* are wildly mistaken or off track, that the species category is vastly more inclusive than long presupposed, with correspondingly very different (or comparatively much less) theoretical import than countless biologists have thought. It seems that experts in biology should then allow that the thin theories *may be accurate*. But it is *only after* being given much

more detail about what it is to *be* a separately evolving lineage (not just details about how to detect or delimit lineages), that experts should also accept that the theories and their consequences *in fact are* accurate.

This does not mean that biologists should cease grappling with the delimitation challenges until they have sufficient reason to accept the thin theories. Of course, let many researchers push on with delimitation meanwhile. Indeed, research communities in biology are relatively massive – many can focus on *only* delimitation, with little regard to theoretical toil, while others continue as well with theories of the species category’s constitutive conditions. Oncologists continued developing incredibly useful ways of detecting tumors for many decades in the late 19<sup>th</sup> and early 20<sup>th</sup> centuries, after having gained a first window into the nature of cancer, but long before achieving the deep theoretical insights about it that came with molecular and genomic methods in the 1980s, 1990s, and 2000s. Likewise, chemists made striking progress from the 1770s through the 19<sup>th</sup> century in detecting separate elements (including remarkably accurate estimates of atomic weights for many elements), long before the nature of elements was uncovered in nuclear charge and corresponding relations between protons and electrons, from about 1910 to the 1930s. But imagine where those disciplines would be now, if, say, in 1950 the community of cancer researchers had said “our theory of cancer’s nature is now comprehensive and exacting enough for us, let’s divert the remainder of our efforts to X-ray technology development”, or the community of chemists and physicists had said, in 1890, “the element is clear enough to us, let’s now only sharpen element delimitation methods and applications.” Among the consequences, my mother would very probably not have survived her HR+, HER2- breast cancer, and you would not have a smartphone at hand. Cancer researchers in 1950 and chemists and physicists in 1890 could not possibly have foreseen such innumerable costs. Neither could biologists now see potential far off costs of stopping work on the nature of the species category.



Or worse (much much worse?), go back to the biology-vs-philosophy distinction, and imagine that these past scientific research communities had added “and let’s leave the continued work on the nature of these categories to our fellow philosophers”. Shiver.

There are two lessons to draw from shortcomings presented in this section. First, it is now advised that at least some researchers seek a theory of the species category’s constitutive conditions that is more *comprehensive and exacting about integrative cohesion* (or evolving separately or having distinct evolutionary roles) than those so far furnished by non-cause-species concepts. Second, we should investigate whether developments can *clarify and constrain* proposals about constitutive conditions in ways that vindicate familiar views about the species category being distinct in fundamental theoretical ways, from other lineage categories or taxonomic categories.

As with the lessons drawn in the previous section, these further lessons are ones that new proposals can heed, as exemplified by the feedback model. Compared to cause-focused species concepts, it suggested a *more* inclusive and dynamic theory of the species category’s constitutive conditions, while addressing *ambiguity* about cohesion. But it was also appropriately *less* inclusive than the different species concepts considered in this section, and less *vague* about cohesion. Putting these innovations together resulted in a much clearer picture of the species category pattern that Section 4 showed to be accepted in more vague and ambiguous form by all functional species concepts.

## 7 Done by Dissolution via eliminative pluralism?

Aside from the above-examined attempts at solving the species category theory problem, the other main way of supporting a We Are Done view is to dissolve that problem. I’ll consider what I think are three of the most interesting and influential ways of attempting this, starting with one of Marc Ereshefsky’s most frequently cited papers (Ereshefsky 1992b). It argues we should think there is no natural, general species category that is important to biological theories, and

that we should eliminate the species concept from biology.<sup>18</sup> This implies there can be no theory meeting the desiderata we have laid out here. That would dissolve the species category theory problem.

In a recent paper I have argued that Ereshefsky's argument fails (Barker 2019b). If that is correct, dissolution does not follow from it. For the details, I refer readers to that paper; here, I will simply run main points from it through the lens of this paper, while also making new points that help show dissolution in general is difficult to defend.

Ereshefsky's focus is on what we are here calling cause-focused species concepts, and especially on the fact there are a plurality of these, each focusing on a different set of evolutionary causes.<sup>19</sup> Three premises are central to his argument. One (1), which I'll call *cross-cutting pluralism*, is that the multiple different sets of causes at issue (e.g., gene flow processes, niche sharing processes, etc.) each operate on and produce different types of "basal lineages", with some of these different lineages cross-cutting each other. For example, according to Ereshefsky there are interbreeding lineages, ecological lineages, and genealogical lineages, and often there are cases like this: populations A and B belong to the same interbreeding lineage, but to different ecological lineages, and to no genealogical lineages. In a way, each cause-focused species concept is finer-grained than a general species concept, and no one of these is always compatible with any other.

A second central premise (2) is that we very probably will not discover a parameter common to all the different types of cross-cutting basal lineages created by the different evolutionary

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<sup>18</sup> In later work (e.g., Ereshefsky 2010), he sees practical value for the concept, but maintains his old view about the category, leaving the old implication for us the same.

<sup>19</sup> Elsewhere (e.g., Ereshefsky 2010, 2017), he argues against some non-cause-focused species concepts.

causes. Call that the *essence cynicism* premise: Ereshefsky doubts there is any underlying essence that could unify all the cross-cutting, finer-grained basal lineage concepts.<sup>20</sup>

Finally, the following premise (3) is needed to move from the other two to the conclusion: *if* cross-cutting pluralism and essence cynicism are true (as is the separate presumption that no non-cause-focused species concepts succeed in general), *then* we should think there is no general functional species category that is of distinctive importance to biological theories.

A first problem for the argument is the appeal to basal lineages. Premise (1) assumes each type of fine-grained group recognised by Ereshefsky shares in being such a lineage. But premise (2) suggests there is no “common parameter” or essence underwriting that category. It seems by the argument’s own lights, (1) and (2) cannot be true at the same time, in which case it cannot issue its conclusion (Barker 2019b).

A second set of problems for the appeal to basal lineage in premise (1) arises even when setting aside its relation to premise (2). What should we take a basal lineage to be? Ereshefsky implies it is to be an evolutionarily cohesive thing that can be produced in a variety of ways – he cites interbreeding causes, ecological causes, and genealogical causes. But this faces the first horn of the dilemma raised in Section 6 for non-cause-focused species concepts: what is it that these causes are producing, and which we associate with being a basal lineage? Moreover, why think interbreeding groups count as basal lineages? Same for ecological groups, and genealogical ones. They may each be biologically interesting groups. But what makes them *lineages*, and what makes them lineages of a *basal* sort? These aren’t rhetorical questions. Rather it seems if there are answers to them for each proposed type of basal lineage, then we have the makings of a theory about a general species category, contrary to the argument’s conclusion.

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<sup>20</sup> Ereshefsky does not use the term ‘essence’ in his paper, though it seems suitable to his claims.

A third problem afflicts premise (3). We should not think cross-cutting pluralism and essence cynicism would, if true, together suffice to take us to the conclusion. Neither of those would help rule out an alternative general theory – or just another theory among the plurality – of the species category that proposes each species lineage consists in dynamic interactions of multiple variables, with variations in these interactions across different examples of species. To see this, suppose cross-cutting pluralism is true, so that populations A and B belong to one “interbreeding lineage”, while also belonging to distinct “ecological lineages”. (Perhaps Templeton’s (1989) cottonwoods and balsam poplars are such a case.) This wouldn’t rule out there being a third interactionist type of lineage, with “feedback lineage” being just one example, and investigating how the two populations relate to it. Already Ereshefsky’s view implies that multiple kinds of lineages can overlap or have some of their member populations be the same. There is no reason to think a further kind of lineage couldn’t also partake in such complexity. We can also model these types of lineage separately or jointly, e.g., the same metapopulations can be plotted in  $M$  space, or in a BSC space, or in an EvSC space, etc., and their relations studied.

Now suppose essence cynicism is true, so that an essentialist standard is not met for the basal lineage category or a general species category. This shouldn’t matter because we have already seen such a standard is neither necessary, nor advised. We have learned that prodigious variation, change, and complexity in the living world challenge such kinds of essentialism, and so we have developed thorough alternatives to accommodate this, including cluster and family resemblance views of categories (e.g., Boyd 1999, Pigliucci 2003, Wilson et al. 2007, Slater 2014).<sup>21</sup> On such views, each of the typically important causal variables can count as one of the constitutive conditions of the species category, without the condition being necessary. Such views are implicitly routine in many other branches of biology, e.g., there is a particular

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<sup>21</sup> The Boyd 1999 paper focuses on individual species taxa, Pigliucci 2003 focuses on the species category, and Wilson et al. 2007 addresses both.

mutation (i.e.,  $\Delta F508$ ) at work in the majority of cases of cystic fibrosis, but not in all, and indeed any one of over 1500 different mutations can play the role (Bobadilla et al. 2002). It does not follow that there is no general cystic fibrosis category.

That example also illustrates the point made above about cross-cutting pluralism not doing the work implied. Ereshefsky's fine-grained "interbreeding lineages" and "ecological lineages" are akin to more fine-grained cystic fibrosis categories distinguished by mutation type, say, " $\Delta F508$ -cystic fibrosis" and "G542X-cystic fibrosis". Each of these four fine-grained categories can have their purposes: there are different treatments for the different fine-grained cystic fibrosis categories; different conservation measures may be advised for the different fine-grained lineages. Nonetheless, there can also be both a more general cystic fibrosis category and a more general species category, whether that be a feedback species category or some other. And these more general categories can have importance additional to that of just the four fine-grained categories listed.

## 8 Done by Dissolution via pessimism?

Brent Mishler is well-known for skepticism about the species category. His argument (1999, 308-309) from failures of past attempts species concepts can be summarised this way:

- (1) "When anyone has looked closely for an empirical criterion to distinguish the species rank uniquely and universally from all others, the attempt has failed" (1999, 308).
- (2) "We are unlikely to have any criterion for distinguishing species" (1999, 309).
- (3) If (1) and (2) are true, then we should think there is no general species category that is of distinctive importance to biological theories. ("Species are not special", 1999, 309.)
- (4) Therefore, we should think there is no general species category that is of distinctive importance to biological theories.

Premise (1) is about *past* work, and our examination of Done by Solution views suggests we should agree with it, *if* by 'fail' we mean: did not succeed in providing the theory we seek. But we should be less sanguine, if 'fail' implies we have not even seen instructive defenses of and

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revisions to functional species concepts, nor learned anything on which we have decent prospects of building. We have, as we've seen.

Mishler's premise (2) is a probability claim about the *future*, and thus difficult to assess. However, note that in (1) he is talking about respective searches for "a" criterion. As with Ereshefsky, that sounds like the assumption of an essentialist standard – that we are seeking a single, necessary and sufficient, constitutive condition for the species category. So there are two problems with (2), and its relation to the other premises. If (2) is pronouncing a low probability for satisfying an essentialist condition, that seems a reasonable inference from (1), but then it will cast doubt on (3). This is because, as we have seen, failed essentialist attempts have taught us better ways to proceed, rather than closing off hope altogether. So those better ways suggest a more optimistic conclusion rather than the pessimistic one that (3) says is in the offing.

If instead (2) is pronouncing poor prospects for un-essentialist attempts as well, then (2) itself seems dubious. Again, we have drawn guidance and hope from the failures; that doesn't *lower* the probability of future success as (2) presupposes.

Last, regarding (3), the point about communities of researchers surfaces again. Suppose Mishler responds with a strong case for thinking past failures suggest poor prospects for even more sophisticated, un-essentialistic attempts in the future. Would those poor prospects be sufficient to conclude once and for all that "species are not special" (p.309), recommending that zero people in the communities should work on the species category theory problem? I don't think so. Given the lessons we've learned, and new kinds of views that heed them such as the feedback model, it would remain wise to have some portion of the research community revving up.

I shouldn't suggest more difference between Mishler's and my own personal views than there is. I too often feel pessimistic about the species category theory problem. But constructing an argument for such pessimism proves difficult.

## 9 Done by Dissolution via phenomenism?

John Wilkins has recently and provocatively argued that species are not “theoretical objects”, and instead are “phenomenal objects” (2018, ch.14; see Wilkins in this volume for more on his views of species). What does this mean?

One function of scientific theories is explanation. The theory of evolution by natural selection, for example, is supposed to offer explanations for many things, including many changes in population trait frequencies. As such, the mechanisms of natural selection count as theoretical objects. Theoretical objects are things that do some explaining according to theories about them. Being “theoretical” is not pejorative here, and doesn’t imply “less real.” It is famously quite the opposite according to W. V. O Quine. Roughly, the more scientific confirmation a theory enjoys, the more assurance we have that the objects to which it appeals for the explanation are real (Quine 1948).

Wilkins thinks that whenever biological theories make reference to a general species category, it is *not* in order to explain anything. A general species category or features associated with it *get* explained, but, he thinks, *do* no explaining. This does *not* imply the category’s unreality. He thinks phenomena that get explained – patterns, cohesive objects, effects, and so on – can also have reality, and he thinks this is the case for the species category. So, he thinks there is a real species category, but that it is like the mountain category in geology – difficult to define and fuzzy at the edges, but a well explained phenomenon nonetheless (Wilkins 2018, 343). Other categories in geology, like tectonic plate, are different – they are theoretical objects that do explaining.

How might this threaten to dissolve the species category theory problem? The general species category we are trying to further uncover by solving that problem is supposed to be of fundamental importance to biological theories. If having such status entails being a category that helps do important *explaining* according to biological theories, but Wilkins is correct to *deny* such an explanatory role to any general species category, then there is no category *of the*

*type sought*. (Again, he will insist there indeed is a real species category, but of a type different than the one sought by the species category theory problem articulated in this essay.) Here is the argument:

- (1) If we should think there is a general species category that is of distinctive importance to biological theories, then some general species concept does important explaining across the living world.
- (2) But it's not the case that some general species concept does important explaining across the living world.
- (3) Therefore, it's not the case we should think there is a general species category that is of distinctive importance to biological theories.

Start with (2). Wilkins provides two interesting reasons in its favour. First, when biological theories seem to appeal to a proposed species category as an explainer, they have actually (so far anyway) been appealing to categories and associated processes at *lower* levels of biological explanation, such as the flow of genes (much lower level) between less inclusive populations (also a lower level). This is a reductionist claim. As he puts it, "the theories used, the explanations, are not theories of species; they are theories of gene exchange, reproduction, fitness, adaptation, and so on" (Wilkins 2018, 342; also see Cracraft 1989b).

This seems incorrect in some familiar cases, including with the BSC and other concepts he discusses under the label "reproductive isolation species concepts" (RISCs). One of the central properties that BSCers think does a lot of explaining is reproductive isolation. That is at least often a property of *groups* of populations (Wilson 1996), and on the BSCer's view it is a property of groups they recognise *as species*. I don't see that we are bound to fully reduce this explanatory property to lower level entities and processes, any more than we are bound to talk about the allele frequency in a population without at least some non-reductive deference, implicit or otherwise, to the whole population (Sober 1980). Populations are what have population allele frequencies and the dynamics that explain changes in these. By analogy,



groups of populations (which BSCers happen to recognise as species) have the property of reproductive isolation.

Indeed, there are many explanatory properties like this, which aren't fully reduced. Trait frequencies across groups of populations, not just within populations, can also help explain how one group responds differently than another group of populations to selection regimes, and some views of species appeal to this (e.g., Barker and Wilson 2010, Barker 2019a). Some putatively explanatory models of speciation also have such non-reductionist aspects (Coyne and Orr 2004), as do attempted explanations of "rules" such as Haldane's rule (e.g., Turelli and Orr 1995), Bateson-Dobzhansky-Muller (BDM) incompatibilities (Cutter 2012), the Island rule (e.g., Lomolino 2005), and Cope's rule (e.g., Hone and Benton 2005).

Then there is what many have proposed is the big-ticket item: why is life clumpy rather than continuous? Or as Mayr put the question, why "has nature, and more precisely natural selection, favored the discontinuities" between some groups of populations but not others? (Mayr 2000a, 161). All cause-focused species concepts attempt to explain that big-ticket item. In doing so, they treat clumpiness as an *explanandum* (thing to explain) but include only the *explanantia* (things that do the explaining) among the conditions deemed constitutive of the species category. Mayr, for example, does this when insisting we exclude phenotypic uniformity from the definition of 'species', while also urging that we explain that uniformity by the processes he *does* reference in the definition: gene flow processes between populations. This is analogous to how chemists treat the chemical element category. They take different sorts of clumpiness as the things to explain, e.g., clumpiness rather than continuity in chemical phenomena such as boiling points, densities, malleability, and so on, across the chemical world. They then explain such clumpiness by appeal to differences in nuclear charge (and associated electron configurations). And when next isolating the conditions that are constitutive of the chemical element category, they appeal only to the explanatory properties and processes (nuclear charge and associated electron configurations), not to the clumpiness they have explained. (As seen above, there is no mention of boiling points, densities, etc., in the IUPAC

definition of ‘chemical element’.) There is at least one apparent difference though. Whereas explanatory and constitutive nuclear charges are intrinsic to their respective atoms, the explanatory and constitutive processes in the case of species are not all intrinsic to populations or species. At least some are unreduced relationships between or across populations and species, according to cause-focused species concepts. Thereby, proponents of those concepts imply that reference to species does a lot of *unreduced* explaining.

On more *general* reductionist grounds, one might try to fully reduce *all* of those sorts of explanations. But although in other work I have defended some reductionist views against hasty anti-reductionist ones (Barker 2013), the prospects of ambitious general reductionist views also seem bleak, given the demise over the past 30 years of such views in biology and philosophy of biology (Brigandt and Love 2017).

If the reductionist point is not available in support of (2), then Wilkins’ second point in its favour becomes more important. It is that none of the species concepts we might regard as explanatory (the functional ones) have succeeded in being accurate *in general*. If we opt for the BSC, for instance, then “the vast bulk of life would not be in species” (2018, 344).

That is a much more promising defense of (2), as our discussion of Done by Solution views would suggest. But it throws a troubling light on (1). It indicates that (1) demands some existing species concept has *already* succeeded with its explanations in general terms, if we are to think there exists a general and important species category of the sort we are discussing. This is even more demanding about past work on functional species concepts than is Mishler. Mishler demanded *more* from past work if we were to see promise for the future; we countered that past work has already provided enough for promise. Wilkins instead demands that past work *already have solved the problem*. So, our counter to Mishler suggests the more demanding view of Wilkins is even further from justified.

## 10 Conclusion

We began with the feedback model of species, which exemplified a new kind of approach we are positioned to develop. Then in Section 3 we zeroed in the hard theoretical species problem which this new kind of approach might help with. This species category theory problem says we lack a theory of the species category's constitutive conditions that meets, to high degrees, the desiderata of being exacting, comprehensive, accurate, and helpful in vindicating the traditional idea that the species category is especially important to many biological theories. We met opposing views about this problem. Revving Up says we are well positioned to begin work on the new approaches to species, thanks to a host of conceptual and empirical lessons learned over recent decades. We Are Done views instead imply we are finished with the species category theory problem, either because we have already solved it, or have dissolved it altogether. Section 4 clarified the relevant extant species concepts that would help us assess Revving Up against some We Are Done views. These are functional species concepts of the cause-focused and non-cause-focused sorts. In Section 5 we saw how the cause-focused sorts don't support We Are Done views that think we've solved the problem at issue; in Section 6 we reached an analogous conclusion for non-cause-focused species concepts. In both cases we drew specific lessons from the challenges to both types of species concept and exemplified via the feedback model that we are well positioned to build on these, thereby supporting Revving Up. Sections 7-9 then examined the other type of We Are Done views that oppose Revving Up, those that say we have dissolved the species category theory problem. These were found problematic. The overall critical conclusion is that We Are Done views have not yet succeeded and there is currently no such view that everyone should endorse. More constructively, Revving Up is plausible, and some proportion of researchers working on species should endorse and further develop it, while others work on We Are Done views.

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