Deep Conventionalism about Evolutionary Groups

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We reject a widespread objectivism about kinds of evolutionary groups in favor of a new conventionalism. Surprisingly, being any one kind of evolutionary group typically depends on which of many incompatible values are taken by suppressed variables. This novel pluralism underlies almost any single evolutionary group concept, unlike familiar pluralisms claiming that multiple concepts of certain sorts are legitimate. Consequently, we must help objective facts determine which candidate evolutionary groups satisfy the definition of a given evolutionary group concept, regardless of whether we also help determine the legitimacy of that concept's applications.

1. Introduction. Most of you probably like objectivity when you can get it, even if you think we seldom can. And researchers widely appreciate the theoretical and practical importance of disputes about the criteria for being this or that kind of evolutionary group—for example, a population, species, or clade. These are reasons why so much attention has been paid in several disciplines to the increasingly popular versions of pluralism that authors such as Philip Kitcher, John Dupré, Marc Ereshefsky, and Helen Longino defend. For many people, those pluralisms have implied that there is a form of objectivism about many kinds of evolutionary groups that we cannot get: in many research contexts, various evolutionary group concepts compete for application, and objective facts alone typically cannot determine which of these concepts is legitimate to use. To make up this shortfall we must also appeal to our research interests, perceptual abilities, values, and so on. For

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brevity, we refer to these things of ours as conventions. Let these and "objective facts" be mutually exclusive by taking "objective facts" to include exactly those facts that obtain independently of our perceptual and mental states. In these terms, Kitcher (2001, 48), for example, implies that in a particular context the conventions of botanists help objective facts determine that applying a morphological species concept is legitimate and applying an interbreeding species concept is not. We are asked to relinquish objectivism about the *application* of evolutionary group concepts.

But familiar pluralisms fail to touch a different kind of objectivism, one about the *satisfaction* of definitions of evolutionary group concepts. In his 2001 book, for instance, Kitcher himself implies that whether a collection of entities satisfies a precisely understood definition of the morphological species concept is not something our conventions influence.[1] Objective facts, and only those, determine such satisfaction. Likewise for whether that same collection of entities, or any other, satisfies the definition of the interbreeding concept, or a definition of some population concept, or clade concept, et cetera.

Most biologists also implicitly or explicitly accept this objectivism about satisfaction. When molecular phylogeneticists and developmental botanists argue that the *AGL6*-like family of genes is a clade that has existed for at least 300 million years, colleagues may dispute whether the *AGL6*-like group really is a clade (Becker and Theißen 2003). But if both sides come to agree (by acknowledged conventions or not) on which concept of clade to apply in the dispute (or on how to define "clade"), they will still insist that objective facts alone determine whether the *AGL6*-like group satisfies the agreed-upon definition of the concept. With the concepts agreed upon, the rest is empirical.

The consensus favoring this objectivism is so widespread that authors rarely discuss it.[2] We aim to show it is mistaken. Given any single evolutionary group concept, typically objective facts alone cannot determine which things are such groups; conventions make up this shortfall. This conventionalism

1. Also consider Kitcher's (1984, 331) reference to "natural partitions," which indicates that for any of the kinds in any set of kinds K_i that he envisions, the objective facts alone determine which entities belong to that kind. The interests of the hypothetical biologists he describes just help determine which of these kinds is relevant in which contexts. He veers from this sort of objectivism in his paper on race (Kitcher 2007).

2. There are many conventionalists about the species rank but they typically presume that the groups we rank conventionally nonetheless objectively satisfy the grouping criteria in terms of which species concepts are defined (e.g., Baum 2009). With respect to populations, Gannett (2003) challenges the consensus, and perhaps some of Godfrey-Smith's (2009) passing remarks are against it. There is also global conventionalism about many or all theoretical concepts that may entail our view (e.g., Sismondo and Chrisman 2001), but our view does not require global conventionalism.

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is independent of standard worries about vagueness, and is of a deep sort because it undercuts hopes of objectivism about evolutionary groups even if the distinct conventionalism about concept application turns out to be false. Arguing for our conventionalism involves uncovering a novel form of pluralism that we express in terms of the key notion of suppressed variables. To clarify this notion, we temporarily suspend biological detail before focusing on cohesive functional units, populations, and clades as exemplar kinds of evolutionary groups.

2. Suppressed Variables. Suppose Charles is at a large picnic with much of Alfred's extended family. Alfred is in a small group of people around a punch bowl, and Charles, walking toward them, senses that the small group is not enjoying the live country music. But the rest of the people at the picnic love the music. Charles asks, "So is this small group of you unified in your response to country music?"

Alfred says "yes," but this is made correct by drawing on context to further specify the question. Alfred gathers that Charles asked his question with certain kinds of responses in mind, and certain kinds of country music. Without presuming particular values for these variables, there is no correct answer to the question.

Suppose the small punch bowl group includes just Alfred and his brother and sister. For the kinds-of-response variable, choose the "emotional response" value. For the kinds-of-country-music variable, choose the "pop-country music" value. Then, given facts about his family, Alfred can assure you that the small punch bowl group is unified in its response to country music. He and his siblings each react with disgust to pop-country music, and more so than any of the attending extended family does. However, with respect to alt-country music the group is not unified. Alfred and his brother like alt-country music, but his sister detests it more than anyone in the extended family. Changing the other variable from "emotional response" to "sensorimotor response" might also make Alfred's affirmative answer incorrect.

In cases like the picnic scenario, semantic facts (as opposed to pragmatic ones) about the meaning of "response to country music" leave many variables open. Short of further pragmatic inputs, there is no fact of the matter about which value the kinds-of-response variable takes. Given that such variables do often get fixed in the face of these shortfalls, something else must help fix the variable values. In the picnic case, that "something else" is pretty clearly our conventions about contextual information. The conventions here imply conditionals such as "if the country music playing is pop-country music in particular, then presume that the kind of country music that the question is about is pop-country music."

The relevant biological variables are like the above linguistic ones and lead to similar results. To see this, consider that in the picnic case we have *in-*

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determinacy pluralism consisting in two conditions. First, variable-dependent unity: whether a group of people is unified in its response to country music depends on variables that can each take one of a plurality of values. Factually, Alfred emotionally responds to alt-country music in one way and to pop-country in another. Second, *unity-indeterminacy*: for some or all of these variables, some different available values would on their own lead to incompatible results, for example, to the punch bowl group having a unified response on some variable values but not on others. So the facts independent of our contributions leave indeterminate whether the punch bowl group is unified in its response to country music. Given that indeterminacy in some cases like this is overcome, our contributions must make up those indeterminacy shortfalls.

The analogous pair of conditions for indeterminacy pluralism typically holds for each particular evolutionary group concept. Each concept picks out some evolutionarily salient relations in terms of which entities belonging to such a group are unified relative to others. Whether a candidate group enjoys this unity depends on variables that can each take one of a plurality of values. This satisfaction of the variable-dependent unity condition of indeterminacy pluralism is underwritten by well-known empirical facts about biological variation, rather than the linguistic underdetermination from the picnic case. And the details of the biological variation within and around any typical candidate evolutionary group typically ensure that the unity-indeterminacy condition of indeterminacy pluralism is also met. That is, the different variable values made available by the objective facts would on their own lead to incompatible grouping results, for example, to a collection of organisms being a particular sort of population on some variable values but not on others. Again we must make up this objective shortfall conventionally.

That puts things abstractly. Discussing exemplar evolutionary groups will make things more concrete. It will also show the futility of trying to use concept splitting to escape suppressed variables. One might try claiming that "unified in response to pop-country music" and "unified in response to alt-country music" are distinct concepts, and that the punch bowl group objectively falls under the former and not the latter. But splitting evolutionary group concepts into more specific ones leads in each case either to further suppressed variables, or to concepts so specific that they are theoretical and practical dead ends—not evolutionary group concepts at all.

3. Functional Units and Cohesion. Many evolutionary groups are what David Baum calls "functional units," characterized by "cohesion or causal efficacy" that allows them to be "players" or forward-looking groups in ongoing evolutionary processes (2009, 74). Although authors typically have species in mind when discussing these units, it is plausible that some non-

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species groups (populations, syngameons, some higher taxa) also enjoy, to greater or lesser degrees or grades, the cohesion that is supposed to make species functional units (Barker and Wilson 2010). But for many systematists, species are special precisely because of their grade of functional cohesion (see Baum 2009, 74–75).

Species cohesion has been important in many articulations of the nature of species since the modern synthesis. This is explicit in some species concepts (e.g., evolutionary species concepts of E. O. Wiley and G. G. Simpson) and implicit in others (e.g., Ernst Mayr's biological species concept; Barker 2007; Barker and Wilson 2010). Species cohesion is also important to various interventional and field studies, such as attempts to explain why conspecific populations together trace a distinct trajectory through the space of evolutionary pressures. Some such projects attempt to discover and mathematically represent relationships between effective population sizes, population subdivision, migration, and species cohesion. An example result: the effective number of migrants, $N_e m$, from one population to another must be ≥ 1 for "maintaining species cohesion" across those populations (Barbará et al. 2007, 1987).

The question for us is whether species cohesion is a conventional sort of unity due to featuring suppressed variables. Recent clarifications of "species cohesion" (e.g., Barker and Wilson 2010) help answer this. Species cohesion is a grade of evolutionary response cohesion that involves organisms or populations responding similarly to evolutionary pressures. Whether a group responds in such a way depends partially on the contrast class. Take a collection of populations. It manifests evolutionary response cohesion exactly when the responses of its populations to evolutionary pressures are more similar to each other than to any outside the collection. Without this relativization to outsiders, it is hard to see how the collection could have the cohesion that supposedly sets it apart from other things—gives it functional unity.

With evolutionary response cohesion distinguishing evolutionary groups that we call functional units, being such a unit clearly depends on the values that suppressed variables take. Imagine two populations, North and South, flanking a mountain. They will face many evolutionary pressures, often concurrently: a drought, a nutrient deficiency, emergence of an advantageous mutation. And there are different responses they can have to any one pressure: this trait declines in frequency in one population and increases in the other; that trait increases in both populations. Minimally, then, two suppressed variables of evolutionary response cohesion (of any grade) that can take many values are these: which evolutionary pressures, and which aspects of response. Typically, these can take an enormous number of values, with different combinations of values leading to different verdicts with respect to evolutionary response cohesion.

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Suppose that in each population, just 1% of organisms have a suite of genes that contribute to their retaining moisture far better than the other 99% of organisms during depressed humidity. Then there is a series of devastating droughts. The suite of genes increases to 35% representation in both populations. In organisms of other nearby populations, genes involved in moisture retention are quite variable, resulting in no pattern of frequency response during the droughts.

Meanwhile, spikes in sunlight hours accompany the droughts. In North, South, and each nearby population, a new sequence at a genetic locus has emerged that dramatically helps utilize increased sunlight hours for energy production. Selection then facilitates a spike in population frequencies of the new sunlight-utilization sequence, except in South where chance events prevented the spike.

Choosing "moisture retention genes" for the which-aspects-of-response variable, and "series of droughts" for the which-evolutionary-pressures variable, would count (or contribute to counting) the two mountain populations as having associated evolutionary response cohesion. The responses of moisture-retention genes in those two populations are more similar to each other than to any responses in other populations. But changing from the "water-retention-genes" variable value to "sunlight-utilization locus" would count (or contribute to counting) the two populations as not having evolutionary-response cohesion.

This clarifies how functional units distinguished by evolutionary response cohesion will typically satisfy the two conditions of indeterminacy pluralism. To help verify that this is typically so, almost any study of population differentiation suffices. Barbará et al. (2007) recently described a model for studying population differentiation across continental radiations. The model involves populations of *Alcantarea* species, perennial plants in Brazil that grow on large granite outcrops (similar to Uluru). Highly varied traits characterized organisms in these populations, for example, all eight microsatellite loci investigated in populations of one species, *Alcantarea imperialis*, "were polymorphic, with up to 14 alleles per locus" (2007, 1985). And the scattering of populations across granite outcrops suggests varied evolutionary pressures across those populations. Together these points indicate there are many values that the responses-to-evolutionary-pressures and which-aspects-of-response variables will take across the studied populations of *Alcantarea imperialis* (first condition of indeterminacy pluralism). Also, evidence suggested that for at least some of these variables, some different available values would on their own lead to incompatible verdicts on whether the populations of the *Alcantarea imperialis* jointly manifest the species grade of evolutionary response cohesion (second condition of indeterminacy pluralism). Genetic distances between populations of *Alcantarea*

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imperialis, for example, were sometimes nearly as large as between that species and another *Alcantarea* species (Barbará et al. 2007, 1986). Genetic variance, too, between conspecific populations was near what it was between the species (2007, 1988). These statistical measures of distance and variance strongly suggest that many particular genetic responses to evolutionary pressures are more similar between populations of distinct species than between conspecific populations.

Generally across functional unit candidates, many of the biological values available for suppressed variables of evolutionary response cohesion would count the candidate group as being a functional unit, while many others would not. Both results cannot concurrently obtain. And the objective facts cannot choose between the diverging values they give. Our conventions must do that. Species cohesion and other grades of evolutionary response cohesion are therefore conventional sorts of unity in light of indeterminacy pluralism. This entails conventionalism about functional units distinguished by such cohesion.

One could concede this and move on to more specific kinds of cohesion in search of objectivity by splitting cohesion concepts into finer-grained ones until convention-implicating suppressed variables vanish. But this would result in concepts such as "functionally cohesive group with respect to trait T1 and pressure P1" and "functionally cohesive group with respect to trait T2 and pressure P2." If one of these applies to a group, it will typically apply to only that group—the one featuring T1 that is subject to P1, for example. Such concepts do not pick out kinds to which many member groups belong and over which theoretically interesting generalizations and predictions hold.

4. Populations and Interaction Rate Exclusivity. Not all forward-looking functional units are distinguished by some grade of evolutionary response cohesion; for others, it is how they or things belonging to them causally interact with each other, rather than how they causally respond to shared evolutionary pressures. Populations are the prime example.

Elaborating and refining earlier work, Millstein (2010) describes a number of population concepts and then defends her own "causal interactionist population concept." On this, a population is any group of multiple conspecific organisms that is the largest group for which the internal rates of survival and reproduction interactions are much higher within the group than outside it (67).

As with evolutionary response cohesion, the evolutionary group-making property that this definition picks out is a kind of unity or exclusivity property. It is relativized to things outside candidate populations. In this case, survival and reproduction interaction rates set apart those belonging to the

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group. Effectively these interaction rates should be greater between members of the same population than between any of them and members of different populations.

This property also features indeterminacy pluralism due to variables that can take many values, some large sets of which would suggest that a group has the property and other large sets of which would imply otherwise. We find these variables at more than one level. At a first level there is a variable, kinds of interaction, that Millstein frees from suppression in similar definitions by explicitly referencing two of its values in her 2010 definition: "survival interaction" and "reproduction interaction." These two values can pull in opposite directions. Many organisms frequently interact with others in a way that changes their life expectancy (e.g., negatively in competition, positively in cooperation) without changing their expected reproductive output. The situation escalates if we omit the stipulated restriction of a population to members of the same species, as Godfrey-Smith (2009) suggests we do to properly understand natural selection, and as one must (on pain of circularity) if one defines "species" in terms of populations. Highest rates of reproductive interactions for some plant in your garden might connect it with pollinators and seed dispersers, while highest rates of survival interactions might connect it with other plants crowding it for soil and sun.

One level down we find two suppressed variables: kinds of survival interaction and kinds of reproductive interaction. These can each take several values, as there are several kinds of each interaction, all of which Millstein means to recognize as forming an "overall" rate of interactions (2010, 67–68). Among the reproductive kind, she cites successful matings, unsuccessful matings, and different offspring-rearing activities. Survival interactions include direct competition, indirect competition, and cooperation. But some of these will simultaneously pull in opposite directions with respect to candidate groupings. Thus we need a weighting scheme for combining them. Simply counting numbers of interactions of any kind is obviously insufficient; some interactions are intense and sustained, others are fleeting with minimal effects. But whether something counts as a relevant interaction or not, and just how much it counts, depends on our conventions.

We again have indeterminacy pluralism, and our conventions are needed to fix population boundaries. Any attempt to split Millstein's population concept until suppressed variables vanish will lead, as before, to theoretically and practically vapid results, such as "population due to rate exclusivity with respect to survival interactions S1 and reproductive interactions R1."

This makes vivid the distinction between our conventionalism and conventionalism stemming from concept pluralism that we flagged in our introduction. For instance, while Stegenga (2010) criticizes Millstein and de-

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fends pluralism about population concepts, any resulting conventionalism is about choosing which population concept to apply. Our distinct point is that whether we settle on Millstein's concept conventionally or objectively, our conventions must help determine which organisms form populations on that concept. Likewise on any reasonable population concept.

5. Clades, Splitting, and Genealogical Exclusivity. In many areas of biology the central evolutionary grouping concept is that of a clade or monophyletic group. Clades are evolutionary groups because they feature a kind of evolutionary unity—they are united by a shared common ancestry, making them backward-looking groups. Relative recency of common ancestry often explains why members of a clade share the traits they do, grounds a variety of inferences about the past, and provides evidence about what unseen traits in members of the group will be like. Such features make clades so important in taxonomy that researchers commonly think biological taxa must be clades. Their importance extends far beyond taxonomy. Phylogenetic trees are recognized as the background information required for a huge number of inferences and explanations, but trees are simply a representation of which groups under examination form clades. Clade divisions do the real explanatory work.

But there is no single "common ancestry" relationship that grounds clade groupings. A standard definition of "clade" is that it is some species and all of its descendants. Yet it is unclear which groups are species. Further, some of the most popular views about species require that they are clades, and so those views cannot define "clade" in terms of species. For these reasons, clades are commonly defined directly in terms of groups of populations or organisms and their relationships (Velasco 2010). But there are different, incompatible ways of understanding the history of populations and of organisms. Take these in turn.

Defenses of phylogenetic concepts of species often talk about trees of populations to argue that all taxa (including species) should be monophyletic groups of populations (Velasco 2008). That is, a clade should be some ancestral population and all of its descendants. This maneuver avoids talking about ancestral species and having delineation of clades depend on delineation of speciation events. But we then meet the problem of delineating populations and population lineage splits. Velasco (2012) argues that lineage splits are context dependent. One rough argument for this is that lineage splits represent a loss of cohesion between groups and the introduction of distinct evolutionary paths. However, for certain kinds of traits a group may still be cohesive, while typically for many other traits the very same group breaks into independent trajectories. Only the context and associated conventions can determine which traits are of interest, and so typically they must help with any determination of lineage splits.

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The history of populations is naturally "loose" in a way that allows for some reticulation between groups. The very idea of migration dictates that it must be possible to have some gene flow between distinct populations without thereby collapsing them. How much reticulation is allowed is precisely what is at issue and what drives the point that lineage splitting (and so cladehood) is context dependent. Grant and Grant (2008) talk about distinct clades of Darwin's finches and place them on a phylogenetic tree, but later discuss hybridization between these groups. There are many reasons to treat sister species of Darwin's finches as distinct clades, but whether the relevant lineages should be considered separate at all depends on context and convention.

While populations are loose, we sometimes want, in other contexts with other purposes, to be strict. Then it is important to think of clades as genealogically exclusive groups of organisms: a group of organisms, all of which are more closely related to each other than to any organisms outside the group. But there are different ways of understanding how organisms are related to one another. Baum and Shaw (1995) first carefully spelled out exclusivity in terms of genetic concordance, but Velasco (2009) defines it in terms of organismal parent-offspring relationships. These two kinds of group are incompatible, with some biological projects concerned with one and different projects the other (Velasco 2010).

When we ask whether a group is genealogically exclusive, we could refer to "recency of organismal common ancestry" or to "genetic concordance." But the biology alone does not determine which we mean. Different answers lead to different groupings. Our research interests, or more generally our conventions, help settle this and so genealogical exclusivity is conventional in our sense.

We do not always want our understanding of common ancestry to be as strict as genealogical exclusivity. After all, a small number of hybrids between two different clades destroys either kind of genealogical exclusivity just described. And often we want to understand the distribution of some "broader level" feature such as biogeography, in which case it seems appropriate to think of the history of whole populations as determined by population lineage splits. But in these cases conventions help fix the variable value "distinct population lineage" in place of "being genealogically exclusive." And we saw that this fixed value itself has deeper suppressed variables because population splits depend on contexts that have incompatible outcomes and which the biological facts alone do not choose between. So at multiple levels there is indeterminacy pluralism and conventionalism.

The general source of this is that different parts of a taxon have different histories. Which parts we care about varies across contexts. Our research interests help decide between the looser "population lineage" definition of clade or the more strict "genealogical exclusive group of organisms" idea.

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What is important to see is that on either of these readings, there are still further suppressed variables whose objective values would incompatibly dictate which things are population-level lineages or which organisms are most closely related to each other. And the biological facts leave us with a plurality of possible values that lead to incompatible grouping of organisms into clades. Further details are needed for any determination of cladehood.

This is most obvious in extreme cases like Thermotogales. While much of the group's history remains uncertain, ribosomal RNA and other "core" operational genes give us strong reason to believe that the Thermotogales are a bacterial group that share a "cellular" history with the bacteria Aquifilales; however, the majority of their genome indicates some other phylogenetic position—including many genes that are clearly of archaeal origins (Zhaxybayeva et al. 2009). Context combined with various conventions helps determine whether Thermotogales is a clade of bacteria, a clade of archaea, or not a clade.

While Thermotogales is among the most extreme cases we know, this kind of conventional dependence is unavoidable. Related concepts free of suppressed variables would not be clade concepts at all. They would be hopelessly overspecific, such as "organism-level clade due to being an exclusive group on the plurality concordance genome tree with respect to all genes and all organisms." There is, then, no unique objective grouping of organisms into clades.

6. Conclusion. The theoretical and practical reasons for caring about the evolutionary group concepts we have focused on are absent for those produced when avoiding our conventionalism by splitting. Better to not split and retain conventional concepts that are important. This is a lesson that emerged upon combining an understanding of what it is for an entity to have relational unity that marks grouphood with an appreciation of empirical facts about the variegated organization and diversity of the biological world.

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