Multilevel Lineages and Multidimensional Trees: The Levels of Lineage and Phylogeny Reconstruction

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Abstract

The relation between method, concept and theory in science is complicated. I seek to shed light on that relation by considering an instance of it in systematics: The additional challenges phylogeneticists face when reconstructing phylogeny not at a single level, but simultaneously at multiple levels of the hierarchy. How does this complicate the task of phylogenetic inference, and how might it inform and shape the conceptual foundations of phylogenetics? This offers a lens through which the interplay of method, theory and concepts may be understood in systematics, which, in turn, provides data for a more general account.

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1 Introduction.

The relation between method, concept and theory is complicated. I seek to shed light on that relation by considering the additional challenges that arise in reconstructing phylogeny not at a single level, but simultaneously at multiple levels of the hierarchy. How does this complicate the task of phylogenetic inference, and how might it inform and shape the conceptual and theoretical foundations of phylogenetics?

The initial contours of these challenges can be grouped into two main projects: epistemological and ontological. How do patterns at one level of the biological hierarchy inform us of patterns at other levels? This is complicated by the presence of multilevel genealogical discordance, namely, when the pattern of phylogeny at one level of the biological hierarchy fails to map onto patterns at other levels. As the degree and kinds of discordance between levels increases, so too do the challenges for inferring phylogeny. How might (or should) discordance be incorporated into phylogenetic methodology and theory? How much can or should this discordance be accounted for in phylogeny reconstruction? How does discordance impact our phylogeny, lineage and species concepts?

To address these challenges, I recommend adopting a *Levels of Lineage* perspective, i.e., a set of commitments about the structure of evolutionary lineages that provide resources for addressing the methodological, theoretical and conceptual challenges raised by reconstruction of multilevel lineages. This offers a lens through which the interplay of method, theory and concepts may be understood in systematics, which, in turn, provides data for a more general account.

I begin with a brief sketch of the levels of lineage perspective, followed by a discussion of the epistemological challenges of producing multidimensional trees, i.e., how incorporating information about different kinds of discordance complicates phylogenetic inference. I then consider the ontological implications of multilevel lineages, characterizing them as complex multiply decomposable objects. This reveals a payoff of the levels of lineage perspective: recognition that biological objects do not simply grade into one another over space and time, but over levels of hierarchy as well. This complicates how we conceive of the edges and boundaries of biological objects, offers a re-boot of the entrenched *species problem*, and a theoretical basis for a constrained pluralism of species, lineages and phylogenies.

2 The Levels of Lineage Perspective.

Specifying the *Levels of Lineage* perspective more precisely will provide the resources to identify the theories, concepts, and methods at play in reconstructing multilevel lineages, and help make sense of the challenges that arise.

The levels of lineage perspective is a commitment to the following propositions:

- The biological world is hierarchically organized;
- A level of the biological hierarchy is constituted by lineage-generating entities;
- Parts of the biological hierarchy are, in part, constituted by and constitutive of other parts of the hierarchy;
- Genealogical discordance is exhibited between levels;
- No single level of lineage offers a privileged perspective of phylogeny.

Some of these are obviously more controversial than others. The point is not to defend these commitments, or even to make the case that they are widely held, rightly or not, among phylogeneticists (though I think they are). Rather it is simply to stipulate the perspective being taken as backdrop. Let's consider each proposition briefly.

The biological world is hierarchically organized. This is an empirical claim, though the facts are in dispute; e.g., Ereshefsky (1992) and Dupré (1995) adopt different pluralist stances towards the hierarchy, whereas Potochnik and McGill (2012) suggest replacing *levels* with *scales*, arguing this better reflects causal significance and interaction. Those disputes aside, in a levels of lineage perspective the hierarchical organization is understood as a product of evolution, so, in part, demands an evolutionary explanation, e.g., why this hierarchy, rather than a different one, or one at all? This requires the adoption of a diachronic approach, aligning this commitiment with diachronic treatments of evolutionary processes, mechanisms and structures (e.g., Griffiths 1974; Maynard Smith and Szathmáry 1998; Szathmáry 2000; Griesemer 2000b; Okasha 2006; Godfrey-Smith 2009). Explaining, describing, and understanding the patterns of hierarchical organization from a phylogenetic perspective sets the research and conceptual problems of the perspective.

A level of the biological hierarchy is constituted by lineage-generating entities. Not just any biological entity will generate a lineage, only those that satisfy certain criteria. What those criteria are, of course, is highly contentious. This is typically framed as a problem of reproduction (Hennig 1966; Griesemer 2000a,b; Godfrey-Smith 2009), and may be generalized across levels, e.g., microbes (Dupré and O'Malley 2009), colonies (Hamilton et al. 2009), evolutionary individuals (Janzen 1977) or clades (Okasha 2003; Hamilton and Haber 2006). Bouchard (2008) adopts a broader framework of differential persistence, regarding reproduction as simply one kind of growth or lineage maintenance. This provides novel (though contentious) ways to account for microbial, colony, and population-level lineages (Simpson 1961; Wiley 1978; Bouchard 2010).

Parts of the biological hierarchy are constituted by and constitutive of other parts of the hierarchy. These part-whole relations are biological, not logical (Haber 2013). Interpreting these relations is central to characterizing the entities, processes, mechanisms and structures of biology in a levels of lineage perspective. This captures a fundamental component of the individuality thesis (Ghiselin 1974; Hull 1976, 1978). Hull notes how this commitment complicates evolutionary processes: "A simple characterization of the units which function in evolution is further complicated by the fact that the units at various levels of organization are related by the part-whole relation, and the functions which they perform are both multiple and variable" (1976, 184). Martens (2010), Okasha (2011) and Haber (2013) extend this complication to biological objects, arguing that some organisms are parts of or constituted by other organisms. This commitment is iterative, though a regress may be avoided by specifying maximal and minimal levels, e.g., a maximal clade, or minimal reproducer (Griesemer 2000b; Gánti 2003).

Genealogical discordance is exhibited between levels. This is an empirical claim about the fidelity of phylogenetic patterns exhibited between levels of the biological hierarchy. Simply put, lineages are leaky, and monophyly at one level of the biological hierarchy does not ensure that the parts of that level will share the same pattern of ancestry and evolution. This is especially notable for microbial organisms, given the extensive presence of lateral gene transfer (Doolittle and Bapteste 2007). Yet discordance is exhibited across the levels of hierarchy, and accounting for it is a central levels of lineage problem (see Doyle 1992; Maddison 1997; Degnan and Rosenberg 2006; Avise and Robinson 2008; Velasco 2008; Dupré 2010; Ereshefsky 2010, among others). Rather than explain away genealogical discordance as a bug, this commitment recognizes it as a feature of the biological hierarchy. Then these discordance patterns may be studied and perhaps explained or predicted by theory, e.g., discordance should be unsurprising on multilevel selection. This is the challenge of incorporating multilevel genealogical discordance into phylogenetic methodology, theory, and concepts.

No single level of lineage offers a privileged perspective of phylogeny. This is a conceptual commitment, and perhaps the most controversial of those listed here. It applies Wimsatt's (1972) work describing reduction and multiple decomposability of complex objects to phylogenetics. It may independently be derived from pluralist stances (e.g., Ereshefsky 1992; Dupré 1995), though pluralism is neither necessary nor sufficient for this commitment.

In addition to these commitments, it will be useful to introduce the following terminology:

- *Multidimensional Tree*: A representation or model of phylogeny including more than one level of the biological hierarchy;

- *Multilevel Lineage*: A lineage consisting of multiple levels of lineages.

The former may be used to represent the latter, though need not necessarily endorse a commitment to multilevel lineages. Multidimensional trees are not new. Hennig uses them to introduce phylogenetic concepts and theory, and to represent the internal structure of lineages, including organismal and developmental lineages (see figure 1). This suggests that a levels of lineage perspective has persisted from the root of phylogenetics.

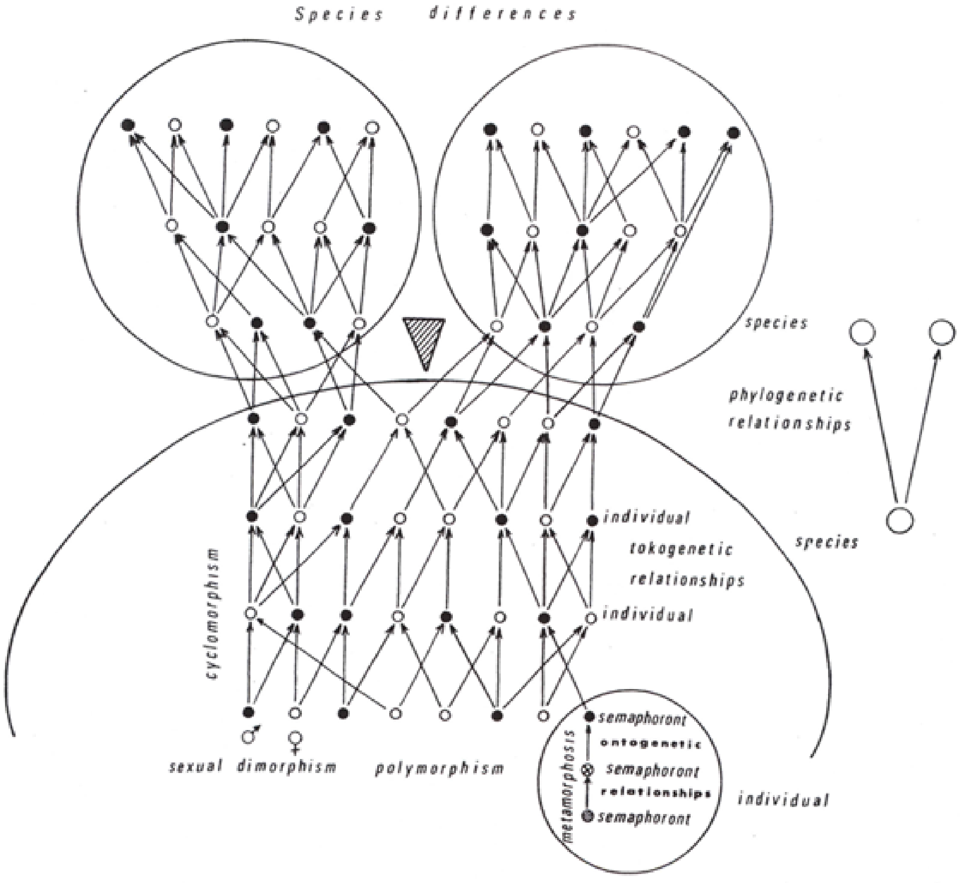

Figure 6. The total structure of hologenetic relationships and the differences in form associated with its individual parts.

Figure 1: Multidimensional trees have been used from the foundation of phylogenetics. Hennig used them to introduce phylogenetic theory and concepts (Hennig 1966, figure 6).

3 Multidimensional Trees.

Phylogeneticists typically suppress the internal structure of phylogenies in order to clearly focus on a single level (e.g., species or population lineages). Idealization of this sort is hardly unique in the sciences, and, arguably, may be central to its success (Cartwright 1983; Giere 1997; Teller 2001). Reconstructing multilevel lineages with multidimensional trees reveals some of this internal structure, and introduces additional methodological hurdles in phylogeny reconstruction. One reason for this is genealogical discordance. Discordance has several causes, including lineage sorting (or deep coalescent events), gene duplication and extinction, horizontal (or lateral) gene transfer (HGT/LGT), hybridization, and recombination (Degnan and Rosenberg 2009). Each carries its own unique epistemic challenges (Maddison 1997), though here I consider how genealogical discordance more generally complicates phylogenetic inference.

Phylogeneticists take genealogical discordance seriously, and advances in technology (theory, etc.) are permitting a deeper look at the internal structure of phylogenies. This is plainly seen as coalescent theory is applied to populations and used to infer phylogeny. Briefly, multispecies coalescent techniques permit the reconstruction of species- (or population-) level phylogeny through analysis of the internal structure of populations (Kingman 1982; Hudson 1983; Tajima 1983). This introduces additional complications for phylogenetic inference. If the shape of the containing tree is short (in number of generations) and wide (in effective population size), then lineage sorting (or deep coalescence) will produce genealogical discordance between gene, organismal, population and species phylogenies (Pamilo and Nei 1988). Avise and Robinson (2008, 503) call instances of this *hemiplasies*, a concept they introduce to capture how "idiosyncratic lineage sorting can lead to fundamental discordances between gene trees and organismal (species) trees" (see figure 2). Though homologous, hemiplasies appear as homoplasies, and may confound phylogenetic inference

Accounting for genealogical discordance in phylogeny reconstruction effectively adds more parameters along which parsimony (or likelihood, or probability) may be disputed. For example, were we simply considering hemiplasies (or HGT, etc.), by what metric should we evaluate what counts as a more parsimonious explanation of genealogical discordance? Should we simply count the number of hemiplasies, selecting the tree requiring the fewest, or should we select the tree requiring the simplest model of evolution that explains the presence of those events? Either case demands a trade-off. In the former, fewer hemiplaies may entail more complex models, whereas in the latter a simpler model may entail more hemiplasies. This is not different in kind from arguments over simple application of parsimony to homology and homoplasy (Felsenstein 2004), though accounting for discordance increases the number of parameters along which this argument occurs. Maddison (1997) offers considerations along these lines, speculating what

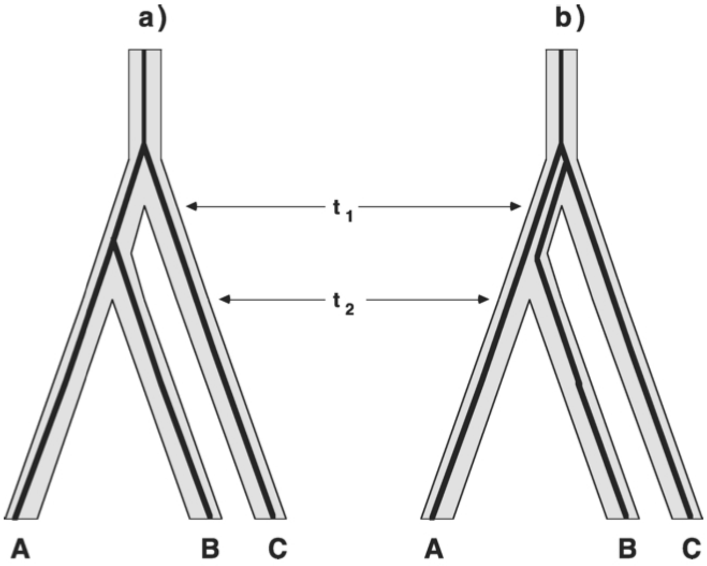

Figure 2: Avise and Robinson (2008, figure 1) introduced the term *hemiplasy* to capture instances of discordance due to lineage sorting (or deep coalescence). In (a) the gene and species trees are concordant, and homology is apparent. In (b) a deep coalescent event presents homologous genes as homoplasies. This is a hemiplasy.

parsimony and ML approaches[1] to inferring species trees from gene trees in the presence of discordance might look like.

Unfortunately, recent studies suggest that accounting for discordance is unlikely to be a simple addition of parameters. Degnan and Rosenberg (2006, 2009) demonstrate that under certain conditions, hemiplasies may outnumber homologies and confound phylogenetic methods such as the multispecies coalescent. That is, when the most common gene tree is discordant with the species tree, a simple parsimony weighting of hemiplasies will systematically select the wrong tree with ever increasing support as data accumulates (they describe such cases as *wicked forests*). Whether these positively misleading errors are likely to manifest with other causes of genealogical discordance is presently not known,[2] though in each case the biological facts are likely to be complicated and demand similar accommodation and analysis in our phylogenetic theories, concepts and methods.

Whether these various sources of discordance should be considered independently, or whether a mixed strategy that simultaneously considers all sources is preferable is both a

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[1] We could add Bayesian analysis.

[2] Though see Galtier and Daubin (2008) with regard to HGT.

theoretical and methodogical problem. This is akin to asking whether sources of discordance should be treated as independent parameters, or as a more dynamic interdependent bunch. Though not different in kind from the sorts of epistemological debates phylogeneticists wrestle with in single-level phylogenetic inference, discordance escalates the problem exponentially. For example, developing methods for these competing strategies requires development of models of evaluation, which, in turn, draw upon phylogenetic theory and concepts (which may themselves require refinement in light of discordance). Again the interplay of method, theory, and concept is on display.

To summarize: The theories, concepts, and methods that are part of the levels of lineage perspective together frame and identify research problems. These are sensitive to empirical facts, and feed back into one another as data are accommodated, discovered, or explained. Conceptually, the internal structure of trees was exploited to establish phylogenetic theory and develop phylogenetic methods (e.g., Hennig 1966). The possibility of genealogical discordance is entailed by numerous biological theories that are more or less well integrated with phylogenetics (e.g., HGT by microbial biology, lineage sorting by coalescent theory).[3] As the extent of the presence of kinds of genealogical discordance became better known, methods and theories were refined to account for these facts and more subtle phylogenetic concepts proposed to capture the theoretically significant patterns and objects previously categorized too bluntly. Together, this provides a snapshot of the interplay of theory, concept and methods in science.

4 Multilevel Lineages.

What is being represented by multidimensional trees? What is a multilevel lineage? A level of the biological hierarchy is constituted by lineage-generating entities, which themselves are constituted by and constitutive of other lineage-generating entities. A lineage, then, will both contain other lineages, and be a part of a broader lineage. This is an iterative definition, bottoming out and topping off at minimal and maximal lineages, respectively. The latter will be something like a maximal clade (or segment thereof); the former generated by minimal lineage-generating biological entities, though what those might be is unsettled.[4] Candidates include self-replicating RNA (Cech 1986) and chemotons (Gánti 2003). Given the diachronic approach implicit in the levels of lineage perspective, it is no accident these coincide with entities hypothesized in origin of life research (e.g., Dupré and O'Malley 2009).[5] Furthermore, these lineages are embedded

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[3] Multilevel selection also likely entails genealogical discordance between inclusive levels of biological individuals, though this has not been formulated precisely.

[4] Griesemer (2000b) uses a similar strategy of iterative definition for *reproducers*.

[5] There may be multiple kinds of minimal lineages, just as there may be multiple kinds of original living things. Likewise, there may be multiple maximal clades, in part due to the poorly resolved basal roots

one in another in complicated patterns which may function as either explanans or explanandum of other biological patterns and processes.

A lot may be said of multilevel lineages. Here the focus will be on specifying multilevel lineages as complex objects in terms of multiple decomposability. This carries implications for species, lineage and phylogeny concepts, and permits a constrained pluralism. The upshot is recognizing that biological gradients apply over levels of the hierarchy, in addition to the more familiar gradients that extend over time and space.

4.1 Multiple Decomposability.

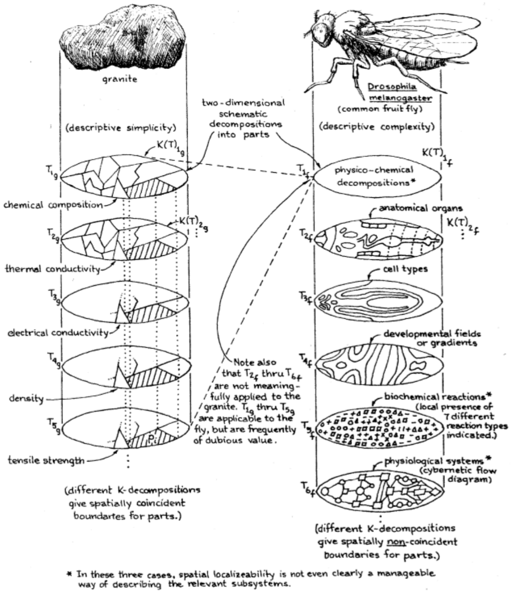

Figure 3: Wimsatt's (1972, figure 1) depiction of complexity and multiple decomposability. **Full-size figure at end of document (labeled as figure 5).**

Wimsatt (1972) introduced the notion of multiple decomposability (figure 3). In the levels of lineage perspective, lineages are recognized as genealogically discordant multilevel objects. These are in part constituted by other lineages and themselves constitutive of lineage-generating entities. These lineages occupy the various levels of the biological hierarchy, and are discordant in ways that bear tracking.[6] Furthermore, at

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of the Tree of Life. A maximal web or network of life may be a better candidate (Doolittle and Bapteste 2007).

[6] What I mean by 'bear tracking' is ambiguous and needs some unpacking. It could mean that reliable

least some levels of the biological hierarchy overlap in complex ways, with different decompositions tracking those various patterns, i.e., lineages are multiply decomposable, and phylogeneticists exploit this fact (compare figures 3 and 4).

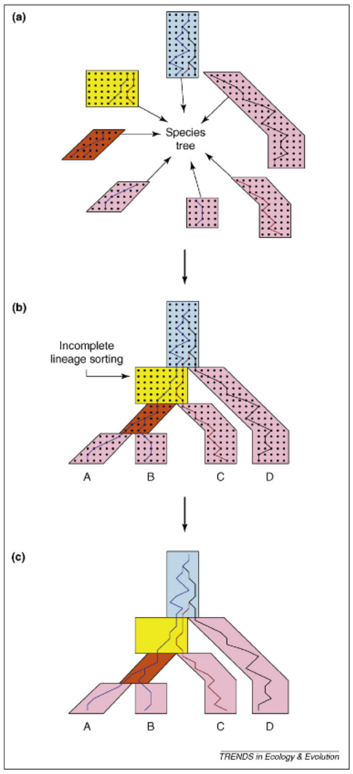

Figure 4: Degnan and Rosenberg's (2009, figure 1) depiction of the multispecies coalescent. This displays various decompositions of the species tree, and the discordances that arise. **Full-size figure at end of document (labeled as figure 6).**

It should hardly be surprising that lineages are multiply decomposable. Wimsatt uses organisms as paradigmatic examples of complex objects (i.e., those that are multiply decomposable). Organisms are complex, in part, due to the fact that they are composed of many kinds of lineage-generating parts.[7]

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inferences may be drawn, good explanations offered, or theoretically relevant biological objects tracked. If multiple decompositions satisfy these criteria, then pluralism may follow. An attractive feature of this account is that specifying what bears tracking both motivates and constrains pluralism. In other words, recognizing what justifies expanding available concepts is to also recognize what restricts those concepts.

[7] Multiple decomposability may also be framed in terms of genomics or selection (see Janzen 1977; Dupré 2010).

Furthermore, organisms themselves generate lineages, at the level of populations, demes, and species. Given both the complexity of ways in which organisms and their parts move and interact through these various lineages, and that organisms themselves are multiply decomposable, we should expect that higher-level lineages would retain this feature of decomposability.

That multilevel lineages are multiply decomposable carries ontological implications. First, it offers a means of cashing out pluralism about species, especially if species are conceived of as segments of lineages of organisms (or populations, or breeding groups, etc.). The various decompositions may produce multiple (inconsistent) patterns of ancestry. This observation may provide a way to break through the entrenched logjam that is the so-called *species-problem* (or, to give due credit, buttress the ontological aspect of Ereshefsky's (1992) eliminative pluralism). Debates over species concepts, at times, turn on patterns that persist in lower-level entities. Presuming a single decomposition, or that one decomposition offers a privileged perspective, generates unwarranted conflict, and may wrongly entail a monist position on species (or, for that matter, lineages). This need not be the case. Biologists might recognize multiple decompositions, and appropriately regard them as equally (or variously) informative, yet still wish to assign to one (or more) of those decompositions the *rank* of species. This, though, is a matter of *ranking* versus *grouping*, i.e., a matter of which groups ought to be designated with the rank *species*. That is a slightly different dispute, and one many are eager to move past (e.g., Mishler 1999).

4.2 Extending Gradients.

If species are lineages (regardless of sort), and lineages are multiply decomposable, then there will be no simple object to identify as a species. Even diachronic approaches (e.g., de Queiroz 1998; Harrison 1998) will be too static. The gradients along which species extend on these views is over time and space; that gradient must be extended over the levels of hierarchy as well.[8]

Ultimately, this is reminiscent of Sober's (1980) treatment of populations, but applied to phylogenetics. Just as Sober rejects the natural state model in favor of variance as central to our concept of a population, and Wimsatt rejects a privileged decomposition, so too should we reject an absolute phylogeny. Maddison recognizes the ontological implications of adopting a levels of lineage perspective:

> When we take a sample from a population and try to understand a statistical distribution by calculating means and variances, we do not single out all of the samples whose values differ from the mean as disagreeing with the mean.

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[8] Baetu (forthcoming) comes close to this.

> They are simply part of the variance, part of the distribution. A simple phylogenetic tree diagram with sticklike branches represents only the mean or mode of a distribution. Phylogeny has a variance as well, represented by the diversity of trees of different genes. This variance does not represent uncertainty due to ignorance or measurement error; it is an intrinsic part of phylogeny's nature. (1997, 533)

It is certainly tempting to stipulate one level as the Archimedean point around which the rest of phylogeny flows. But this is a mistake, if we accept Wimsatt's lesson about multiple decomposability and the lack of privileged perspective. This is the phylogenetic analogue to Sober's contrast of population thinking to the natural state model view. Just as we abandoned Newton's notion of absolute space for relativity, the lesson to draw here is that there is no absolute phylogeny, no privileged perspective from which all others derive. We can just as well hold organismal as interbreeding population lineages constant, and, indeed, this is just what population geneticists do (e.g., Avise and Wollenberg 1997; Coyne and Orr 2004). That conflicts with other evolutionary histories (of organisms, or genomes, etc.) may arise is not an indicator of incoherency, but of facts in need of explanation (*contra* Velasco 2008). This is part and parcel of the complexity of biology, and hardly unique to phylogenetics. Indeed, in so far as there are laws in biology, their utility is often most perspicacious when they fail to hold true (e.g., Mendel's laws of inheritance, or the Hardy-Weinberg equilibrium). Why should phylogenetics be different? That the edges and boundaries of biological objects grade into each other over space and time is well appreciated. The lesson here is that biological gradients also span levels of hierarchical organization. The added dimensions of how we ought to conceive of biological objects are, admittedly, difficult to grasp. Yet recognizing this challenge is the first step, and the levels of lineage perspective, along with multidimensional trees and a rich multilevel lineage concept, provide the resources to account for this complexity.

5 Conclusion.

Recall that the initial framing concerned the interplay of method, concept and theory in science. I considered how this plays out in systematics when phylogeneticists aim to reconstruct phylogeny not at a single level, but simultaneously at multiple levels of the hierarchy. Methods of phylogeny reconstruction require both a theoretical and conceptual basis. Incorporating coalescent theory into phylogeny reconstruction is attractive for various reasons, e.g., it permits a point of contact between phylogenetics and population genetics. Using the multispecies coalescent to reconstruct phylogenies, though, draws bare the underlying genealogical discordance exhibited between gene trees and species or population trees, and demands refining existing methods or developing new techniques. Furthermore, under some circumstances the discordance is so great as to generate a positively misleading error, i.e., wicked forest anomaly zones. This reinforces the need to account for genealogical discordance in our lineage, species and phylogeny concepts in order to offer plausible biological interpretations of these findings. This re-conceptualization, in turn, demands further refinement of phylogeny reconstruction in order to appropriately capture the complexity of multilevel lineages in multidimensional trees.

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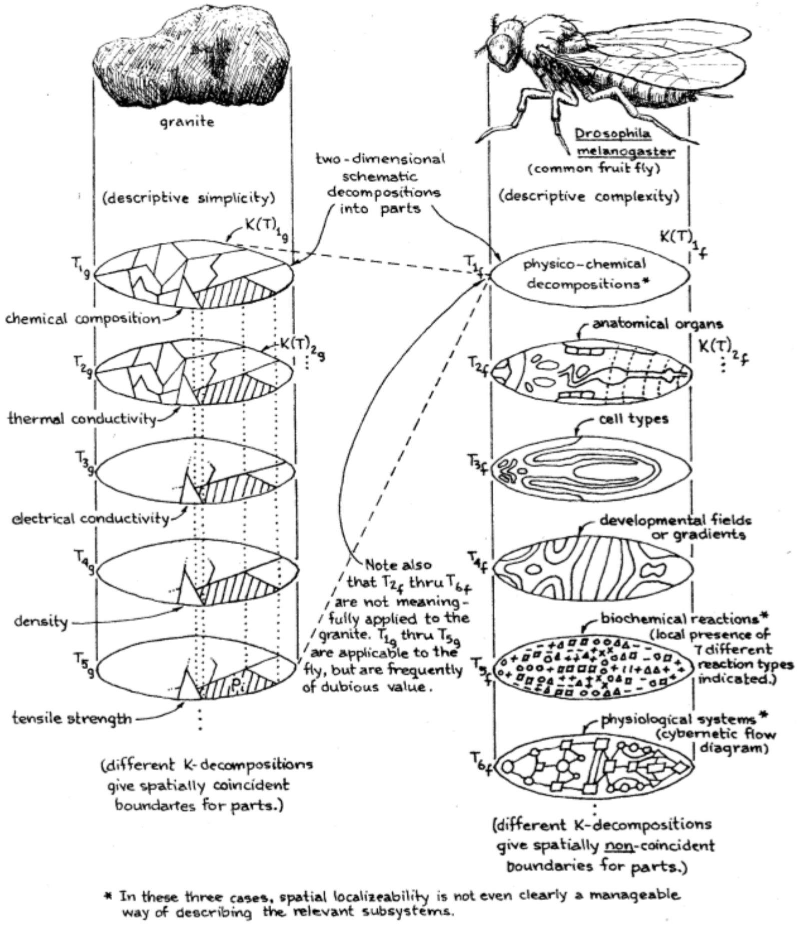

Figure 5: Wimsatt's (1972, figure 1) depiction of complexity and multiple decomposability.

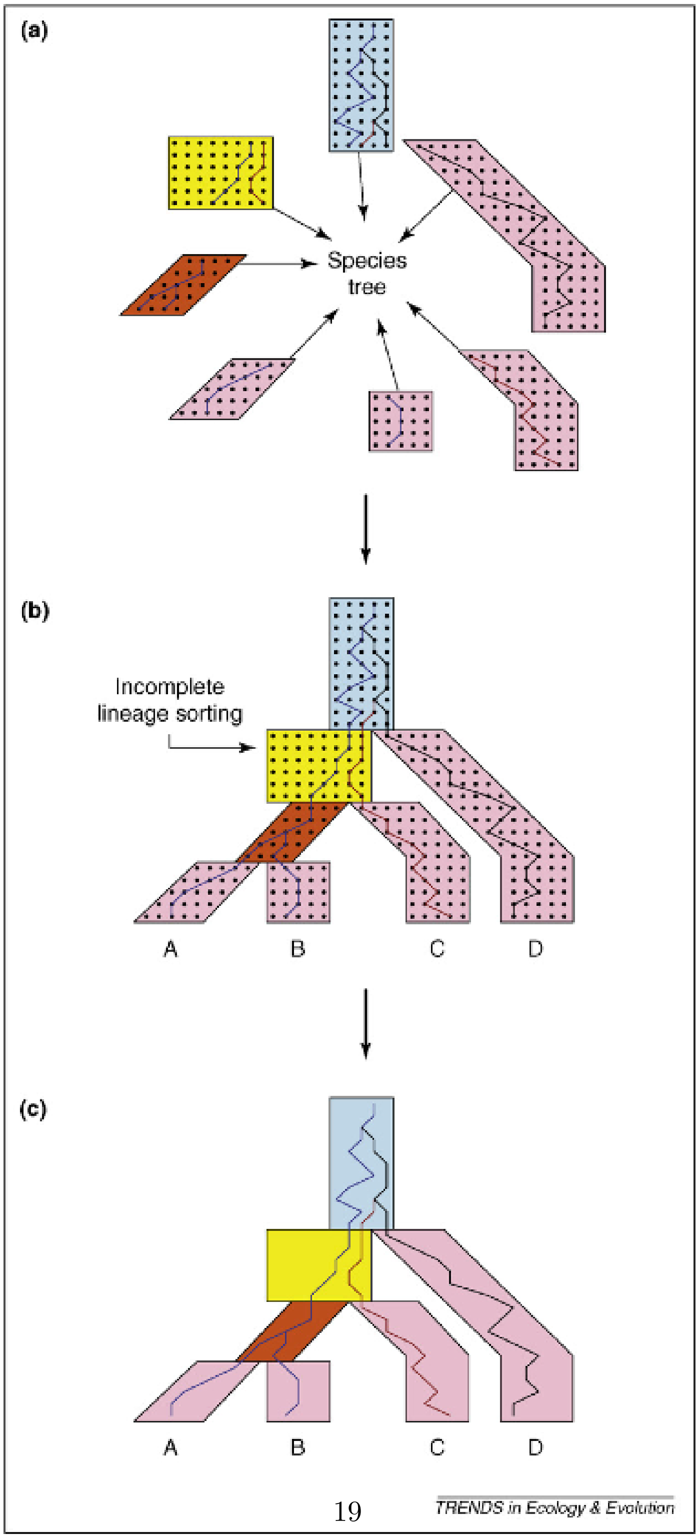

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Figure 6: Degnan and Rosenberg's (2009, figure 1) depiction of the multispecies coalescent. This displays various decompositions of the species tree, and the discordances that arise.