

Species in the Age of Discordance: Meeting Report and Introduction

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In 2017, three interdisciplinary workshops were held on whether and how biological discordance might impact our views on species. Though the prompting focus of these workshops was genealogical discordance, the precise sense of ‘discordance’ was left intentionally ambiguous. This was to encourage an examination of the question from many different perspectives and to foster connections across disciplines. Participants included philosophers, historians, and other social scientists, alongside a range of biologists representing microbiology, population genetics, phylogenetics, invasion biology, herpetology, and ecology, among other areas. Here, context is provided for those workshops and to help motivate why biological discordance generates useful interdisciplinary research problems, along with brief summaries of the workshop papers included in this special issue.

Keywords

species • discordance • conference • phylogenetics • genealogical discordance • phylo-evo-devo

Part of the special issue Species in the Age of Discordance, guest-edited by Matthew H. Haber and Daniel J. Molter.

1 Varieties of Discordance

The papers included in this special issue were selected from a series of three interdisciplinary workshops titled Species in the Age of Discordance. Participants including philosophers, phylogeneticists, systematists, population geneticists, invasion biologists, historians, social scientists, botanists, herpetologists, ichthyologists, and microbiologists, among others, were asked to consider species in the context of discordance. The sense of “discordance” was left intentionally ambiguous in the call for abstracts, as our goal was to examine this question from many different perspectives, to seek out connections across disciplines, to think about the different ways discordance surrounding species is conceived, and to ascertain how the varieties of discordance might inform each other.

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Genealogical discordance, the fact that component lineages of biological systems often have conflicting or incongruent histories, is the kind of discordance that prompted this project. Consider for example the polar bears. Phylogenetic analysis of the history of mitochondrial DNA, which is inherited matrilineally, reveals that the ancestors of polar bears and brown bears diverged into isolated lineages about 150,000 years ago. Phylogenetic analysis of nuclear DNA, on the other hand, which is inherited from both parents, reveals a much earlier divergence around 750,000 years ago. Did polar bears split from brown bears 150,000 years ago or 750,000 years ago? The answer is “yes.” Nuclear genes show that brown bears and polar bears began diverging at the earlier date, but at the later date a female brown bear mated with one or more male polar bears and, by hybrid introgression, became the maternal ancestor of all extant polar bears (Hailer et al. 2012; Kutschera et al. 2014).

Hybridization events, like the one that scrambled polar bear phylogeny, are just one way to generate genealogical discordance, which also arises from horizontal gene transfer, gene duplication, and incomplete lineage sorting (Degnan and Rosenberg 2006). Attending to genealogical discordance forces us to reimagine what species and other evolutionary lineages are like, as discordance runs counter to idealized conceptions of evolutionary lineages as spatiotemporally discrete branches on an evolutionary tree. We’ve known since at least Hennig (1966) that phylogenetic trees are, to some extent, idealizations of history, but recent work in genomics (work that attends to all the genes in a specimen, rather than sampling one or a few genes for barcoding) suggests that the phylogenetic history of species might be so complex that tree models cannot capture it. In place of tree thinking, some authors have suggested a switch to cloud thinking, such that species are conceived as “clouds of gene histories” and represented with “cloudograms” (Maddison 1997).

Though genealogical discordance was a primary focus of these workshops, other sorts of discordance were centrally considered. Ecological disturbance, human intervention, migration and invasion, and political/national boundaries all generate discordances that can impact species identity and integrity, as well as the ways theoretical and operational species concepts are employed. A broad range of biologists, philosophers, historians, and social scientists were included so that we could explore how these different kinds of discordance are interconnected. The workshops were interdisciplinary in the sense that researchers from many fields participated, but they were also interdisciplinary in a further sense that they were directed towards very different audiences at different venues.

The first meeting was a stand-alone workshop held at the University of Utah in March 2017; forty-one papers and posters were presented by over fifty scholars, half of whom were biologists, the other half philosophers, historians, and social scientists of biology. Presenters ranged from pre-doctoral students to senior scholars in their fields. The second and third workshops were integrated into larger professional meetings. A session presented at the Society of Systematic Biologists Pre-Conference Workshop, prior to the 2017 Evolution Meeting, included presentations from three biologists and three philosophers and was enthusiastically received by a standing-room-only audience of mostly evolutionary biologists. There was a great deal of interest in stepping back to examine how recent advances in systematics impact the study of diversification and divergence of evolutionary lineages. The final workshop was an organized session at the 2017 International Society for History, Philosophy, and Social Studies of Biology (ISHPSSB) meeting.

2 Paper Summaries

Matthew J. Barker's (2019) "**Species and Other Evolving Lineages as Feedback Systems**" offers a programmatic paper, proposing a hypothetical account of species conceived as evolving metapopulation lineages, each held together as a unit of evolution by feedback processes. On Barker's theory, spatiotemporal and trait-space cohesion are both affected by feedback systems, which, perhaps surprisingly, include trait similarity as part of the feedback process. Capacity to interbreed and capacity to occupy a common niche are hallmarks of many species concepts, and they function as elements of Barker's feedback system. But given the post-Darwinian demise of essentialism, trait similarity has recently been viewed as merely an effect of other factors which mold a group of organisms into a single evolutionary unit. Barker argues that trait similarity is no mere effect; trait similarity participates in feedback processes along with factors such as gene flow and ecological niche to maintain a species as a single evolving unit.

Barker proposes a 3D model of metapopulation cohesion space, reminiscent of Godfrey-Smith's (2009) cube of graded Darwinian individuality. Beginning with a broadly promiscuous metapopulation concept, one which includes any and all groups of organisms, Barker maps each metapopulation onto a 3D space of M values, where M is the sum total of cohesive factors operating in the metapopulation. The members of most arbitrarily defined metapopulations do not participate in any common feedback processes at all, and therefore have M values of zero. Paradigm, evolving metapopulations, characterized by high gene flow, universal mating compatibility, and shared ecology, appear at the top of the M value scale. Barker speculates that species might be metapopulations whose cohesion values cluster in a single region of M space, and if this hypothesis is correct, then that region of M space could serve to define the species category. Barker describes possible experiments to test this hypothesis and encourages researchers to allocate resources to do just this.

Considering species of microbes, Ford Doolittle's (2019) "**Speciation without Species: A Final Word**" argues for an eliminative pluralism which recognizes multiple ways prokaryotes sort themselves into species, but which denies there is one ontological species category. Central to Doolittle's approach is the idea that species are cohesive processes, and that processes can cohere in a number of different ways. First, homologous recombination in bacteria can hold lineages together as evolving units, similar to the way sexual recombination holds interbreeding plant and animal species together, even though horizontal gene transfer blurs the boundaries of microbial lineages and homologous recombination provides less cohesion than sex. Second, adaptation to an ecological niche, especially when enabled by a point mutation that allows the offspring of a single microbe to colonize a new substrate, results in "ecotype" species. These are characterized by a strong founder effect, but, due to horizontal gene transfer, need not be composed wholly of bacteria sharing a recent common ancestor. Pangenomes—groups of genes propagating vertically and horizontally in a microbial network, but which are only partially instantiated in any one microbe—mark the boundaries of yet another kind of cohesive and evolving microbial lineage. Each of these kinds of cohesive groupings are taken to be species by microbiologists, meaning that a selfsame bacterium can be a part of more than one species. Doolittle argues this is not problematic. Species concepts are for Doolittle as gene concepts and biological individuality concepts are for Ken Waters: tools of scientific investigation that need not carve the world into discrete, non-overlapping units. Doolittle suggests that we can "save all the babies" of speciation while throwing out the bathwater of a univocally defined species category.

Noting that many biologists and philosophers embrace species pluralism, Marco Nathan's (2019) "**Pluralism Is the Answer! What Is the Question?**" argues that this term lacks a univo-

cal meaning. Some authors use “pluralism” in reference to species heterogeneity—the view that there are various kinds of species in nature, such as interbreeding species and species of asexual microbes. Other authors use the term “pluralism” in reference to what Nathan calls theory dependence—the idea that demarcating species is something scientists do, and do so always according to some theory, aim, or purpose. Species heterogeneity recognizes multiple different natural arrangements that count as species, and theory dependence recognizes no species apart from those identified and classified for some scientific purpose. Nathan argues that neither heterogeneity nor theory dependence implies anti-realism, as species monists have suggested pluralism must.

Nathan examines three perspectives that have been described as species pluralism, the first two exemplifying heterogeneity, and the third theory dependence. “Second order pluralism” holds that all species are units of evolution, and hence provides a monistic definition of species ontology, while recognizing a variety of ways to epistemically assess whether organisms belong to a single evolving unit. “Eliminative pluralism”, a second kind of heterogeneity, holds that there are multiple kinds of naturally demarcated lineages (clades, interbreeding lineages, and ecological lineages), each of which should be recognized as distinct rather than lumped into a single species category. Nathan argues that eliminative pluralism is actually species monism, because if the species category is replaced by other categories of cohesive lineages, then the species category remains monistically defined, even though it is an empty category.

On the other hand, Nathan considers “species pragmatism” to be true pluralism. Pragmatism holds that the species concept is central to biology, so it cannot be eliminated, but because species are always demarcated according to some purpose, and because there are many cross-cutting purposes, the species category cannot be univocally defined. While Nathan takes theory dependence to be a more genuine form of pluralism than species heterogeneity, his aim is not to police the language, but rather to show that species heterogeneity and theory dependence need not come together as a package. Because “pluralism” refers both to heterogeneity and theory dependence, and because these two come apart, “pluralism” cannot be univocally defined. Nathan concludes that the question “Should we be species pluralists?” is not well formed, and would be better replaced by more precise questions about heterogeneity and theory dependence.

Makmiller Pedroso’s (2019) “**Forming Lineages by Sticking Together**” notes that “Individual thinking” identifies species with evolving lineages, and treats reproducing parts of species as individuals, on account that reproduction is what generates a lineage. Here he suggests that individual thinking can be extended to include multispecies aggregates of microbes as lineage-generating individuals, but in order to do so, we must recognize that ‘lineage generating’ is a graded rather than a bivalent condition, and we must attend to lineages beyond those which connect parents and offspring. Biofilms composed of multiple species of bacteria do not reproduce by generating well-defined parent-offspring lineages, but Pedroso argues they are nonetheless individual lineage generators, insofar as they have evolved such that some of their component species lineages propagate in tandem.

Biofilms are aggregates of numerous microbial species which do not reproduce together as a unit. However, biofilms are spatially structured, because cells of cooperating species tend to stick together and segregate themselves from non-cooperating species. Because the lineages of certain component microbes stick together in a biofilm, when environmental conditions break the biofilm apart, lineages of stuck together microbes can disperse as a unit and found biofilms in new locations. It follows that even though a biofilm as a whole does not generate parent offspring lineages, it can still achieve a degree of evolutionary individuality, by generating lineages in which some of its components co-disperse.

Aleta Quinn's (2019) "**Diagnosing Discordance: Signal in Data, Conflict in Paradigms**" identifies debates over the principle of total evidence as an important thread tracing through three recent debates in phylogenetics: (i) parsimony versus maximum likelihood methods, (ii) character congruence versus consensus trees, and (iii) concatenation versus coalescence approaches. This provides an illuminating and novel way to understand these debates and how they are connected, while offering opportunities to add clarity to those (ongoing) discussions. For example, Quinn convincingly argues that Nixon and Carpenter's (1996) defense of "simultaneous analysis" ought to be understood in terms of defending the principle of total evidence. On Quinn's account, Nixon and Carpenter are advancing this argument in service of a defense of parsimony approaches in phylogenetics. Quinn suggests that this is to conflate debates over the utility of total versus partitioned evidence with debates over particular methodologies in systematics, where how the former plays out need not be decisive with regard to debates on the latter. With regard to the more recent debates over concatenation versus coalescence methods, Quinn argues that concatenation (total evidence) approaches may conflate genuine genealogical discordance with error, and, thus, fail to reconstruct trees correctly when subsets of data ought to be prioritized. Quinn's analysis also provides an important case study for how the principle of total evidence plays out in scientific practice, and an examination of the way that entrenched commitments in the sciences can weave in and out of different debates. Seeing those contributions helps identify those debates that appear novel as part of a longer-lived and larger recurring disagreement.

Jason Sexton's (2019) "**The Adaptive Continuum and How Species Succeed and Fail**" argues that a species' failure to adapt can have three causes: chance, time, and speciation. Chance events, especially those which cause large-scale rapid changes to the environment, are well-recognized causes of extinction. Sexton argues that lack of time to evolve after a speciation event can also lead to extinction, as can the budding off of new species. Sexton compares the emergence, evolution, and budding off of new species to life cycles of organisms, and he argues that species can fail to adapt at each of these stages. Species can fail in the early stage of this cycle by not acquiring sufficient genetic variation to adapt to changing environments, and they can fail in later stages by budding off incipient species. The incipient species' reproductive isolation deprives the parent species of part of its pool of genetic resources, thus inhibiting its ability to evolve in response to changing environments, including competition from the newly generated species.

Sexton describes an adaptive continuum in which extinction events, while decreasing adaptation at the level of species, can increase adaptation at other levels of organization. The adaptive continuum ranges from genes, at the bottom of the hierarchy, up through species to supraspecific clades and the entire tree of life. The adaptive continuum also cuts across species boundaries, as gene combinations from multiple species are frequently adaptive at the level of symbiotic collectives. Sexton describes a continuously expanding tree of life, evolving into ever new niches, in which adaptation occurs at numerous of levels of organization, such that losses in adaptation through extinction at one level are offset by increases in adaptation at other levels. A species' failure to adapt, and hence its extinction, is not a net loss for adaptation, as new adaptive lineages replace those which are extinguished through chance, lack of time to evolve, or the ordinary replacement of parent species by daughter species at the end of parent species' life cycles.

As biological taxonomy was emerging as a science in the eighteenth and nineteenth centuries, European invaders were colonizing the New World, and their views of the indigenous peoples they conquered, and interbred with, were heavily influenced by the new biology. Erica Torrens and Ana Barahona's (2019) "**Castes and Trees: Tracing the Link between European and Mexican Representations of Human Taxonomy**" relates the role of pre-Darwinian

and Darwinian thinking to popular views of races and castes in the colonial period of Mexico. Visual representations of humans as parts of a larger biological order, specifically tree models from thinkers such as Ernst Haeckel and Manuel Ortega, as well as Ignacio María Barreda's artistic representations of a hierarchy of mixed-race castes, profoundly informed the national consciousness before and during Mexico's transition into a nation state. White Europeans were universally depicted at the top of these hierarchies, which often misconstrued evolution as an orderly and progressive march toward increasing perfection. Unsurprisingly, these images, which represented false and misleading evolutionary histories, were frequently misunderstood by the public as providing scientific support for the racist zeitgeist and white supremacy of the colonial period.

One prominent understanding of species is that they are monophyletic groups, clades, or branches on the tree of life. These branches are parts of a larger phylogeny, but what exactly is a phylogeny? Joel Velasco's (2019) "**The Foundations of Concordance views of Phylogeny**" notes that phylogenies can be conceived as mapping the branching patterns of organism lineages, as they are held together by reproductive interactions and diverge according to reproductive isolation, or phylogenies can be understood as mapping the branching structures of replicating gene lineages. The first kind of phylogeny Velasco calls "species trees" and the latter "gene trees". Attempts to map species trees onto gene trees is complicated by genealogical discordance—the fact that genes in a species have their own unique histories and branching patterns, each different from the others and from the branching patterns of species trees. Velasco argues that if we want to define phylogeny in terms of the actual flow of genetic information, including horizontal gene transfer, then it makes sense to attend to all the gene trees within a species. Using a genealogical concordance approach to phylogenetic systematics, we sort organisms into monophyletic groups just in case their gene trees coalesce more recently within the group than outside the group.

Velasco considers five different algorithms used to generate concordance trees, including full coalescence, majority coalescence, and plurality coalescence, along with mathematically more complex models such as the "greedy tree", which combines elements of the other approaches. Any of these algorithms can be used to generate a primary concordance tree that is taken for taxonomic purposes to be an estimate of the species tree. The concordance tree is only an estimate; concordance trees and species trees can come apart. Velasco argues that the mismatch between species trees and genealogical concordance trees is unproblematic. When a concordance tree fails to map onto a species tree, it does not make the concordance tree a bad estimate of the phylogeny, as the concordance tree just is the phylogeny. Species trees and concordance trees represent two distinct aspects of evolutionary history, and both are useful, though perhaps for different purposes. Velasco concludes that if phylogeny is understood to be a history of the flow of genetic resources, then taxa are best understood in terms of primary concordance trees, irrespective of whether the primary concordance tree is coincident with a species tree understood in terms of reproductively isolated organism lineages.

Matthew H. Haber's (2019) "**Species in the Age of Discordance**" offers a broad view of how genealogical discordance is impacting the way we consider species. He argues that as the relatively recent appreciation for the degree and breadth of different kinds of discordance in biology has grown, this is becoming increasingly impactful on conceptualization, theory, and practice in phylogenetic systematics. More specifically, he considers how discordance is changing the contours of debates over species, and how a finer-grained understanding of the different kinds of discordance presents both opportunities and challenges for phylogeny reconstruction. In both cases, entrenched commitments are being challenged, but the upshot is a more nuanced and sophisticated approach to studying divergence and diversification in biology. Haber identifies these as examples of scientific progress that he calls "productive disruptions". Moreover,

the breadth of modes of discordance have also spurred biologists to work across disciplines, partnering in exciting ways to utilize what we are learning about discordance to gain a deeper understanding of a range of systems from developmental, evolutionary, and phylogenetic traditions.

3 Summary

Biological discordance is a timely and relevant topic to examine. Biologists are still coming to grips with the extent and scope of genealogical discordance, and we are still in the early stages of reflecting on the implications it might have for central conceptual, methodological, and theoretical commitments in biology. Because the mechanisms of genealogical discordance draw from other fields, e.g., developmental biology and microbiology, this also presents an opportunity to synthesize work across disciplines, in what Minelli (2009) calls a ‘phylo-evo-devo’ approach. For fields beyond systematics, the topic is pressing due to the accelerated impacts on threatened or endangered species due to climate change or human-mediated migration and displacement. The cross-disciplinary interest in these workshops is evidence that biologists are keen to engage with philosophers and other humanists and social scientists on how to navigate the intersection of scientific investigation with the practical and political implications of their work (see too Laplane et al. 2019). We hope this special issue will help facilitate that ongoing discussion.

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