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Review

Reconsidering cytonuclear discordance in the genomic age

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Abstract

Historically, phylogenetic datasets had relatively few loci but were over-represented for cytoplasmic sequences (mitochondria and chloroplast) because of their ease of amplification and large numbers of informative sites. Under those circumstances, it made sense to contrast individual gene tree topologies obtained from cytoplasmic loci and nuclear loci, with the goal of detecting differences between them—so-called cytonuclear discordance. In the current age of phylogenomics and ubiquitous gene tree discordance among thousands of loci, it is important to distinguish between simply observing discordance between cytoplasmic trees and a species tree inferred from many nuclear loci and identifying the cause of discordance. Here, we examine what inferences one can make from trees representing different genomic compartments. While topological discordance can be caused by multiple factors, the end goal of many studies is to determine whether the compartments have different evolutionary histories: what we refer to as "cytonuclear dissonance." Answering this question is more complex than simply asking whether there is discordance, requiring additional analyses to determine whether genetic exchange has affected only (or mostly) one compartment. Furthermore, even when these histories differ, expectations about why they differ are not always clear. We conclude by pointing to current research and future opportunities that may help to shed light on topological variation across the multiple genomes contained within a single eukaryotic cell.

Keywords: chloroplast capture, cytonuclear discordance, cytonuclear dissonance, mitonuclear discordance, mitochondrion capture, phylogenetic discordance

Introduction

Eukaryotic organisms possess one or more kinds of membrane-bound organelles, including mitochondria and chloroplasts, which were acquired through ancient endosymbiotic relationships. Both mitochondria and chloroplasts (or, more generally, plastids) have retained reduced, self-replicating genomes that are integral to cellular metabolism (Martin et al., 2015). In addition to the functional importance of these organelles, their DNA has been a widely used source of phylogenetic information since the dawn of molecular systematics. There are several reasons for this, including high copy-number and highly conserved sequences, for which PCR primers can be easily designed. Given these features, cytoplasmic genes have been used many times for estimating relationships among taxa.

The field of phylogenetics has a long history of studying inconsistencies between tree topologies inferred from cytoplasmic sequences and trees inferred from nuclear loci—commonly referred to as cytonuclear discordance (reviewed in Sloan et al., 2017; Toews & Brelsford, 2012). Early studies in both animals (Ferris et al., 1983; Gyllensten & Wilson, 1987; Powell, 1983) and plants (Doebley, 1989; Rieseberg et al., 1990a, b) presented the contrast between cytoplasmic and nuclear markers as an effective and unique tool for revealing introgression between species. Many of these studies sampled multiple individuals across a geographic range, which often allowed them to infer introgression of cytoplasmic DNA (cytDNA) across species without an accompanying signal of introgression among a modest number of nuclear genes. These patterns invited numerous biological explanations, from selection against nuclear introgression, to selection for cytoplasmic introgression, to sex-biased dispersal (Rieseberg & Wendel, 1993). Importantly, before the explosion in availability of nuclear sequences, cytonuclear discordance was viewed as one of the only ways to infer introgression between species.

However, simply observing differences between phylogenetic tree topologies based on cytoplasmic and nuclear DNA does not always present a straightforward interpretation. In this paper, we aim to provide an overview of several important considerations that should be made when comparing the evolutionary histories of nuclear and cytoplasmic genomes. We introduce a new term, "cytonuclear dissonance," to emphasize the concept of differing evolutionary histories between the nuclear and cytoplasmic compartments and clarify that such dissonance is distinct from the empirical observation of conflicting tree topologies (i.e., cytonuclear discordance), and numerous related concepts in the literature (Box 1). Because the concept of cytonuclear dissonance applies to the phylogenetic history of lineages and clades, our discussion will largely focus on inferences made at evolutionary scales above the level of individuals or single populations.

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Box 1. Discordant terminology

Cytonuclear discordance is the most common term for describing inconsistencies between phylogenetic trees inferred from nuclear and cytoplasmic loci. Observations of cytonuclear discordance are linked to multiple biological explanations (see main text), with a commensurate number of terms used to describe the patterns, processes, and outcomes.

Several phrases have been used to suggest the magnitude and underlying biological basis of cytonuclear (but usually cytoplasmic) introgression. For example, cytoplasmic capture is often used as a synonym for cytoplasmic introgression (Rieseberg & Soltis, 1991; Tsitrone et al., 2003). This term—or a similar one, like mitochondrial capture or chloroplast capture—is also used to describe a species possessing the cytoplasmic haplotype of another species while lacking signal for nuclear introgression (Good et al., 2015; Secci-Petretto et al., 2023; Wielstra & Arntzen, 2020). Although the term "capture" could imply a benefit to the recipient species, these terms are often used without reference to adaptive introgression. A less suggestive alternative to "capture" is cytonuclear mismatch (Beresford et al., 2017; Lee-Yaw et al., 2014; Pritchard & Edmands, 2013), which itself may suggest functional consequences (see below).

Cytonuclear disequilibrium was first used to formalize models that describe associations between cytoplasmic and nuclear genes and to infer their biological basis (Arnold, 1993; Arnold et al., 1988; Asmussen & Arnold, 1991; Asmussen et al., 1987; Latta et al., 2001). In many papers, this term is also used as a synonym for cytonuclear discordance (Fields et al., 2014; Monsen et al., 2007; Won et al., 2003). In a more applied context, the introgression of foreign cytoplasmic genes can be referred to as cytoplasmic rescue when used as a tool for escaping the burden of genotypes with many deleterious mutations in threatened or endangered populations (Gemmell & Allendorf, 2001; Havird et al., 2016) or as a preventative mechanism against negative interactions between nuclear and organellar genomes (Barnard-Kubow et al., 2017).

When investigating the molecular interactions between cytoplasmic- and nuclear-encoded proteins, a different but sometimes confounding set of terms are used. Cytonuclear integration or cytonuclear interactions can describe how proteins that originate from cytoplasmic organelles and the nuclear genome interact to conduct important functions, such as cellular respiration (McDiarmid et al., 2024; Rand et al., 2004; Sloan et al., 2018). Differences in mutation rates, effective population sizes, and mode of inheritance between compartments may select for sequence changes in the other because of these interactions, generally described as cytonuclear coevolution (Rand et al., 2004; Wang et al., 2021; Weaver et al., 2022) or cytonuclear coadaptation (Edmands & Burton, 1999; Sackton et al., 2003). More specifically, it is proposed that the nuclear genome may undergo cytonuclear compensation (Havird et al., 2015; Sloan et al., 2014; Zhang & Broughton, 2013) in response to deleterious alleles that appear in cytoplasmic genes (Hill, 2020).

As a result of coevolutionary processes, protein products from cytoplasmic genes that work well with their native nuclear genes may be reduced in function when present on another nuclear background. Cytonuclear interactions may be disrupted via hybridization and backcrossing, and many authors have documented corresponding reductions in metabolic performance and fitness (e.g., Klabacka et al., 2022). These situations can be referred to as cytonuclear incompatibility (Chou et al., 2010; Hoekstra et al., 2013; Meiklejohn et al., 2013; Moran et al., 2024; Sambatti et al., 2008) and are part of a broad class of postzygotic incompatibilities between cytoplasmic- and nuclear-encoded proteins (Burton & Barreto, 2012; Burton et al., 2013; Dobler et al., 2014; Sloan et al., 2017). In addition, cytonuclear conflict can describe the situation in which cytoplasmic and nuclear genomes are under opposing selection pressures. For instance, any process that benefits the transmission of mitochondria at the cost of reducing transmission of the nuclear genome (Havird et al., 2019).

The breadth of these terms is potentially confounding. Does a pattern of cytoplasmic introgression between two species imply cytonuclear coevolution? Does a lack of cytoplasmic introgression suggest cytonuclear incompatibility? Depending on which field authors are approaching the concept from, cytonuclear discordance may include pattern, process, consequence, or all of these (Dong et al., 2014; Funk & Omland, 2003; Lee-Yaw et al., 2019; Rose et al., 2021; Toews & Brelsford, 2012).

Our primary goal is not to provide mechanistic explanations of how cytoplasmic and nuclear phylogenetic histories usually come to differ, nor is it to present an exhaustive review of the vast array of biological phenomena involved in shaping nuclear and cytoplasmic histories and interactions. Rather, we hope to provide readers with a clearer view of what cytoplasmic discordance can and cannot tell us about evolutionary history. To do this, we first briefly review the causes of gene tree discordance, followed by a more in-depth discussion of analytical approaches that can be used to determine whether cytonuclear dissonance has occurred. We end with a discussion of some of the possible biological causes of cytonuclear dissonance, as well as several outstanding questions in the field.

A multispecies coalescent view of species tree and gene trees

Modern population genetics theory provides a view of the species tree, wherein gene tree discordance is expected under a wide range of biological scenarios (Maddison, 1997). The multispecies coalescent model (MSC) describes the expected genealogical relationships between sampled species for many loci across the genome resulting from stochastic population processes (Hudson, 1983; reviewed in Rannala et al., 2020). The genealogical history of each locus is represented by a gene tree, whereas the species tree represents the population history. Individual gene trees evolve within the species tree. The topology of a gene tree can be discordant with the species tree when coalescence at a locus does not occur in the most recent ancestral population, but instead occurs in a more distant ancestral population; this phenomenon is called incomplete lineage sorting (ILS; Figure 1). Under the MSC, species tree branch lengths are often represented as time (t, measured in number of generations) divided by twice the effective population size (N_e). More ILS is expected when there are shorter branches in the species tree, either because the time between speciation events is short or population sizes are large. Importantly, it is the length of branches that determines how much ILS there is, not the age of branches. Phylogenetic conflict arising from ILS is the same for recent divergence and ancient divergence, and does not decrease over time (Maddison, 1997). Population histories involving introgression, horizontal gene transfer, or

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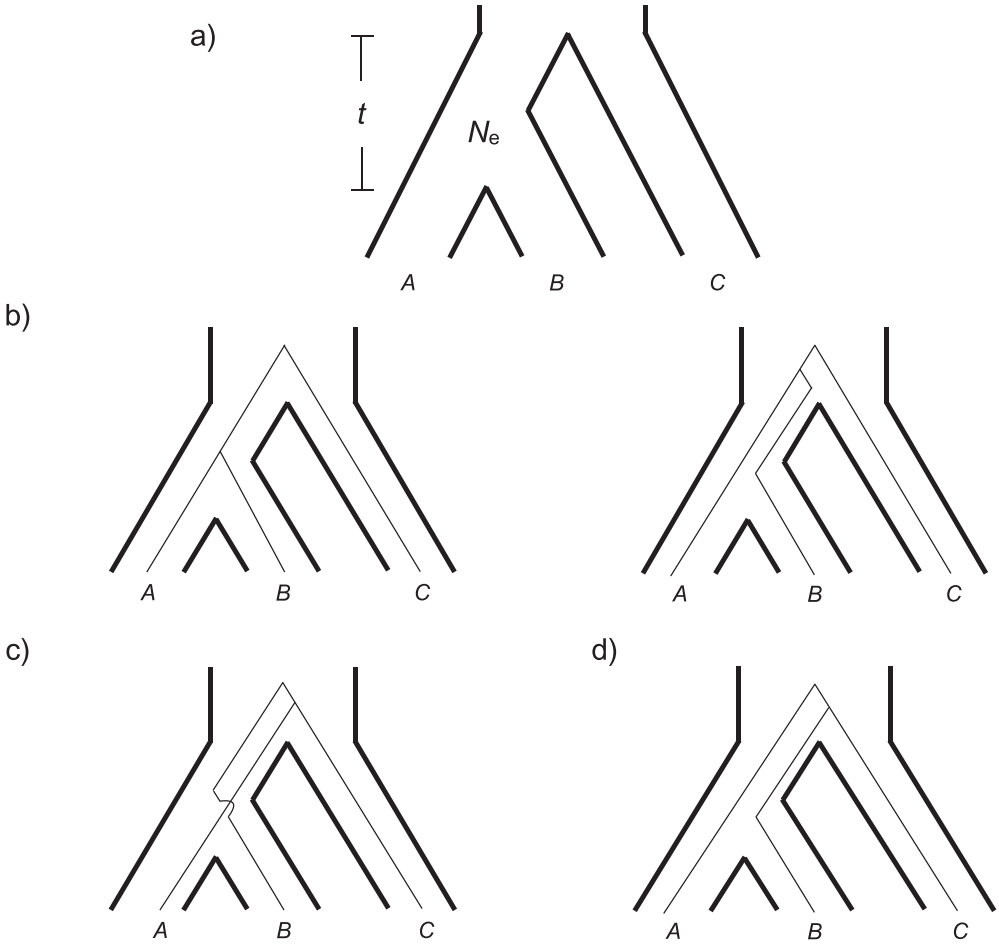

Figure 1. The multispecies coalescent model and incomplete lineage sorting (ILS). Under the multispecies coalescent model, many different gene trees can be produced by a single species tree due to ILS. (a) The species tree provides information about hierarchical relationships and divergence times among species. Here, we emphasize information about the time between the two speciation events (t) and the effective population size (N_e) of the ancestral population that exists between these two events. Together, t and N_e determine the amount of ILS that will occur in this population. (b) The two concordant gene trees that are produced by this species tree. The one on the left coalesces in the ancestor of species *A* and *B* (i.e., lineage sorting), while the one on the right does not (i.e., ILS). Panels (c) and (d) show the two discordant gene trees that can be produced by ILS in this species tree, one with species A and C more closely related (panel c) and one with species B and C (panel d) more closely related.

other evolutionary reticulations can be accommodated by species networks. Such networks are typically represented as a species tree with additional edges, sometimes given weights according to the proportion of the genome inferred to have followed a given edge. Recent empirical phylogenetic studies, no longer limited to sequencing a small number of genes, routinely observe high levels of gene tree discordance due to both ILS and introgression (Cai et al., 2021).

As is made clear by the MSC, a species tree or species network does not represent the same thing as a single cytoplasmic or nuclear gene tree. Species histories shape the many locus histories that exist among groups of organisms; locus histories are often investigated to infer the species history. This fact is particularly explicit when using species tree methods (Edwards, 2009), which take a collection of individual gene trees and use them to infer a species history. Depending on the model assumed, these methods can infer divergence histories and sometimes introgression as well, resulting in the "nuclear tree" to which a cytoplasmic tree is often compared. While the inferred species tree from the nuclear loci is not exactly an average of the underlying marginal gene trees (because of some quirks of coalescent genealogies; Degnan & Rosenberg, 2006), neither does it have to match any of the individual gene trees, even without introgression. In other words, in some datasets, all gene trees are discordant with the species tree (e.g., Jarvis et al., 2014; Larson et al., 2025; Pease et al., 2016; Wu et al., 2018).

While methods to estimate a phylogenetic tree or network from a set of gene trees can rely on a solid foundation of established population genetic and mathematical theory, it is a different challenge to accurately infer individual locus trees in the nuclear genome. This is because there are many interacting biological processes such as recombination, homoplasy, and evolutionary rate heterogeneity that complicate both decisions about how to define loci and how to best estimate their histories. In practice, estimating gene trees is usually accomplished by selecting loci that are short enough that recombination is low within each locus, and then using maximum-likelihood methods to infer the tree topology and branch lengths. Gene tree inference error can result when one or more assumptions of the model used to estimate the tree are violated, including that the sequence evolved under treelike, stationary, reversible, and/or homogeneous condi-

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tions (Naser-Khdour et al., 2019). Methods that make use of site patterns, such as SVDquartets (Chifman & Kubatko, 2015), eliminate the need to delimit loci to infer a species tree, but these methods still require assumptions about the independence of individual genomic sites included in the analysis.

A multispecies coalescent view of cytoplasmic discordance

Considering the description of species trees and gene trees given in the previous section, we believe there is an important distinction to be made between differing evolutionary histories and differing phylogenetic trees when comparing nuclear and cytoplasmic compartments. To emphasize this distinction, we use the term "cytonuclear discordance" strictly to describe the *observation* of mismatching topologies between phylogenetic trees or networks from the nuclear and cytoplasmic compartment(s). Cytonuclear dissonance, on the other hand, is a *hypothesis* about evolutionary history—an inference that one or more cytoplasmic genomes are thought to have moved among species or lineages in a way that is different from the histories comprising the nuclear genome.

To illustrate this point, imagine that instead of a cytoplasmic locus, we had a high-confidence gene tree from the nuclear-encoded *alcohol dehydrogenase* (*Adh*) gene, a classic focus of many evolutionary studies (McDonald & Kreitman, 1991). How would we interpret discordance between *Adh* and the species tree? This alco-nuclear discordance could signify introgression among species at the *Adh* locus, possibly even tied to coevolution between *Adh* and its interacting proteins. But without additional evidence, one cannot rule out that it is discordant due to random genealogical processes and ILS. Phylogenetic discordance with cytoplasmic loci can often be viewed in much the same way: a mitochondrial or plastid tree topology may essentially be one random draw from the multitude of genealogies that the species history comprises. Differing tree topologies alone does not provide evidence that the nuclear and cytoplasmic genome(s) ever spent time evolving in different lineages (Neigel & Avise, 1986).

While cytDNA is subject to many of the same biological processes as nuclear DNA, there are also important differences. In sexually reproducing species, there is usually frequent recombination within the nuclear genome. This results in the nuclear genome having a mosaic of histories in a way that mitochondrial or plastid genomes usually do not (Doyle, 2022), though there are examples of phylogenetic discordance within cytoplasmic genomes seemingly caused by recombination during periods of heteroplasmy (e.g., Leducq et al., 2017; Sullivan et al., 2017; Kao et al., 2022). Indeed, recombination among mitochondrial genomes is relatively frequent following experimental crossing of *Saccharomyces* yeast species, which show biparental inheritance of the cytoplasm followed by a rapid return to homoplasmy (Leducq et al., 2017; Poláková et al., 2021). However, in general, the difference in recombination means the history of the nuclear compartment as a whole is not directly comparable to that of a cytoplasmic compartment. Instead, the history of a cytoplasmic genome is probably better compared to the histories of individual nuclear loci, which together comprise the nuclear history. Cytoplasmic genomes also experience differences in effective population size compared to nuclear loci. In most plants and animals, the mitochondrial and plastid genomes are haploid and uniparentally inherited, causing the cytDNA to have lower effective population size than a typical nuclear locus. Under idealized conditions, N_e for cytDNA is expected to be four times lower than nuclear loci in a diploid species with separate sexes, or two times lower in outcrossing hermaphroditic or monoecious species (Birky et al., 1983; Latta, 2006). However, this varies greatly depending on several biological factors and is difficult to measure empirically (Wright et al., 2008). The smaller N_e of cytoplasmic genomes means that coalescence will occur more quickly on average. Therefore, we might not expect a cytDNA tree to experience as much ILS as the average nuclear locus. As we discuss in the next section, some approaches for assessing cytonuclear dissonance are better able to account for this difference in N_e than others.

Investigating whether the histories of the cytoplasm and nucleus are dissonant

Given that there is discordance between a cytoplasmic locus and the species tree, one may want to know the extent to which the observed discordance is due to error, ILS, and/or past genetic exchange among lineages. To be clear, we refer to the species history as the entire series of divergences and evolutionary reticulations that populations of organisms have experienced (Figure 2a). This species history determines what locus histories could possibly have occurred. When there is a reticulation in the species history, different loci can follow different locus histories. Some loci will follow the strictly vertical inheritance history, or what we will call the "speciation history" (Figure 2b), while other loci will follow the "introgression history," which includes horizontal movement among lineages (Figure 2c). Cytonuclear dissonance occurs when the cytoplasmic genome follows a different history (i.e., either Figure 2b or c) than the loci that comprise the nuclear genome.

Several important points should be clarified about cytonuclear dissonance. First, there can be multiple reticulations in a species history. Therefore, a locus (including cytoplasmic loci) may follow the speciation history at some points in a tree and may follow the introgression history at other points. Second, we consider evolutionary reticulation to comprise several processes, including introgression between species via sex and backcrossing, horizontal gene transfer, and allopolyploidy. For our purposes, the outcomes of these various types of reticulations are generally the same: they can result in loci having differing histories (Figure 2). Thus, here we generally refer to "introgression" and "introgression histories" when discussing reticulations that may have led to cytonuclear dissonance and/or discordance. However, it is important to consider the possibility that reticulation other than strict introgression may have produced the differing locus histories observed in any particular system; such considerations may alter expectations for the tests described below.

There are also several considerations to be made in determining whether the cytDNA has a history that is dissonant with that of the nuclear genome. Cytonuclear dissonance can only occur as the result of genetic exchange between diverged lineages, whereas cytonuclear discordance can result from introgression as well as other biological and

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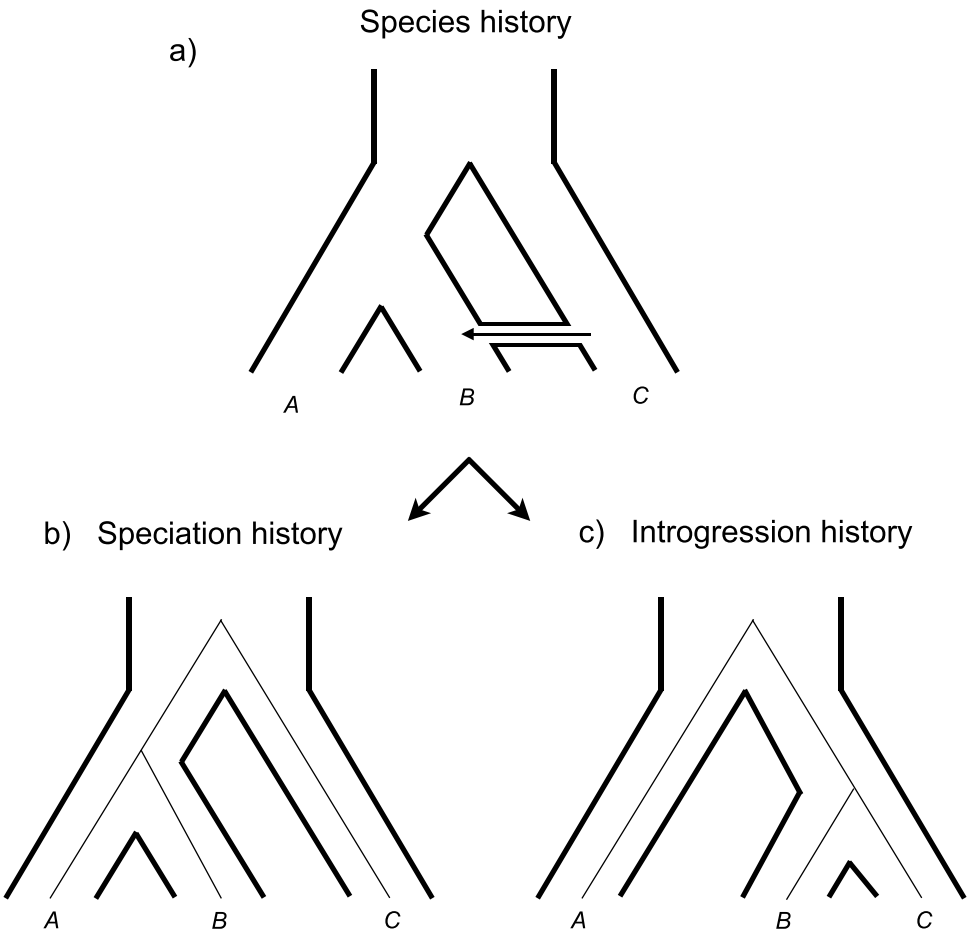

Figure 2. Evolutionary reticulation leads to loci with differing histories. (a) An example of a species history that includes introgression from species C into species B. (b) Nonintrogressed loci have evolved along the speciation history. (c) Introgressed loci have evolved along the introgression history in which species B and C share a more recent ancestor than either does with species A. Loci that have evolved along either the speciation or introgression histories could also have experienced ILS. Discordance between cytoplasmic and nuclear gene trees may occur due to incomplete lineage sorting within the context of a shared inheritance history, or because the cytoplasmic locus sampled happens to follow an inheritance history that only a subset of the nuclear genome follows. Testing for cytonuclear dissonance involves testing whether the cytDNA has a history that is different from the nuclear history, which comprises the many individual nuclear-locus histories.

methodological causes. When cytonuclear discordance can be explained by the coalescent sampling processes and ILS, there is no reason to conclude that the history of the cytoplasm is different from the overall nuclear history. Similarly, if the nuclear history includes reticulations that can explain the cytDNA tree(s), there is little reason to conclude that the compartments do not share the same introgression history. Here, we provide suggestions for the kinds of tests that can help to determine whether the cytoplasm and nuclear have dissonant histories. We provide example studies that have implemented these approaches and therefore may be useful for developing specific workflows and pipelines appropriate to the clade of interest.

Testing for cytonuclear discordance

The first consideration when evaluating cytonuclear dissonance should be the extent to which the nuclear and cytoplasmic trees truly differ. If there are no well-supported branches that differ between the cytDNA tree and an inferred species tree, then there is no reliable signal of cytonuclear discordance, and the observed differences may be due to tree estimation error or some other violation of the model used to estimate the tree. Even with whole cytoplasmic genomes, one should not ignore gene tree inference error as a possible source of discordance (Kimball et al., 2021; Shen et al., 2017; Weisrock, 2012). Sequence alignments should be inspected to check whether taxa with particularly high levels of missing data are causing discordance or whether the gene tree shows signals of biologically unreasonable branch lengths, possibly due to misidentified orthologs, sequence alignment issues, or assembly errors. Species misidentification or taxonomic uncertainty can also be issues for some studies (Toews & Brelsford, 2012). It is important to note that any statistical assessment of cytonuclear discordance should generally only use a single tree per organellar genome—one cannot use each gene in the mitochondrial or plastid DNA separately, as doing so would require assumptions about recombination within cytoplasmic genomes that are generally not aligned with their biology (Doyle, 2022; Edwards & Bensch, 2009). If there is support for cytonuclear discordance, the next step is to determine whether there is evidence of nuclear introgression, since this aspect of the species history will deter-

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mine which are the most appropriate tests for cytonuclear dissonance.

Testing for nuclear introgression

The shape of the species tree or network determines the probability of observing any particular gene tree topology. Thus, characterizing any past introgression involving the nuclear genome is an important step toward understanding whether the cytoplasm has a different history. There are currently many methods that can be used to detect introgression among nuclear loci (reviewed in Hibbins & Hahn, 2022), including *D*-statistics (Durand et al., 2011; Green et al., 2010) and *F*-statistics (Reich et al., 2009). These tests generally rely on differences in the overall counts of gene tree topologies or site patterns across the genome, as introgression can cause some to occur more often than others. When testing for introgression, ILS is generally used as the null hypothesis and the absence of evidence for introgression is generally taken to be evidence for ILS. However, ILS is always occurring, even (or perhaps especially) in the same circumstances where introgression is likely to occur—among closely related populations or species. Introgression inference at individual loci (such as the plastid or mitochondrion) requires that a determination about introgression history be made about a single gene tree, which requires a different approach than testing for genome-wide introgression in the nuclear genome.

Testing for cytonuclear dissonance

Ultimately, establishing cytonuclear dissonance requires showing that the cytDNA and nuclear genomes have different introgression histories. In other words, one must show that the inferred nuclear species tree or network could not have produced a gene tree like that observed for the cytDNA. Only introgression of either the cytoplasmic genome or nuclear genome, to the complete (or near-complete) exclusion of the other, produces cytonuclear dissonance. Thus, the approach one takes to testing for cytonuclear dissonance depends on an understanding of the nuclear introgression history. If there is no evidence of nuclear introgression, and the species history can be reasonably modeled as a bifurcating tree, then establishing evidence of cytonuclear dissonance involves asking whether the inferred nuclear tree could generate a tree like the cytDNA topology due to ILS. If nuclear introgression has occurred among species, then demonstrating evidence for cytonuclear dissonance involves determining whether the species network, including the hypothesized history of introgression, could generate the cytDNA tree(s). The approaches for identifying which gene trees are realistically possible, given the species tree or network, fall into two broad categories: examining the distribution of empirical nuclear gene trees estimated from sequence data (see the section "Method I" below) and generating gene trees through simulation based on an inferred species tree or network (see the section "Method II" below). We next discuss these two approaches in greater detail, as well as the strengths and drawbacks of each.

Method I: compare cytoplasmic tree to nuclear gene trees

A straightforward approach to determining which gene trees a species tree or network is likely to produce is to examine the set of empirically estimated nuclear gene trees. One could compare the cytDNA tree topology to each estimated nuclear gene tree topology, but with any moderate number of tips it might not be expected that any two match completely, even under the same evolutionary history. Instead, one can compare the nuclear gene trees to the species tree topology using a distance metric such as Robinson–Foulds distance (Robinson & Foulds, 1981) or "extra lineages" distance (Maddison, 1997; Than & Rosenberg, 2011) and then compare the cytDNA tree in the same way to ask whether the cytDNA tree is unusually distant (i.e., in the extreme tail of the distribution of distances). This approach provides a consistent empirical comparison because both sets of gene trees must be inferred from data and may therefore experience similar estimation error. If the cytDNA tree has a greater phylogenetic distance than is observed in any of the nuclear gene trees, this can be taken as evidence that the cytoplasmic genome has a dissonant history. Several recent studies have taken such an approach and provide good examples of specific tools that can be used to carry out these kinds of analyses (e.g., Gardner et al., 2023; Kimball et al., 2021).

An alternative approach asks whether there are specific branches that differ between sets of gene trees. If a reasonably large number of nuclear loci have been sampled, one can determine whether there are specific, well-supported branches in the cytDNA tree(s) that are not present among the nuclear gene trees. If they are not present in any nuclear trees, this is evidence that the cytoplasm has a different history. This approach can provide information about where in the tree introgression has occurred, which is not possible using methods that only consider overall tree dissimilarity. Examples of this approach can be found in Buckley et al. (2006), Folk et al. (2017), and Gardner et al. (2023).

Method II: simulate data and compare

A second general approach is to simulate gene trees with ILS using the species tree or network, but with tree branches lengthened to resemble those resulting from cytoplasmic inheritance. As discussed above, cytoplasmic loci have an effective population size that is smaller than an average nuclear locus and are therefore expected to experience less ILS. Species tree branch lengths can be estimated in coalescent units ($=t/2N_e$) experienced by the nuclear genome; however, one cannot estimate a tree in coalescent units from cytDNA directly. Instead, simulating the amount of ILS experienced by the cytDNA can be done by simply lengthening the branches of the nuclear-based tree by a factor of four (or a different scaling factor appropriate based on the focal clade's biology). A variety of different coalescent simulators can then be used to generate a null set of gene trees expected under the nuclear history, but with the amount of ILS approximately experienced by the cytoplasm.

Once a set of cytDNA-like trees has been simulated, one can apply the same two approaches as described above for the empirical nuclear gene trees. That is, one can determine whether the total tree distance from the species tree is greater for the cytDNA tree(s) than the simulated cytDNA-like trees (Baldwin et al., 2023; Gardner et al., 2023; Zhou et al., 2022) or investigate whether branches present in the

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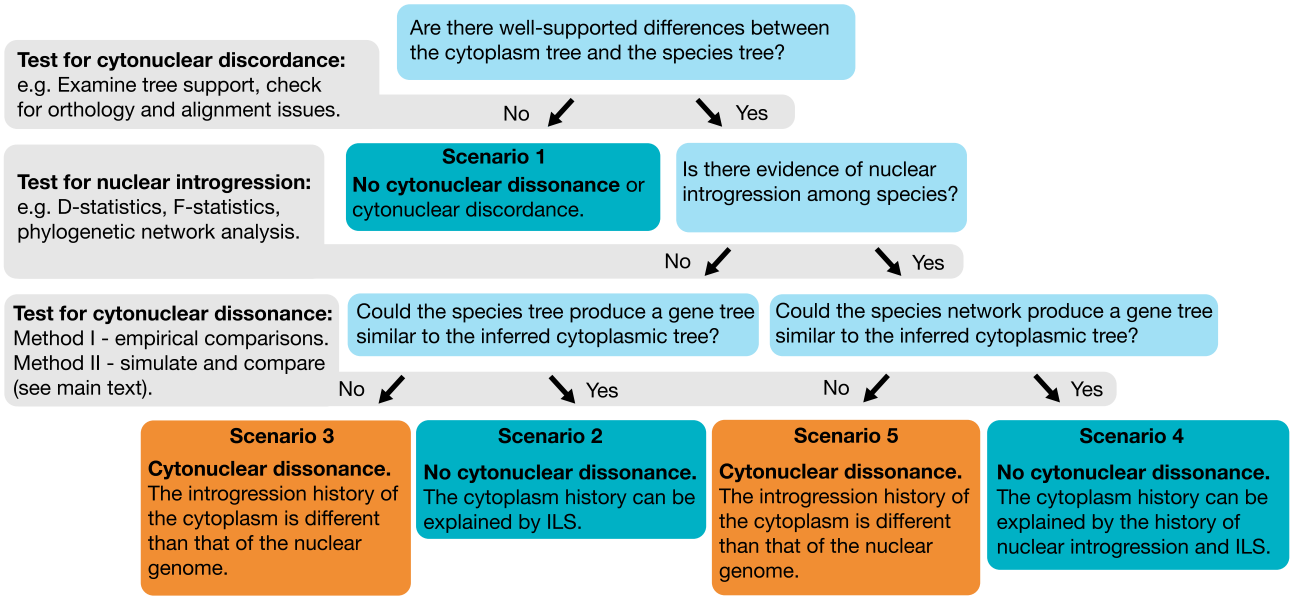

Figure 3. Framework for assessing whether there is evidence of cytonuclear dissonance. Here, we focus on introgression as a potential cause of cytonuclear dissonance, but similar ideas apply to other reticulations, including horizontal gene transfer and allopolyploidy, which all have the effect of leading to network-like species histories.

cytDNA tree(s) are also observed among simulated gene trees (Folk et al., 2017; García et al., 2017; Morales-Briones et al., 2018; Zhou et al., 2022). While simulation-based approaches are capable of accounting for differences in N_e experienced by the cytoplasm—an advantage not available when using only empirical gene trees—they also have several disadvantages. First, the cytDNA tree is inferred from data, while the simulated trees are not. Therefore, the cytDNA tree might be more different from the species tree simply because it contains more error. Second, misspecification of the species tree or network used to simulate gene trees could lead to an incorrect distribution of gene trees.

Tests involving branch lengths

The tests we describe above rely mainly on identifying differences in tree topologies; however, branch length information can also be useful for determining evidence of introgression (e.g., Hahn & Hibbins, 2019; Suvorov et al., 2022; Vargas et al., 2017). Under ILS alone, the divergence time of cytDNA should be older than a given species divergence, whereas introgression can result in cytDNA divergences that are more recent than the species divergence (Joly et al., 2009; Rosenzweig et al., 2016). However, it is important to ensure that genetic distances or branch lengths are comparable between compartments, as both mutation rates and effective population sizes differ (Allio et al., 2017; Smith, 2015; Wright et al., 2008). Fair comparisons require making clear distinctions between allelic divergence times and species divergence times (cf. Edwards & Beerli, 2000) and making use of scaling factors that account for differences in mutation rates between compartments (e.g., Lee-Yaw et al., 2019; Mikkelsen & Weir, 2023).

Interpreting the evidence: what can we infer?

Thus far, we have introduced multiple biological processes that can lead to gene tree discordance, as well as multiple different tests that can be used to distinguish whether cytonuclear discordance is due to dissonant histories. Importantly, comparisons involving tree topologies do not necessarily tell us much about the particular events or processes that have occurred, and there are often multiple possible combinations of ILS and introgression that could lead to similar sets of empirical evidence for or against dissonance. Here, we discuss what the evidence can tell us about the histories of the nuclear and cytoplasmic genomes, focusing our discussion on five scenarios implied by the tests described in the previous section (Figure 3).

Scenario 1: no cytonuclear discordance

If there is little support for cytonuclear discordance, the most straightforward interpretation is that the cytDNA has the same history as much of the nuclear genome. However, even introgressed loci do not necessarily have a discordant tree topology. It is still therefore possible that introgression (and ILS) has occurred in one or more genomic compartments in this, or any other scenario, even if there is no signal of discordance.

Scenario 2: cytonuclear discordance, but not support for cytonuclear dissonance in the absence of nuclear introgression

If there is support for cytonuclear discordance, and nuclear introgression is not suspected, one can use the tests outlined above to establish whether the cytDNA tree could reasonably be produced by the inferred species tree. If the cytDNA tree is sufficiently similar to the nuclear gene trees observed, only ILS is needed to explain the discordance (e.g., DeRaad et al., 2023). It is important to note that even if the inferred cytoplasmic tree is not shown to match any particular nuclear gene tree exactly, pervasive ILS can lead to a large number of possible trees, not all of which will be necessarily be observed in the nuclear genome.

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Scenario 3: support for cytonuclear dissonance in the absence of nuclear introgression

If one has established that the cytDNA tree cannot be explained by ILS given the species tree, and there is no evidence of introgression within the nuclear genome, then there is evidence that the introgression history differs between nucleus and the cytoplasm. However, one cannot necessarily conclude that the cytoplasmic element is the one that introgressed. The biology of cytoplasmic genes alone does not necessarily provide a strong argument for or against introgression of the cytoplasm (Sloan et al., 2017), and it is possible that the nuclear genome was replaced by introgression rather than the cytoplasm (see discussion of possible mechanisms below).

Scenario 4: cytonuclear discordance, but not support for cytonuclear dissonance in the presence of nuclear introgression

If there is evidence of both cytonuclear discordance and nuclear introgression, finding support for cytonuclear dissonance requires showing that the cytDNA tree could not result from the proposed species network. If the species network could reasonably generate a similar tree through a combination of ILS and introgression, then there is no evidence that the history of the cytoplasm differs from those of the nuclear genome, and therefore no evidence of cytonuclear dissonance. Several studies have found cytonuclear discordance that is well-explained by a history of introgression also observed among nuclear loci, including in bats (Foley et al., 2024), seabirds (Mikkelsen & Weir, 2023), and wild pigs (Frantz et al., 2013).

Scenario 5: support for cytonuclear dissonance in the presence of nuclear introgression

If one has established cytonuclear discordance and shown that the nuclear history of introgression cannot reasonably explain the cytDNA history, then there is evidence to support an inference of cytonuclear dissonance. Folk et al. (2017) used empirical tree comparisons and simulations (i.e., Methods I and II here) to show that neither cytDNA tree could be explained by ILS based on the histories inferred to comprise the nuclear genome in the plant genus *Heuchera*.

Considering the causes cytonuclear dissonance

There are a multitude of biological scenarios that could lead to cytonuclear dissonance. For example, hybridization between species followed by backcrossing, possibly with strong selection, could result in cytoplasmic introgression to the exclusion of long-term nuclear introgression. During reproduction via androgenesis or gynogenesis, one parent passes on their entire nuclear genome to the next generation after mating (Hedtke & Hillis, 2011; Schlupp, 2005). There are very few, if any, examples of multispecies androgenetic or gynogenetic clades, which could theoretically generate apparent cytonuclear dissonance through only speciation and ILS (due to completely linked inheritance of all nuclear genes). However, it is possible that interspecies mating, followed by ejection or destruction of one parent's nuclear DNA could lead to "mismatched" nuclear and cytoplasmic genomes in a single generation (Hedtke & Hillis, 2011). If this introgressed genome became widespread or fixed in a lineage, this process could result in cytonuclear dissonance. For example, a lineage of salamanders in the genus *Ambystoma* originated via hybridization and subsequent replacement of the parental species' nuclear DNA, establishing starkly different histories between mitochondrial and nuclear loci (Bogart et al., 2007, 2009; Denton et al., 2018). Other modes of transfer do not necessarily rely on reproductive strategies; interspecies cellular interactions resulting from parasitism or injury could result in horizontal transfer of plastids or mitochondria, which could be passed on to offspring. Transfer of plastids between species has been demonstrated in plants grafted in the lab (Stegemann et al., 2012; Thyssen et al., 2012), and there are numerous examples of apparent horizontal cytDNA transfer occurring in nature (e.g., Davis & Wurdack, 2004).

Which cellular compartment introgressed?

In most cases where there is evidence of cytonuclear dissonance, the topology of a phylogenetic tree alone is not sufficient to reliably determine what events caused it, or even which genome introgressed. Some particularly clear examples of cytonuclear dissonance come from population-level analyses, where cytoplasmic genome variation within a species allows inference of the directionality of introgression (Denton et al., 2014; Soltis et al., 1991; Toews & Brelsford, 2012). For example, Good et al. (2015) used targeted sequence capture to show that there was no evidence of nuclear introgression, despite clear, unidirectional introgression of the mitochondrial genome in populations of *Tamias* chipmunks. It is important to note that monophyly of a species within a gene tree does not necessarily rule out introgression, since an introgressed locus or genome can also fix within a species (e.g., Bossu & Near, 2009).

There are many explanations in the literature for why genes in one or the other compartment might have introgressed, given that cytonuclear dissonance can have important functional consequences. For example, mismatches between cytoplasmic genes that cause male sterility and nuclear restorer elements underlie hybrid male sterility in several groups of plants (Fishman & Willis, 2006). Several organellar protein complexes are derived from subunits that originate from both the cytoplasmic and nuclear genomes, which coevolve to maintain the structure and function of the protein complex (Rand et al., 2004; Sloan et al., 2018; Weaver et al., 2022; Yan et al., 2019). Mismatches between these coadapted subunits can result in genetic incompatibilities through poor physiological performance or lethality in hybrids (Barnard-Kubow et al., 2017; Chou et al., 2010; Lamelza & Ailion, 2017; Moran et al., 2024; Willett & Burton, 2001). Therefore, some arguments point to the central role of mitochondria and chloroplasts in metabolism and emphasize that their genomes (and any nuclear genes to which they are coadapted) should generally be resistant to gene flow due to reduced fitness of early hybrids (Burton & Barreto, 2012; Hill, 2016). Thus, from this point of view, introgression of the cytoplasmic genomes should be rare relative to the nuclear genome.

Other arguments emphasize that the uniparental inheritance and limited recombination among cytoplasmic genomes could lead to the accumulation of deleterious mutations. In such cases, a species might benefit from acquiring an overall less-impaired cytoplasmic genome through in-

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trogressive hybridization with another species (reviewed in Sloan et al., 2017). Similarly, introgression during a species' range expansion could also allow the acquisition of more locally adapted cytoplasmic genomes (Hill, 2019). In these cases, one might argue that the cytoplasmic genome is more likely than most nuclear genes to introgress, though as mentioned above discordance by itself is also usually uninformative about the direction of introgression, so determining who "captured" which genome of whom requires additional data.

Other biological factors may also influence the relative likelihood of nuclear versus cytoplasmic introgression. For example, there is a bias toward greater introgression of cytoplasmic loci in haplodiploid animals (Patten et al., 2015). Differences in average dispersal between males and females, and between pollen and seeds in plants, can also lead to differences in introgression rates between compartments (Petit et al., 1993), as can sex-biased asymmetries in hybrid fitness (Toews & Brelsford, 2012).

In other cases, there may be little or no functional difference in the cytoplasmic genomes of related species. For example, the mitochondria of land plants typically have a strongly conserved set of core genes that, in contrast to animals, have high coding sequence similarly, with substitution rates that are generally much lower than nuclear genes (Allio et al., 2017; Smith, 2015). If there are no selectively meaningful differences among the cytoplasmic genomes of potentially hybridizing species, the cytoplasmic genomes may be free to introgress.

Finally, it may be that nuclear genes can cointrogress with coadapted cytoplasmic genes (Forsythe et al., 2020; Moran et al., 2024). If a small number of nuclear genes appear to share an introgression history with the cytoplasm, should one consider there to be cytonuclear dissonance? In a sense, the history of those cointrogressed nuclear genes could be considered dissonant with the rest of the nuclear history and any threshold for how many nuclear genes can cointrogress alongside the cytoplasm before the cytoplasmic and nuclear histories should be considered consonant is largely a matter of terminology. What is more biologically important is whether this pattern is due to coevolution and/or selection for cointrogression between nuclear and cytoplasmic genes. One approach to detecting such scenarios is to test whether introgressed nuclear loci are enriched for genes involved in plastid or mitochondrial interactions (e.g., Forsythe et al., 2020; Lee-Yaw et al., 2019). If there are more genes involved in cytonuclear interactions than expected by chance, this could be evidence that selection has caused these genes to be preferentially introgressed after or during the introgression of the cytoplasm. One should also consider the possibility that these genes are among the only ones that have not introgressed within a background of near-total nuclear replacement. Determining which situation is more likely requires additional information.

Conclusions and future directions

We have argued for a clearer distinction between cytonuclear discordance and cytonuclear dissonance. Such a distinction will allow researchers to better differentiate between patterns observed in phylogenetic analyses and evolutionary processes, including introgression and interactions between the cytoplasmic and nuclear genomes. Many of the ideas discussed here are also relevant to studies of symbionts and their hosts, particularly bacterial endosymbionts (e.g., Perez-Escobar et al., 2016; Symula et al., 2011). Populations of such organisms would be expected to undergo ILS in much the same way as does a mitochondrial or plastid genome. This means that discordance between a host clade's phylogeny and that of their endosymbiont does not necessarily indicate dissonant histories (i.e., host switching). Rather, one must establish evidence that the endosymbiont's history cannot be explained by the species history (i.e., the phylogenetic tree or network) of the host clade.

Demonstrating that there is cytonuclear discordance is relatively easy; providing evidence for cytonuclear dissonance requires much more work. Advances in DNA sequencing have provided a broader view of the frequency with which nuclear gene trees will be discordant with the species tree. Depending on the tempo of speciation and the history of introgression, many cases of cytonuclear discordance may be well-explained by processes that affect all cellular compartments.

There are several areas of research that may yield advances in our understanding of the causes of cytonuclear discordance and dissonance. One pattern that we find particularly interesting is that cytoplasmic gene trees often appear to be more different from the species tree, and with higher support, than any particular nuclear gene tree (e.g., Gardner et al., 2023; Hendriks et al., 2023; Zhou et al., 2022). The reasons for this pattern are unclear: it could be because cytDNA introgresses more often, or simply that the signature of introgression is more easily observed in the relatively long, generally nonrecombining cytoplasmic genome. In other words, it could be that the length of recombination-free loci within the nuclear genome are generally too short to yield strongly supported, highly conflicting tree topologies. Another explanation could be that the conserved functions of chloroplasts and mitochondria mean that their genomes are capable of introgressing across further evolutionary distances without experiencing the same levels of genetic incompatibilities as the average nuclear gene.

Scientists cannot meaningfully investigate the potentially powerful consequences of cytonuclear discordance and dissonance until they are defined and reliably identified. Doing so will allow empirical studies to better assess other related processes, such as the prevalence of cointrogression of nuclear and cytoplasmic loci, signatures of compensatory molecular evolution, or the functional costs of cytonuclear mismatch. Taxonomic systems that demonstrate strong signals for cytoplasmic dissonance can be used to test for potential negative effects on these types of traits (e.g., mitochondrial efficiency, organismal metabolic rate, and fertility). Several studies have demonstrated that cytonuclear mismatch can carry a negative or lethal consequence, particularly in F1 hybrids or asexual lineages of animals (Cullum, 1997; Denton et al., 2017; Klabacka et al., 2022; Moran et al., 2024; Willett & Burton, 2001). However, it remains unclear how common these cytonuclear scenarios are, especially compared to nuclear incompatibilities, or if the fitness costs are meaningful. Systems with a history of cytonuclear dissonance, particularly without cointrogression of nuclear genes, should provide better insight to the ubiquity of this phenomenon.

Reliably differentiating between patterns of cytonuclear discordance and cytonuclear dissonance is an important step

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forward, especially as these concepts become applied to other biological disciplines. For example, cytonuclear dissonance is increasingly studied as a contributor to phenotypes associated with aging (e.g., Serrano et al., 2024). These studies often conduct crosses among strains to create new combinations of mitochondrial haplotypes on different nuclear backgrounds (Serrano et al., 2024) or to quantify selection between or within individuals that are heteroplasmic (Battersby & Shoubridge, 2001; Jenuth et al., 1997). In these instances, phylogenetic methods could help to quantify cytonuclear dissonance to contextualize experiments that measure putative physiological outcomes. The above guidelines could also contribute to the further development of ecological models that consider cytonuclear dissonance as a parameter that influences community composition, abundance, and distribution (e.g., Princepe et al., 2022). The dizzying array of terminology surrounding cytonuclear discordance and dissonance (Box 1) makes these connections across fields challenging, but we hope that the conceptual clarifications offered here help to make them more likely.

Data availability

No new data were generated or analyzed in support of this research.

Author contributions

M.W.H. and R.D.D. conceptualized the project. D.A.L. wrote the manuscript with contributions from M.W.I., R.D.D., and M.W.H.

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Conflict of interest

The authors declare no conflict of interest.

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