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COMMENTARY

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Will molecular phylogenetics help decrease nomenclatural instability?

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In the process of compiling a flora for Montana (Lesica, 2012, 2022), we came to realize that many published nomenclatural changes are only weakly supported by the data presented which has often been based on recent findings in the field of molecular evolution. In this essay we attempt to present a summary of the reasons why taxonomic changes may be less than robust and our guidelines for accepting newly proposed nomenclature that we attempted to follow in our work.

Taxonomy is an orderly classification that reflects presumed natural relationships (https://www.merriam-webster.com). Although we think that elucidating the process of evolution should be a goal of taxonomy, we also believe that the primary function of taxonomy should be communication. As a classification, taxonomy should provide standardized names with a significant degree of stability and descriptions for groups of organisms (taxa) which facilitate communication among biologists including ecologists, restorationists, conservationists, land managers, the general public, as well as taxonomists. Taxonomy applies a different name to every distinct entity and groups similar entities together. Taxonomy allows biologists to know that they are communicating about the same or different organisms. This is useful for many reasons. For example, one can accurately compare the species composition of a forest taken at two locations or at the same location at two different times. The U.S. Forest Service Forest Inventory and Analysis Program (www.fia.fs.usda.gov) monitors permanent plots every ten years to understand how vegetation is changing. This becomes more difficult when species have been assigned a different name between the sample periods. Changes in taxonomy may also interfere with conservation efforts by affecting whether endangered or threatened populations are given species status (Garnett and Christidis (2017), but see Thomson et al. (2018)). Other reasons for maximizing taxonomic stability, such as communication between researchers in different countries, are presented by Lowry et al. (2019; but also see Nesom et al., 2019).

Taxonomy also attempts to portray the evolutionary relationships among different taxa, a function that serves primarily taxonomists and evolutionary biologists. Our understanding of these relationships has often changed over time. As a result, plant taxonomic nomenclature has been unstable. In the past the greatest reasons for instability have been disagreements in taxon concepts and individual taxonomic philosophies (e.g., lumpers and splitters; see Endersby, 2009). In addition, digitization of global botanical literature has allowed nomenclatural experts to identify illegitimate names based on priority issues. Although these are still sources of taxonomic instability, in recent decades changes due to molecular phylogenetics research have come to the forefront.

There is no question that molecular phylogenetics has provided an abundance of interesting and useful insights into the evolution of vascular plants. For example, phylogenies informed by molecular phylogenetics are a powerful way of exposing cases of cryptic species (Soltis et al., 2007; Monro, 2022) and convergent evolution (e.g., *Aster*; Noyes and Rieseberg, 1999; Losos, 2017). Over the past several decades evolutionary biologists have been using molecular markers to provide information on evolutionary relationships that does not also rely on morphological appearances.

While phylogenetic studies usually provide valuable information, nomenclatural changes resulting from these studies have made communication more difficult. A certain amount of instability is inherent in plant taxonomy. However, recognizing the limitations of molecular phylogenetic methods may help taxonomists, database managers, authors of local and regional floras, as well as the botanical community at large to minimize nomenclatural instability, thereby increasing the communication functionality of taxonomy.

Prior to adopting nomenclatural changes for databases or floristic manuals, phylogenies should represent the evolution of species (i.e., species trees). However, not all members of the botanical community realize that gene trees obtained from molecular studies may be discordant with species trees for several reasons. One reason for this discordance is the interspecific transfer of genetic material (Maddison, 1997; Degnan and Rosenberg, 2009; Long and Kubatko, 2018; Morales-Briones et al., 2018b; Du et al., 2019; Matveeva and Otten, 2019; Stull et al., 2020). Interspecific introgressive hybridization has been common in the plant kingdom and has played an important role in speciation (Soltis and Soltis, 2009). Hybridization followed by backcrossing between distantly related species can result in reticulate rather than bifurcating evolution of the nuclear genome (Soltis and Kuzoff, 1995; Christin et al., 2012; Leache et al., 2014; Soucy et al., 2015; Morales-Briones et al., 2018a; Dunning et al., 2019; Nelson et al., 2021; El Baidouri et al., 2023), and provide an inaccurate phylogeny.

Taxonomists and non-taxonomic botanists should also realize that another source of discordance between gene trees and species trees is transfer of mitochondria or chloroplasts across species boundaries. Introgressive hybridization can result in the transfer of chloroplasts and mitochondria across species boundaries (Sun et al., 2015; Folk et al., 2017; Morales-Briones et al., 2018b). This may also happen through grafting and organelle capture (Richardson and Palmer, 2007; Bock, 2010; Stegemann et al., 2012; Fuentes et al., 2014; Gao et al., 2014; Taylor et al., 2015; Yang et al., 2019; Yoshida et al., 2019; Wickell and Li, 2020). Gene sequences of these organelles have often been and still are used in phylogenetic studies even though they may not reflect the true species trees.

The discordance between a gene tree and a species tree may also be caused by incomplete lineage sorting (ILS) of genetic polymorphisms that were retained across successive nodes in the species tree (Avise and Robinson, 2008; Naciri and Linder, 2015; García et al., 2017), although this problem is often unappreciated outside of the phylogenetics community. Methods of phylogenetic analysis that assume tree-like evolution may not be robust to histories that include interspecific hybridization, horizontal gene transfer or incomplete lineage sorting and gene duplication (Daubin and Szollosi, 2016; Solis-Leymus et al., 2016; Morales-Briones et al., 2022). Ultimately many phylogenies cannot properly be represented as a tree but should be thought of as a network (Linder and Rieseberg, 2004). One potential answer to this problem is network analysis (Posada and Crandall, 2001; Bapteste et al., 2013; Morales-Briones et al., 2018b, 2021), although network analysis may not be compatible with current taxonomic principles.

Another problem with determining evolutionary relationships from molecular phylogenetics or morphology results from less than adequate quality of the data (Sun et al., 2020). Robust taxonomic delineations require adequate sampling across and within putative taxa. Unfortunately, this has not always been the case (Lavin and Pennington, 2022). We would argue that populations from across the range of a taxon must be sampled adequately to determine the relationship with other closely related taxa. A single sample of a widespread species cannot represent that species when delineating taxa within a genus much less a genus within a family. Inadequate sampling is likely to generate distinct taxa that would be less distinct with more complete sampling. Regardless of these problems, many plant taxonomists promote nomenclatural changes relying on research involving insufficient taxon or genetic sampling. Many of these changes will not stand the test of time but will contribute to nomenclatural instability.

While a large proportion of plant systematists recognize the aforementioned potential problems, many non-taxonomic botanists may not realize that nomenclature changes based on less-than-adequate data continue to be published. We believe that it is fair to assume gene phylogenies may not always accurately reflect species phylogenies. We are not suggesting that taxonomic nomenclature should remain static, only that systematics studies based solely on molecular or morphological data, while presenting useful information, should refrain from proposing taxonomic changes until sampling is comprehensive and relevant branches of gene trees are consistently well-supported. In this way we can avoid a great deal of nomenclatural instability. Some botanists who write floristic treatments and some taxonomists who assemble databases assume that the most recent taxonomic treatments should be followed whether there are problems with sample size, marker choice, poorly supported phylogenies, or lack of consistency among data sets. We believe that it is fair to assume that gene-based or morphology-based phylogenies alone may not always accurately reflect species phylogenies. Therefore, when making or adopting nomenclatural changes, we suggest that phylogenetic studies should include the following hallmarks:

1. Comprehensive taxon sampling, i.e., species and genera represented by multiple conspecific and congeneric samples from throughout their geographic ranges.
2. Coherent results derived from at least ten multiple nuclear loci (Scott Edwards, Museum of Comparative Zoology, Harvard University, personal communication) or phylogenomic analysis of large regions of the nuclear genome (e.g., Escudero et al., 2020) because different regions of the genome can be impacted differently by evolutionary processes.
3. Relevant phylogenetic branches at the genus and family levels have high support and are congruent

with some additional combination of ecological, geographical, or morphological data (Doyle, 1992; Grant, 2003; Monro, 2022).

Ornithologists have, to some extent, dealt with the nomenclatural instability problem by having an elected group of experts, the American Ornithological Society (https://americanornithology.org), who decide what names should be used. A similar strategy has been proposed for all living organisms (Garnett and Christidis, 2017), but for plant taxonomy this is not likely to happen soon (Thomson et al., 2018). There are several taxonomic databases (e.g., IPNI [www.ipni.org], ITIS [www.itis.gov], Tropicos [www.Tropicos.org], USDA Plants [https://plants.usda.gov], Plants of the World [https://powo.science.kew.org]), but they do not necessarily arbitrate taxonomic nomenclature and they don't always agree on accepted names.

Biologists, especially those who compile floristic treatises or databases, should sufficiently consider whether taxonomic name changes are derived from a species tree rather than a gene tree. They should realize that in some cases proposed nomenclatural changes are simply evolutionary hypotheses, which need not be adopted if supporting evidence is weak. This can best be surmised using the guidelines listed above as well as provided by others (Monro, 2022). In the end, uncritical adoption of taxonomic nomenclature is one of the main causes of taxonomic name proliferation and nomenclatural instability. Taxonomy should reflect phylogeny as much as possible, but the phylogeny should be firmly established to reduce taxonomic instability. Most phylogenetic studies advance our knowledge of evolution to some degree. However, we believe that because taxonomic name changes affect the broader biological community, they should reflect not simply the most recent gene tree, but an assembly of congruent data derived from adequate sampling, statistical confidence, and congruence with non-genetic data. In this way taxonomy can serve the communication needs of ecologists, other biologists, and the field of evolutionary biology equally well.

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Both authors contributed equally to conceptualization as well as writing, reviewing, and editing the manuscript.

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No new data were generated for this manuscript.

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