Title: Phylogenomic conflict coincides with rapid morphological innovation

Authors: Caroline Parins-Fukuchi[a,1], Gregory W. Stull[b,c], Stephen A. Smith[d,1]

[a]Department of Geophysical Sciences, University of Chicago, Chicago, IL, USA

[b]Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650201, China

[c]Department of Botany, Smithsonian Institution, Washington, DC 20013, USA

[d]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109, USA

[1]To whom correspondence may be addressed. Email: parinsfukuchi@uchicago.edu or eebsmith@umich.edu.

Abstract

Evolutionary biologists have long recognized that rates of phenotypic change vary widely throughout time and across lineages. Researchers have been particularly fascinated with evolutionary 'radiations'--periods during which novel phenotypic characteristics and new species emerge at an unusually high rate. Despite considerable speculation and empirical testing of the geologic, environmental, and ecological contexts coinciding with the radiations of major lineages, our understanding of how population processes during these epochs contribute to emergent macroevolutionary patterns in phenotypic change remains poor. However, the increasing prevalence of phylogenomic datasets over the past decade has revealed that phylogenomic conflict, frequently caused by population-level processes, is often highest at the origin of major lineages. We reconstruct patterns in both rates of morphological change and levels of phylogenomic conflict across six clades to identify whether the large spikes in the rate of phenotypic change that accompany major radiations coincide with elevated conflict. We found that the most conflict-rich regions of the six clades also tended to experience the highest rates of morphological evolution, suggesting that the complex population processes that underlie evolutionary radiations leave signatures at deep phylogenetic scales in both genomic and phenotypic data. Thus, closer examination of the drivers and implications of phylogenomic conflict may permit us to make improved connections between micro- and macroevolution, vastly increasing our understanding of the processes that shape the origin of major lineages across the Tree of Life.

Introduction

Phylogenetic conflict, where gene-trees disagree about species tree resolution, is common across genomes and throughout the tree of life (Smith et al. 2015; Chen et al. 2017; Smith et al. 2020). Conflict is often driven by population processes such as incomplete lineage sorting (ILS), hybridization, and rapid evolution. Regions of high conflict often coincide with the emergence of major clades, such as mammals (e.g., Song et al. 2012), angiosperms (e.g., Wickett et al. 2014), and metazoa (e.g., Nosenko et al. 2013). This suggests that heterogeneity in the population

processes underlying the origins of modern biodiversity has been recorded in particular nodes across the tree of life (e.g., Smith et al. 2020, Leebens-Mack et al. 2019).

Most large-scale phylogenetic and phylogenomic studies meant to resolve species relationships have treated conflicting gene regions as an analytical nuisance to be filtered or accommodated (e.g., Song et al. 2012; Wickett et al. 2014; Leebens-Mack et al. 2019). However, since conflict might be thought of as the phylogenomic imprint of past population genetic processes, studying its correlation with other macroevolutionary patterns may shed light on the microevolutionary processes underlying major transitions across the tree of life. Researchers have long recognized that rates of morphological change vary across the tree of life, with pronounced bursts in morphological change interspersed with periods of relative stasis (Simpson 1944, Eldredge and Gould 1972). However, the relationship between rates of morphological change and genomic evolution is not well-understood. In particular, it may be worthwhile to examine whether phylogenomic conflict tends to coincide with periods of rapid morphological change. This may help to identify whether genomic conflict and morphological innovation detectable over macroevolutionary timescales stem from the same population processes.

Anecdotally, conflict often appears to coincide with important episodes of morphological differentiation among major lineages. For example, the major differences in life history and body plan that distinguish mammalian orders emerged rapidly following the K-Pg mass extinction (O'Leary et al. 2013). The phylogenetic resolution of these early diverging lineages has proved difficult and attempts at resolution have included the use of both sophisticated methodological approaches and the generation of large-scale genomic datasets (Morgan et al. 2013; Romiguier et al. 2013; Teeling et al. 2013). The early avian radiation has experienced similar challenges and is notable for the establishment of disparate lineages and morphological innovation leading the extant diversity. Several large-scale studies using massive genomic datasets have revealed extensive conflict among phylogenetic branches coinciding with the early radiation of crown Aves (Jarvis et al. 2014; Prum et al. 2015). Since the origin of land plants, there have been numerous major phases of morphological and ecological innovation, including the initial radiation of vascular plant body plans in the late Silurian (Kenrick and Crane 1997); the origination of major lycophyte and euphyllophyte structures (e.g., roots, megaphyllous leaves, seeds, wood) by the late Devonian or earlier (Gensel et al. 2020); radiations of ferns, seed ferns, and lycophytes with diverse life histories during the Carboniferous (Stewart and Rothwell 1993); radiations of various gymnosperm lineages in the Permian and different parts of the Mesozoic (Beck 1988); and distinct phases of angiosperm radiation from the Cretaceous to the present (Friis et al. 2011). As with the vertebrate lineages, the origins of many major plant clades show elevated levels of phylogenomic conflict. Many of these have been the subject of intense analysis and debate (e.g., Drew et al. 2014; Leebens-Mack et al. 2019; Smith et al. 2020) and recent sequencing efforts have failed to confidently resolve most of these challenges.

Here we examine whether periods of high genomic conflict coincide with episodes of rapid morphological evolution across several phylogenetically disparate clades. Many clades show qualitative evidence that time periods with particularly rampant conflict are often associated with important phenotypic changes. However, if phylogenomic conflict indeed represents the remnants of complex population processes that are adaptively important, we reasoned that there should be a correspondence between areas of high conflict and elevated rates of phenotypic evolution. To examine whether this is the case, we reconstructed concurrent patterns in phylogenomic conflict and phenotypic evolution across six major clades of the

eukaryotic tree of life: crown Aves, Mammalia, and four major lineages of vascular plants (Ericales, Caryophyllales, Polypodiopsida, and Acrogymnospermae).

Results

We assembled and analyzed six genomic datasets for plants, mammals, and birds. Specifically, we examined published phylogenomic datasets including 624 genes of Caryophyllales from Yang et al. (2018); 387 genes of Ericales from Larson et al. (2020); 1332 gene regions of Polypodiopsida from Shen et al. (2018); 1308 gene regions representing Acrogymnospermae from Ran et al. (2018); 424 genes of Mammalia from Song et al. (2012); and 259 gene regions of Aves from Prum et al. (2015). We gathered publicly available phenotypic matrices corresponding to each of these datasets (see Materials and Methods). For the Caryophyllales, a suitable morphological matrix is not available, and so we examined the phylogenetic locations of major changes in the betalain and photosynthetic pathways. Generally, broad phenotypic matrices that cover the taxa in each of these datasets are rare or non-existent. Furthermore, overlap between the genomic and phenotypic matrices was such that each needed to be reduced to ensure comparable edges were being compared. Divergence times continue to be controversial across the tree of life. To overcome these difficulties, we used one set of divergence times and one topology for both the morphological and molecular analyses (see Materials and Methods).

We found that mammals experienced elevated levels of conflict near the K-Pg boundary, coinciding in time with the origin of most placental orders (Fig. 1). We compared these genomic patterns to phenotypic rates calculated from two independent datasets: a dataset of mammalian body masses (Jones et al. 2009), which we interpreted as a proxy for many strongly correlated aspects of life history and ecology (Calder 1983), and a massive 'phenomic' matrix of >4000 qualitative characters (O'Leary et al. 2013). These analyses revealed that, in addition to witnessing extensive phylogenomic conflict, the epoch coinciding with the early divergence of major placental lineages also witnessed a peak in rates of phenotypic evolution. The two phenotypic datasets displayed remarkably similar patterns, showing that both life history and anatomical characteristics diversified rapidly during the early divergences of placental lineages. Unlike the angiosperm examples, but more similar to the fern and gymnosperms examples (albeit with an order of magnitude higher sampling of characters), the 'phenomic' dataset examined here sampled characters at all phenotypic levels. Although skeletal and dental characters comprised the majority of the dataset, characters representing internal and external organs, musculature, and behavior were also included. It has previously been recognized that the life history habits displayed by major mammalian lineages were established early during the radiation of major mammalian clades (Stearns 1983), but our analyses demonstrate that these changes occurred as rapid bursts during a single temporal episode that also witnessed both rapid rates of anatomical change and high phylogenomic discordance.

Our genomic analysis revealed rampant conflict among early-diverging avian lineages immediately following the K-Pg boundary (Fig. 1). We also identified an additional episode of increased conflict that occurred at the onset of the Miocene. We compared this genomic pattern to those displayed by two morphological datasets: a large qualitative character matrix (Livezey and Zusi 2007) and a dataset representing the scores calculated from the first three axes of a principal component analysis performed on a dataset of linear measurements that corresponded to body size, relative beak size, and relative wing size, respectively (Pigot 2019). In both phenotypic datasets, we found evidence for elevated rates of evolution during the epoch

immediately following the K-Pg, coincident with the elevated levels of genomic conflict. Although qualitatively similar in this regard, we found that each dataset displayed outliers in rate not shared by the other, with the qualitative character matrix displaying two instances of extremely high rate coinciding with the K-Pg boundary and the quantitative dataset displaying two such instances during the late Miocene. The outliers displayed by the qualitative dataset are consistent with the overall pattern of coincidence between episodes of conflict and rapid morphological change, differing from the quantitative dataset only in magnitude. However, we could not identify a clear explanation for the outliers present in the quantitative dataset. In addition to the congruence between patterns of conflict and phenotypic evolution near the K-Pg, the quantitative dataset displayed weak evidence for an overall increase in morphological rate coinciding with the Miocene increase in phylogenomic conflict. Although the qualitative dataset did not display a Miocene rate increase, this is likely a result of taxon sampling rather than biological reality, since the genomic data also fail to display the Miocene boost in conflict when the dataset is reduced to reflect the same taxa as the qualitative data matrix.

Acrogymnospermae (known colloquially as "gymnosperms") show dramatic and coincident spikes in genomic conflict and rates of morphological evolution, with several of these spikes occurring near major stratigraphic boundaries marked by mass extinction or, at least, major ecological upheaval (Fig. 2). The largest spike, for both conflict and innovation, occurs before the P-T boundary and corresponds to the divergence of Gnetales. The phylogenetic placement of this lineage has long been contentious, with different molecular datasets (or analytical methods) resulting in different topologies (e.g., Zhong et al. 2010). Morphologically, Gnetales is also highly derived, which has led to various hypotheses concerning its placement, including sister to angiosperms (Crane 1985), given that both lineages share several (presumably independently derived) traits such as vessels in the wood, net veined leaves (in some Gnetales), and siphonogamy, as well as flower-like sporangiate structures in Gnetales. Genomic datasets, however, appear to be reaching a consensus that Pinaceae may indeed be the closest living relative of this enigmatic order (e.g., Ran et al. 2018; Smith et al. 2020). Our results, which follow this placement of Gnetales (sister to Pinaceae), suggest that the divergence of the order involved a coordinated burst in both genomic and morphological evolution; the possible causes are unclear but deserve further study. Although no whole-genome duplications have been detected in the stem of Gnetales and polyploidy in gymnosperms is generally considered less common than in other vascular plant lineages (Leebens-Mack et al. 2019), this phenomenon has nevertheless been relatively understudied in gymnosperms. It is noteworthy that WGDs have been detected in two of the three genera comprising Gnetales, *Welwitschia* (Li et al. 2015) and *Ephedra* (Ickert-Bond 2020), with the latter including a large number of recently formed polyploids. Two of the other major (coincident) peaks in gymnosperms correspond to the divergence of Ginkgo and cycads (ca. 290 Ma) and the divergence of *Gnetum* and *Welwitchia* (ca. 114 Ma). As with the Gnetales divergence, these two spikes in morphological innovation include the acquisition of novel states spanning the plant bauplan (including, for example, changes in stem anatomy, leaf structure, microsporangia and pollen, and megasporangia and seeds). The monotypic genus *Welwitschia*, in particular, is characterized by highly unique and bizarre morphology, with continuously growing strap-shaped leaves that sprawl along the desert floor. The significance of WGD as a possible driver of phenotypic novelty in this genus deserved further study.

The Ericales also exhibit a high amount of conflict during their early evolution. This conflict coincides with the rapid evolution of perianth merism, androecial structure (e.g., stamen

number and anther orientation and attachment), and carpel number. Similar variation in floral morphology is evident in some of the earliest fossil representatives of this order (e.g., Schönenberger and Friis 2001; Crepet et al. 2013; Martínez et al. 2016) and likely relates to early co-evolution with insect pollinators, particularly hymenoptera (Crepet 1996; Nixon and Crepet 1993). This observed genomic conflict and innovation in floral morphology precedes the evolution of the major families and also correspond to several life history shifts and movements out of the tropics (Rose et al. 2018) occurring by ~79-90 MYA based on available fossil evidence (e.g., Crepet et al. 2013) and between ~100-110 based on molecular divergence-time estimates (Magallón et al. 2015; Rose et al. 2018). These early ecological shifts in the Cretaceous may have involved adaptation to fire-prone habitats of the mid-latitude Northern Hemisphere, based on taphonomic information from some of the earliest fossils (charcoalified flowers; Friis et al. 2011; Crepet et al. 2013).

In Polypodiopsida (=monilophytes, Pryer et al. 2001; or "ferns" more colloquially), as with gymnosperms, there are major coincident spikes in morphological rate and genomic conflict. These correspond to the most contentious deep nodes in fern phylogeny. The monilophytes are a heterogeneous assemblage of ancient lineages—including horsetails (Equisetiidae), marratioid ferns (Marattiidae), whisk and ophioglossid ferns (Ophioglossidae), and leptosporangiate ferns (Polypodiidae)—that trace back to the Devonian radiation of vascular plants ca. 393 to 359 Ma (e.g., Kenrick and Crane 1997; Gensel et al. 2020). Prior to phylogenetic analyses including molecular data (e.g., Pyrer et al. 2001), the lineages comprising the monilophytes were not thought to form a clade, but analyses have continued to recover this relationship with strong support (Pryer et al. 2001; Wickett et al. 2014; Leebens-Mack et al. 2019). However, relationships among the four major constituent lineages remain contentious (e.g., Shen et al. 2018; Leebens-Mack et al. 2019). Here, we show that the conflict underlying earliest divergences in monilophyte phylogeny coincides with pronounced phases of rapid morphological innovation. The two largest bursts (dated here at ca. 290 Ma and ca. 245 Ma) correspond, respectively, to the divergence of leptosporangiate ferns, and the split of marratioid and whisk/ophioglossid ferns (topology following Shen et al. 2018). Various aspects of morphological evolution across these lineages remain poorly known, including the origin(s) of megaphyll leaves, which show divergent morphologies and range from complex and highly diverse, to reduced, to entirely absent across the different groups of monilophytes (Harrison and Morris 2017). Major changes in sporangial structure also characterize (and serve as the namesake for) the largest extant monilophyte clade, the leptosporangiate ferns (Pryer et al. 2001). Overall, these pronounced bursts of rapid morphological innovation across the early radiation of monilophytes appear to correspond to major genomic upheavals. These events render the resolution of relationships difficult, but also may hold insight into the evolutionary origins of complex morphological features. It is likely that WGD played an important role in the early evolution of this group, as WGD events have been identified in all major monilophyte lineages, with events particularly clustered on the earlier branches of the monilophyte radiation (e.g., Leebens-Mack et al. 2019). In addition to other population level processes, WGD provides an important mechanism whereby major genomic changes/conflict may both signal and underlie major leaps in morphological novelty.

The Caryophyllales show substantial conflict at the edges preceding the emergence of the major clades that correspond to Linnean families (Fig 2). Based on available divergence times, these conflicts occurred between ~59-101 MYA with the most extensive conflict at ~77 MYA. In particular, there are hotspots of conflict along the backbone of the "core Caryophyllales" and

then several within the Caryophyllaceae and Phytolaccaceae+Nyctaginaceae. Major floral innovations have been observed along these nodes including changes in the number and configuration of perianth and androecial parts (e.g., Brockington et al. 2009, 2013); the lineages stemming from these nodes have been claimed to show the highest diversity in androecial patterns among all flowering plants (Ronse De Craene 2013; Ronse De Craene and Brockington 2013). Morphological sampling beyond floral characters would likely reveal other major instances of innovation given the many distinctive phenotypic features documented across this ecologically diverse clade (e.g., betalain pigments, carnivory, succulence, successive cambia). In particular, successive cambia and betalains likely evolved in high-conflict areas of the Caryophyllales backbone (e.g., Carlquist 2010; Brockington et al., 2011; Timoneda et al. 2019), and both traits show complicated yet intriguing patterns of presence/absence across the phylogeny. We found that genetic innovations in the betalain pathway, major whole genome duplications, and transitions in photosynthetic pathways transitions throughout the evolution of the group experienced an increase in evolutionary rate coinciding with the highest peak in gene-tree conflict (Fig. 2).

Discussion

We demonstrate that several instances of high phylogenomic conflict correspond to instances of high morphological innovation. This has implications for understanding both phylogenomic conflict and morphological evolution. First, biological processes, perhaps in addition to error, have a large impact on the patterns of conflict, even at deep time scales and when filtering for strongly supported signals. That biological processes can cause conflicting signals in gene-trees is well known. However, typically, researchers attempt to overcome this conflict through modeling or methodological developments intended to construct a species tree. We suggest that conflict itself is important to dissect and not just accommodate in phylogenetic reconstruction. Importantly, we do not suggest a perfect correlation between instances of morphological novelty and conflict. There are many processes that might lead to increases in both of these measures and so it is unlikely that there will be an exact correspondence of rapid morphological rates and conflict at all nodes across the tree of life. Nevertheless, we suggest that the events that led to high conflict in the past (e.g., dramatic episodes of population expansion or contraction during rapid speciation events) had such a large impact that many aspects of these lineages, including morphological evolution, were significantly affected.

Disentangling the sources of conflict within phylogenomic datasets is fraught with difficulties. In the datasets examined here, while there may be instances of hybridization and, to a lesser extent, horizontal gene transfer that are contributing to the patterns of conflict, there is no published evidence that these phenomena are the source of biological conflict at the nodes that correspond to morphological innovation. There has been some suggestion of ancient hybridization early in the Caryophyllales (e.g., Morales-Briones et al. 2019); however, there are challenges of identifiability that have yet to be overcome. Whole genome duplications (perhaps in many cases stemming from hybridization, i.e., allopolyploidy events) may also result in conflicts across the tree of life, especially as they may create errors as a result of misidentified paralogy. Other systematic errors and background noise may be a source of conflict, especially when exacerbated by rapid evolution (Smith et al. 2020; Larson et al. 2020). Furthermore, conflicts may be the result of errors due to uncertainty resulting from rapid evolution. Finally, incomplete lineage sorting has been recognized as a major source of gene-tree disagreement at all depths of the tree of life (Maddison and Knowles 2006). Conflicts due to incomplete lineage

sorting will be exacerbated by changes in population processes such as changes in effective population size from selection, bottlenecks, or other phenomena and/or rapid evolution (Pease and Hahn 2013). While errors also, undoubtedly, have contributed to some of the conflict we document, the vast majority of the nodes we highlight have been demonstrated to be difficult to resolve using multiple data types and analytical techniques (Jarvis et al. 2014; Prum et al. 2015; Wickett et al. 2015; Walker et al. 2017; Leebens-Mack et al. 2019; Larson et al. 2020).

One notable attribute of several of the clades examined (e.g., Ericales, Caryophyllales) is that many phenotypic traits show complex patterns of presence/absence across lineages stemming from regions of high conflict. In most cases, such a distribution of states would be interpreted as independent gains and losses (i.e., homoplasy). However, it is possible that the inheritance of phenotypic traits, from a polymorphic ancestral population, might in some cases follow an ILS-like process (i.e., hemiplasy; Avise and Robinson 2008; Guerrero and Hahn 2018). If the genes underlying phenotypic traits are subject to ILS, it follows that phenotypic traits themselves are also subject to this process. This might serve as a better explanation than independent gains/losses for complex distributions of phenotypic states in some clades. Hypothetically, this would imply that patterns of trait evolution during rapid “adaptive” radiations in some cases might be partly or largely stochastic--a byproduct of the sorting of underlying genetic variation. However, combinations of traits inherited through such a process could subsequently prove adaptive. These possibilities are speculative but deserve further attention, although demonstrating ILS-driven phenotypic evolution at macroevolutionary scales would likely be a major challenge.

We suggest that population processes occurring episodically in the past exacerbated gene-tree conflict and were correlated or causal in generating new morphological innovations. A link between population processes and phenotypic innovation has long been theorized (Wright 1932). Although the specific relationship between microevolutionary processes and phenotypic changes observable at a macroevolutionary scale is not well-understood, previous work has considered how demographic events such as rapid fluctuations in population size and and genic exchange between diverging populations might work synergistically with subsequent environmental adaptation to drive the exploration of diverse areas of morphospace by facilitating the emergence of both new phenotypic features and novel combinations of character states (Simpson 1944, Marques et al. 2019, Parins-Fukuchi 2020, McGee et al. 2020). Importantly, these processes are also likely to cause phylogenetic conflict if they persist over many generations and coincide with lineage divergences. We therefore suggest that phylogenomic conflict observable at deep timescales may often stem from the same population processes that facilitated the rapid and dramatic episodes of phenotypic change underpinning the radiation and morphological diversification of major clades. For example, the rapid speciation events that occur during evolutionary radiations may both generate conflicting phylogenomic signal due to population-level processes (e.g. rapid fluctuations in population size and selection) and drive the emergence of novel morphologies as diverging lineages carve out new ecological niches. In particular, a large population size will result in a smaller probability that two lineages will coalesce within a particular time. This should result in high conflict between gene trees. Several episodes of high conflict observed here (for example, in Ericales) are succeeded by periods of low conflict. This would suggest population size reduction if ILS can safely be assumed to be the source of conflict.

In addition to the notable coincidence of nodes with high conflict and rapid morphological innovation, many of these nodes also appear to correspond with major geologic

events. As has long been observed, major radiations in mammals and crown birds seem closely tied to the KPg mass extinction; our results here linking conflict to morphological innovation hint at underlying processes that may have driven these radiations into the wake of KPg ecological collapse. Gymnosperms and ferns show coincidence spikes near the Permian-Triassic boundary, another widely studied mass extinction event (Benton and Twitchett 2003). But given our limited sampling of these particular clades, this association is much more tenuous. Unfortunately, examining these patterns in greater detail requires a reliance on accurate divergence times, which are challenging to estimate from molecular phylogenies. A better integration of fossil and phylogenomic data may offer a clearer understanding of how major geologic events have influenced coordinated bursts of conflict and phenotypic innovation.

Conclusion. This study provides an important link between genomic and morphological evolution at deep timescales. We suggest that episodic evolutionary and population events leave signatures of conflict within genomes that may offer important insight on the processes responsible not only for conflict but also for massive changes in phenotype across disparate lineages. Moving forward, we suggest that closer examinations using more densely sampled molecular and morphological datasets representing taxa across the tree of life will help us to generate a deeper understanding of the micro- and macroevolutionary processes that drive major organismal changes from the genomic to the phenotypic level.

Materials and Methods

Genomic datasets. We examine several published phylogenomic datasets including 624 loci of Caryophyllales from Yang et al. (2018); 387 loci of Ericales from Larson et al. (2020); 1332 loci of ferns from Shen et al. 2018; 1308 loci of gymnosperms from Ran et al. (2018); 424 loci of mammals from Song et al. (2012), respectively; and 259 loci of Aves from Prum et al. (2015). Species trees were all based on those presented in the original publications. Gene trees were re-estimated using iqtree (v. 1.6.11) with support calculated using the approximate likelihood ratio test (-alrt 1000) and with the GTR and Γ model for nucleotides (-m GTR+G) and the LG and Γ model for amino acids (-m LG+G).

Morphological datasets. Large morphological datasets for major clades of flowering plants are surprisingly few, and additionally most available datasets are relatively limited in their sampling of either taxa and/or characters. For the Caryophyllales, we coded characters representing genome duplications (from Yang et al. 2018), presence of betalains, betalain pathway related duplications (from Sheehan et al. 2020), and photosynthetic pathway type (i.e., C3, C4, and CAM). This matrix is available in the data supplement. For the gymnosperms, we used the published data from Nixon et al. (1994) where the data are primarily scored at family level. The taxon circumscriptions applied in Nixon et al. (1994) for their OTUs are monophyletic and consistent with our current understanding of gymnosperm phylogeny, and thus were applicable to the clades examined here. Thus multiple exemplars within a clade corresponding to one of their OTUs will be identical in their states. For the Ericales, we used the published matrix developed by Chartier et al. (2017) focused on floral characters. For mammals, we used the O'Leary et al. (2013) published dataset that covers mammal morphology broadly as well as body size data gathered from the panTHERIA database (Jones et al. 2009). For the ferns, we used the morphological dataset from Pryer et al. (2001), which was developed for analysis of fern (i.e.,

monilophyte) relationships within the context of vascular plant phylogeny. Finally, for the birds, we used the morphological matrix compiled by Livezay and Zusi (2007) as well as the principal component scores calculated from the large dataset of linear measurements presented by Pigot et al. (2019). Many of the morphological datasets were sampled across more taxa than the genomic datasets-- in these cases, we pruned the morphological datasets to include only the taxa present in the genomic data.

Phylogenomic analyses. Conflict analyses were conducted with the program ***bp*** (available from https://github.com/FePhyFoFum/gophy) using species and gene trees. We used the options -tv to print the concordance, conflict, and noninformative values back to the species tree and -scut 80 to ignore edges that had less than 80% for the aLRT statistic as calculated from the iqtree analyses.

Divergence-time analyses. Although divergence-time estimates were not required for conflict analyses, they were required for calculating rates of morphological evolution. They are also useful for visualizing the concurrence of conflict and morphological innovation and placing these in a geologic context. Therefore, for each dataset, regardless of the source of divergence time estimates, both the morphological and genomic phylogenies used the same dated tree. The Aves phylogeny used the published dates from Prum et al. (2015). The final pruned topology contained 82 taxa matching both the morphological and genomic datasets, from an original 198. The Caryophyllales dataset uses divergence time estimates from Smith et al. (2017) with a final topology of 166. For the Ericales dataset, we used the divergence times and topology from Chartier et al. (2019). For the fern dataset, we used the divergence times and topology from Shen et al. (2018). For the gymnosperms dataset, no suitable dated phylogeny was available. Instead we used the topology from Ran et al. (2018) and then constructed a set of calibrations based on the available fossil data as well as divergence times available in TimeTree (Supplemental Text). For the mammal dataset, we used the chronogram produced in the course of the original genomic study (Chen et al. 2017).

Morphological analyses. We calculated rates of discrete character evolution by estimating the number of character transitions using parsimony occurring along each phylogenetic branch and dividing this estimate of the amount of character divergence along each branch by the amount of time represented by the corresponding branch in the time-scaled tree. Rates calculated from discrete-character matrices were therefore presented in units of inferred character transitions per unit time. For quantitative traits, we calculated the average character divergences along each branch by estimating ancestral states for each character under a Brownian motion model of evolution and then representing the amount of change along each edge as the absolute value of the difference between the trait value inferred for the ancestor and that displayed by the descendant. Like with the qualitative analyses, we then transformed these raw divergences to rates by calculating their ratio to the corresponding amount of elapsed time for the corresponding edge in the timetree.

Selection of species tree topology: We used the same topology for both the morphological and molecular analyses. Conflict and morphological rates were mapped onto the species tree resolved in the study from which the genomic data were sourced.

Data availability

Gene trees and dated species trees for each of the datasets examined are available from Figshare.

Figures

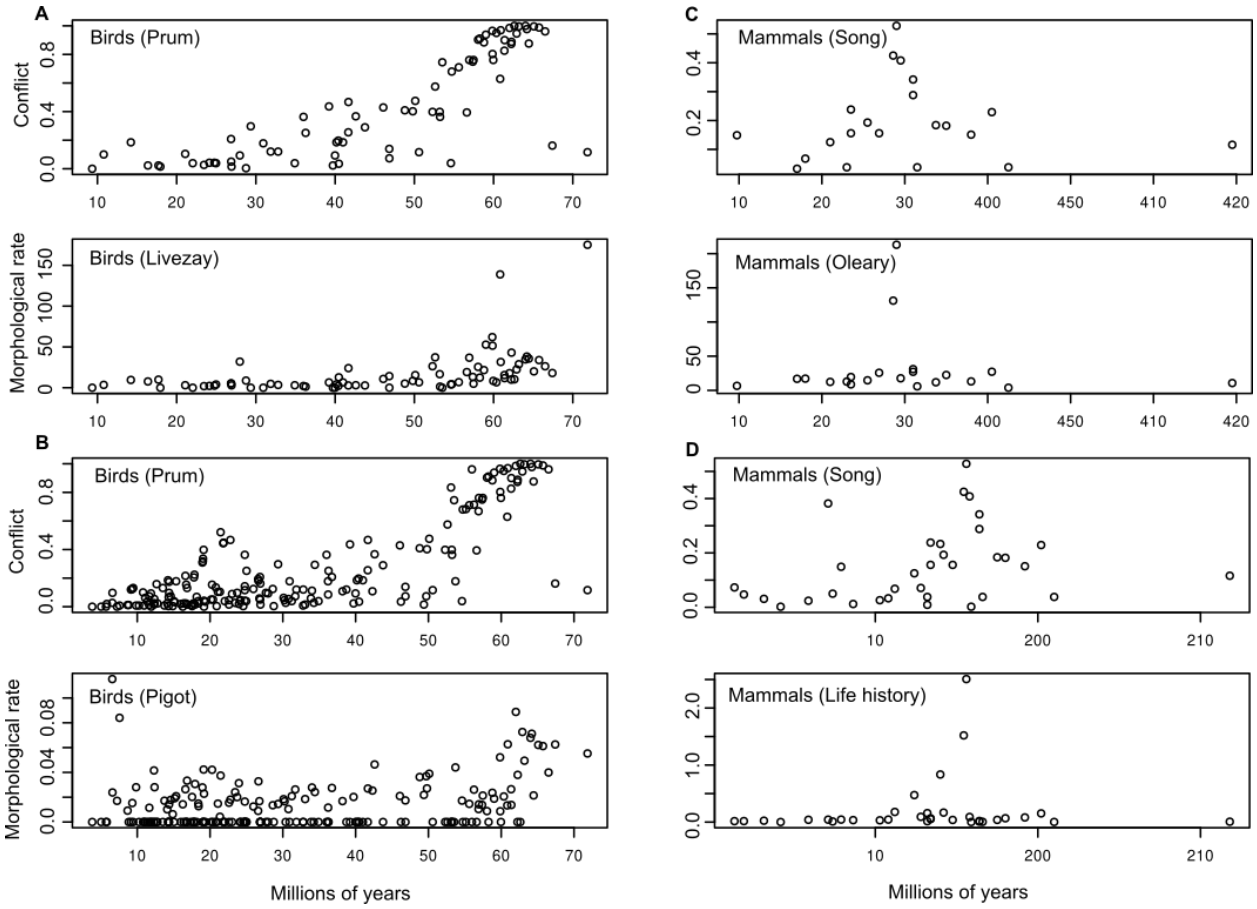

Figure 1. Co-occurring patterns in gene-tree conflict and morphological rates of evolution across bird and mammal datasets.

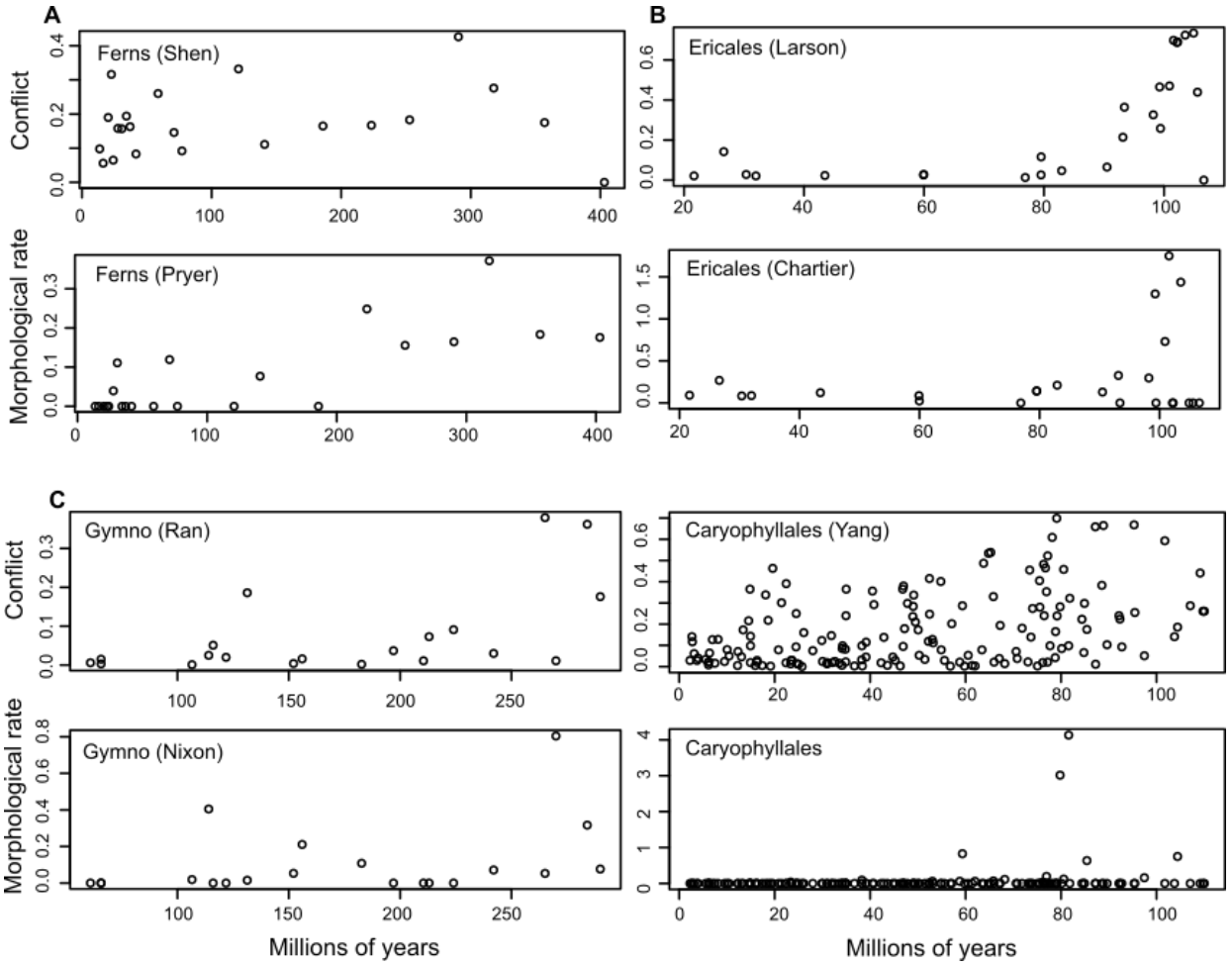

Figure 2. Co-occurring patterns in gene-tree conflict and morphological rates of evolution across major plant clades.

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