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Review

Reticulate evolution: Detection and utility in the phylogenomics era

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ABSTRACT

Phylogenomics has enriched our understanding that the Tree of Life can have network-like or reticulate structures among some taxa and genes. Two non-vertical modes of evolution – hybridization/introgression and horizontal gene transfer – deviate from a strictly bifurcating tree model, causing non-treelike patterns. However, these reticulate processes can produce similar patterns to incomplete lineage sorting or recombination, potentially leading to ambiguity. Here, we present a brief overview of a phylogenomic workflow for inferring organismal histories and compare methods for distinguishing modes of reticulate evolution. We discuss how the timing of coalescent events can help disentangle introgression from incomplete lineage sorting and how horizontal gene transfer events can help determine the relative timing of speciation events. In doing so, we identify pitfalls of certain methods and discuss how to extend their utility across the Tree of Life. Workflows, methods, and future directions discussed herein underscore the need to embrace reticulate evolutionary patterns for understanding the timing and rates of evolutionary events, providing a clearer view of life's history.

1. Introduction

Phylogenomics – phylogenetic analysis using genome-scale data – has been used to infer the evolutionary history of diverse lineages across the Tree of Life, including animals, fungi, plants, bacteria, archaea, and viruses (Dunn et al. 2008; Misof et al. 2014; Wickett et al. 2014; Worobey et al. 2016; Simion et al. 2017; Parks et al. 2018; Shen et al. 2018; One Thousand Plant Transcriptomes Initiative 2019; Zhu et al. 2019; Coleman et al. 2021; Galindo et al. 2021; Li et al. 2021; Tahon et al. 2021). These studies have resolved numerous phylogenetic controversies, deepening our understanding of life's history (Capella-Gutiérrez et al. 2012; King and Rokas 2017; Williams et al. 2019; Pipes et al. 2021; Steenwyk et al. 2023 Jun 27). Phylogenomics has also proven useful for delineating lineage relationships at taxonomic scales ranging from species to higher-order taxa (Díaz-Tapia et al., 2017; Muñoz-Gómez et al. 2017; Mateo-Estrada et al. 2019; Bringloe et al. 2021; Steenwyk, Balamurugan, et al. 2022; Sierra-Patev et al. 2023). Species trees inferred using phylogenomics provide the framework for comparative evolutionary genomic studies, such as determining gene duplication and loss events or studying phenotypic innovation (G. Zhang et al. 2014; Steenwyk, Opulente, et al. 2019; Fernández and Gabaldón 2020; Shen et al. 2020; Phillips et al. 2021; Li et al. 2022 Nov; Opulente et al. 2023; Title et al. 2024).

Incongruence between the evolutionary histories of single loci and organisms (locus-tree-species-tree incongruence or discordance) can arise from various biological processes (Steenwyk et al. 2023 Jun 27). This includes two processes of reticulate evolution – hybridization/introgression and horizontal gene transfer – that are so categorized because they involve genetic exchange among distinct evolutionary lineages. In contrast, incongruence can also be caused by several within-lineage processes, including incomplete lineage sorting, recombination, and gene conversion. The purpose of this review is to outline methods of detecting and distinguishing the phylogenomic incongruence patterns that arise from reticulate (among-lineage) evolutionary processes as distinct from those that arise from within-lineage processes. We will first define these reticulate processes and then outline a full phylogenomic workflow for diagnosing the most likely causes of detected incongruence patterns.

Hybridization/introgression – the sexual interbreeding between divergent lineages – has been documented in plants, algae, fungi, animals, and other lineages, and can disrupt inferences of both the timing and pattern of historical divergences (Rieseberg et al. 2007; Neafsey

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et al. 2010; Stukenbrock 2016; Mixão and Gabaldón 2020; Steenwyk, Lind, et al. 2020; Wang et al. 2022). Among humans, loci originating from admixture events between early humans and Neanderthals have been associated with adaptation, phenotypic variation, and disease risk, including for severe COVID-19 (Sankararaman et al. 2016; Simonti et al. 2016; Dannemann et al. 2017; Dannemann and Kelso 2017; Zeberg and Pääbo 2020). Hybridization can also result in allopolyploidy wherein the genome of the hybrid organism encodes (nearly) the entire genome of both parents. Allopolyploidy has been observed in numerous plants, fungi, and a few vertebrates (Ozkan et al. 2001; Session et al. 2016; Edger et al. 2019; Steenwyk, Lind, et al. 2020; Chen et al. 2022; Session and Rokhsar 2023). Genome evolution in allopolyploids can be rapid – marked by pronounced loss of genetic material (Ozkan et al. 2001) – or relatively stable, resulting in retention of both parental genomes (Steenwyk, Lind, et al. 2020; Steenwyk et al. 2023; Salojärvi et al. 2024). In either case, introgression/hybridization results in novel combinations of genes and genetic backgrounds that can, in turn, lead to distinct phenotypic profiles (Steenwyk, Lind, et al. 2020; Bautista et al. 2021).

Another mode of reticulate evolution, horizontal gene transfer (or lateral gene transfer) – the transfer of genetic material without sexual reproduction – also causes discordance between locus trees and the organismal history. Horizontal gene transfer has been documented in diverse organisms, especially among prokaryotes and archaea (Galtier 2007; Yue et al. 2012; Van Etten and Bhattacharya 2020; Arnold et al. 2022; Gonçalves and Gonçalves 2022; Gophna and Altman-Price 2022; Li et al. 2022; Steenwyk et al. 2023). Horizontal gene transfer can be advantageous, endowing recipient organisms with potentially novel functionality (Gonçalves and Gonçalves 2019; Kominek et al. 2019; Li et al. 2022). In certain cases, complex patterns of horizontal gene transfer or lateral acquisition of entire gene clusters can occur, resulting in new metabolic capabilities such as alcohol fermentation and the biosynthesis of thiamine and siderophores in yeast (Gonçalves et al. 2018; Gonçalves and Gonçalves 2019; Kominek et al. 2019). Horizontally acquired genes can also facilitate adaptation to extreme environments. For example, ice-binding proteins originating from bacteria are thought to contribute to algal adaptation to Arctic environments (Dorrell et al. 2023), and mercuric reductase, an enzyme responsible for converting mercury to a less toxic form, was transferred from bacteria to extremophilic algae commonly isolated from environments with a high mercury concentration (Schönknecht et al. 2013). Among protists, approximately 1 % of gene repertoires are estimated to have been horizontally acquired (Van Etten and Bhattacharya 2020). Among plants and animals, horizontal gene transfer events appear to be far more rare, but the transfer of microbial loci has been detected in some lineages (Yue et al. 2012; Li et al. 2022) and the exchange of transposable elements among lineages may be more common than previously expected (Osmanski et al. 2023). These observations emphasize the significance of horizontal gene transfer as a major evolutionary mode across the tree of life.

Here, we briefly outline notable steps for species tree inference – a common prerequisite for detecting reticulate evolution – and then compare methodologies for detecting and differentiating reticulate evolution from other biological factors contributing to incongruence between loci and organismal histories, such as incomplete lineage sorting, recombination, and gene conversion. In doing so, we aim to also pinpoint current considerations and identify future avenues for methodological advancement in detecting reticulate evolutionary processes using phylogenomic data and methods. To do so, We also discuss how determining the relative timing of introgression/hybridization and horizontal gene transfer can inform the order of speciation events. For a more in-depth discussion of analytical sources of phylogenomic incongruence and methods to mitigate them, we refer the reader to previously published literature (e.g., (Philippe et al. 2017; Kapli et al. 2020; Steenwyk et al. 2023 Jun 27)). We also acknowledge that reticulation encompasses several evolutionary processes and that there are existing literature reviews for individual topics. Thus, throughout this review, we point the reader to other reviews and key literature – for example, see (Xu 2000; Spencer et al. 2006; Keeling and Palmer 2008; Mallet et al. 2016; Stapley et al. 2017; Lorenz and Mpaulo 2022) for articles on recombination, gene conversion, hybridization, horizontal gene transfer, and phylogenetic analysis in the presence of reticulate processes. The application and development of these methods holds promise for unraveling the confluence of evolutionary processes that shape the Tree of Life.

2. Overview of a phylogenomic workflow

The first step of phylogenomic tree inference involves acquiring high-quality genomic/transcriptomic data from the target taxa (Fig. 1A) (Cheon et al. 2020; Kapli et al. 2020; Turnbull et al. 2023). We note that best practices for generating new sequence data involve depositing voucher specimens (preserved whole organisms and/or tissues) in an accredited biorepository for use by future researchers (Buckner et al. 2021). Moreover, phylogenetic inference using genomes and transcriptomes may require specific considerations, such as transcriptomes having more transcripts than genes (Cheon et al. 2020).

Thereafter, orthology inference is conducted among gene sequences (nucleotide or amino acid) encoded in the genomic/transcriptomic data. Relationships among orthologous genes can be described as one of three categories: one-to-one, one-to-many, and many-to-many (Fernández et al. 2019). Considering two haploid genomes, one-to-one orthologs are encoded in each genome once; one-to-many orthologs are encoded in one genome once and the other multiple times (implying gene duplication or loss); and many-to-many orthologs refer to a gene with multiple copies in each genome. Species tree inference often relies on one-to-one orthologs as phylogenomic markers because they (presumably) have not experienced duplication or loss (Li et al. 2017). Because phylogenomic markers can also be noncoding sequences, the reasoning extends to loci more generally, not just genes. Single-copy orthologs are often the substrate of many downstream molecular evolutionary analyses, such as selection measures, relative evolutionary rates, and gene-gene coevolution (Chikina et al. 2016; Kowalczyk et al. 2019; Steenwyk et al. 2021; Steenwyk, Phillips, et al. 2022; Álvarez-Carretero et al. 2023). Alternatively, predetermined phylogenomic markers may be used, such as in RADseq, where restriction enzymes are used to select markers, or the use of near-universally single-copy genes from OrthoDB or similar databases (Eaton and Ree 2013; Waterhouse et al. 2018; Kriventseva et al. 2019).

Once a curated set of phylogenomic markers has been obtained, the next step is multiple sequence alignment and trimming of each marker individually (Fig. 1C). Multiple sequence alignment aims to determine the site-wise homology across a group of sequences, typically derived from different organisms (Katoh and Standley 2013; Sievers and Higgins 2018; Edgar 2022). Thereafter, alignments for each marker are commonly subjected to trimming, which involves the removal of specific sites or blocks of sites within the alignments (Talavera and Castresana 2007; Criscuolo and Gribaldo 2010; Tan et al. 2015; Steenwyk, Buida, et al. 2020). Next, an optimal model of sequence evolution is determined for each alignment for use in conducting phylogenetic inference (Kapli et al. 2020). The resulting single-locus phylogenies represent the inferred genealogical history for that locus among the sampled taxa.

Species tree inference often follows, which seeks to unite information from the genealogical histories among the sampled markers. Two commonly used approaches for species tree inference from genome-scale datasets are multiple sequence alignment concatenation (or simply concatenation) and coalescence (Fig. 1D) (Rokas et al. 2003; Liu, Yu, Kubatko, et al. 2009; Steenwyk et al. 2023 Jun 27). Each approach employs a different theoretical framework. Concatenation places the multiple sequence alignments from each marker end-to-end (concatenates them column-wise) to form a supermatrix, which then may be analyzed using a single model of sequence evolution or else partitioned with separate models for different markers or sites (e.g., third codon

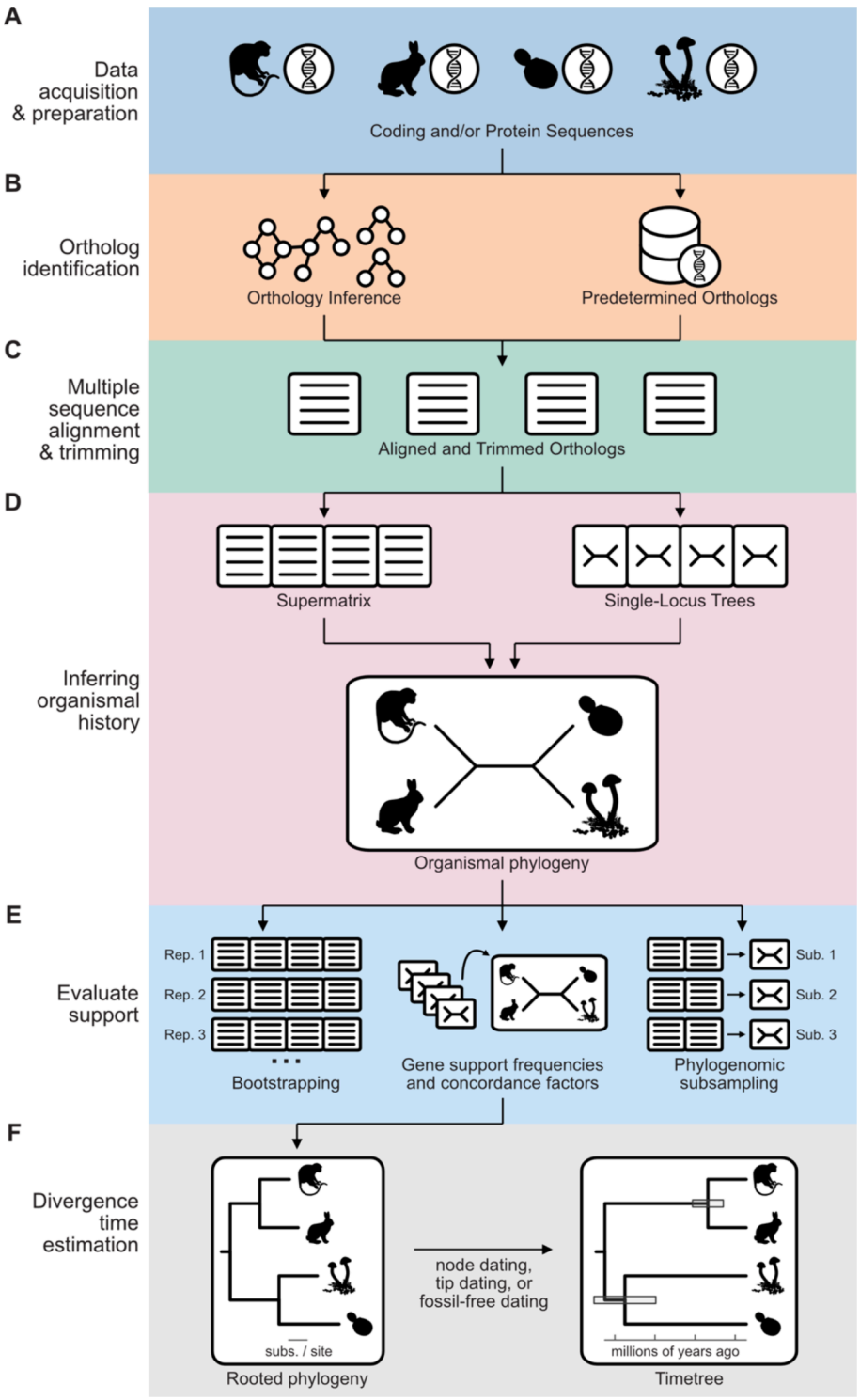

Fig. 1. A workflow for phylogenomic inference. (A) The first step in a phylogenomic workflow is data acquisition and preparation. This often entails identifying gene boundaries in genome assemblies or assembling transcripts in transcriptomes. (B) The next step is to identify orthologs using (left) *de novo* approaches – for example, all-by-all sequence similarity calculations followed by graph-based clustering – or (right) from predetermined sets of orthologs. (C) Orthologous groups of genes suitable for phylogenomics (i.e., one-to-one orthologs and SNAP-OGs) are subsequently aligned and trimmed. (D) The resulting multiple sequence alignments can be (left) concatenated into a supermatrix or (right) collections of single-locus phylogenies can be used in a coalescence-based approach. (E) Support for the inferred phylogeny can be evaluated using multiple approaches, such as bootstrap statistics, gene support frequencies / concordance factors, and phylogenomic subsampling. (F) Divergence time estimates can be inferred using node dating, tip dating, or fossil-free analyses. Branch lengths represent substitutions per site in the phylogeny on the left and time on the right. Grey boxes in the timetree represent confidence intervals. Silhouette images were obtained from PhyloPic (https://www.phylopic.org/); credit goes to their respective contributors.

positions may evolve faster than first or second positions and different protein domains may benefit from distinct substitution models; (Kainer and Lanfear 2015)). Concatenation approaches either assume that all locus trees reflect the same species tree or that all locus trees are independent of each other and the species tree (Edwards et al. 2007; Gatesy et al. 2017). In contrast, coalescence relies on the multi-species coalescent model, which jointly accounts for discordance between locus trees and the species tree stemming from processes like incomplete lineage sorting (i.e., when locus histories fail to coalesce before species divergence, as viewed from the present (Edwards et al. 2007)). There are two main coalescent-based approaches. In the one-step coalescent approach, single-locus phylogenies are estimated simultaneously with the species tree (Liu et al. 2008; Yang and Rannala 2010; Douglas et al. 2022). In two-step coalescent approaches, single-locus phylogenies are individually inferred and then used to construct a summary species-tree phylogeny (Liu, Yu, Pearl, et al. 2009; Zhang et al. 2018).

Support for the resulting phylogeny can be assessed using, for example, bootstrapping, single-locus or −site support frequencies (also known as concordance factors), and phylogenomic subsampling (Fig. 1E) (Edwards 2016; Zhang et al. 2018; Minh et al. 2020; Steenwyk et al. 2021; Steenwyk et al. 2023 Jun 27). Gene support frequencies coupled to concatenation tree inference can also help determine how common the topology is among single-locus trees. Calculations of internode certainty may help to determine if single-loci support one or more competing hypotheses (Salichos and Rokas 2013; Salichos et al. 2014). Thus, comparing topologies from concatenation with partitioned loci or coalescent approaches relative to those from single-locus trees is a powerful method to evaluate support for a putative species tree.

Additional parameters to consider during phylogenomic inference, including ways to identify and ameliorate analytical sources of error, are reviewed elsewhere (Philippe et al. 2017; Kapli et al. 2020: 20; Steenwyk et al. 2023 Jun 27). Furthermore, although we focused on multiple sequence alignment-based phylogenomics, we acknowledge the relevance of relatively new alternative data types in the phylogenomic era, such as synteny, retrotransposon insertion, and structure (Doronina et al. 2019; Moi et al. 2023; Parey et al. 2023; Schultz et al. 2023 May 17; Steenwyk and King 2024).

3. Reticulate Evolution: Identification and relevance of relative divergences

Reticulate evolutionary processes of hybridization/introgression and horizontal gene transfer result in loci that record different evolutionary histories than the whole organism (Dobzhansky 1982; Abbott et al. 2013; Steenwyk et al. 2023 Jun 27). There are diverse outcomes for hybridization ranging from adaptive changes due to ecological selection or compromised viability or fertility due to hybrid incompatibilities (Racimo et al. 2015; Moran et al. 2021). For example, due to hybridization, sunflowers have adapted to novel environments and reabsorbed incipient species (Mallet 2005; Mallet 2008; Racimo et al. 2015; Buck et al. 2023). Hybrid progeny can have improved growth and reproductive success or be sterile (Zanewich et al. 2018; Qiao et al. 2019; Allen et al. 2020; Adavoudi and Pilot 2021). Similarly, horizontal gene transfer endows recipient organisms with novel genetic material and can be adaptive (Schönknecht et al. 2013; Gonçalves and Gonçalves 2019; Arnold et al. 2022; Gophna and Altman-Price 2022; Li et al. 2022; Dorrell et al. 2023). For example, hybridization has been observed in microbial pathogens and thus may contribute to higher or lower organismal virulence (Lin et al. 2009; Depotter et al. 2016; Mixão and Gabaldón 2020).

3.1. Signatures of hybridization/introgression across the genome, gene trees, and sites

Comparative genomic and phylogenetic methods are available for identifying hybridization/introgression events (Scannell et al. 2006; Marcet-Houben and Gabaldón 2015; Ortiz-Merino et al. 2017; Mixão and Gabaldón 2020; Steenwyk, Lind, et al. 2020; Steenwyk et al. 2023). (Note, we use the terms hybridization and introgression interchangeably throughout the manuscript.) In the context of allopolyploid hybrids – where the genome of the hybrid organism contains (nearly) the complete genetic complement of both parental genomes and, therefore, two or more copies of most genes – ancient events can be identified by a burst of gene duplications and are supported by other lines of evidence such as synteny information (Chain et al. 2011; Marcet-Houben and Gabaldón 2015; Session et al. 2016). For example, the allopolyploid event leading to the radiation of Hawaiian mints was identified by signatures of ancient hybridization coupled with subgenome duplication (Tomlin et al. 2024).

Among phylogenetic approaches, it is crucial to discriminate between incongruences among single-locus phylogenies stemming from hybridization between species versus incomplete lineage sorting – the random sorting of ancestral alleles that can, at times, result in single-loci with evolutionary histories distinct from the organismal history (Yu et al. 2013). Hybridization is favored when two nearly equally supported topologies (one of which is the species tree) are found among genome-wide single-locus phylogenies, which should especially be the case if hybridization was a recent event. Incomplete lineage sorting is favored when three topologies are observed equally frequently for a given node, especially among cases of more recent divergences (Steenwyk, Shen, et al. 2019); roughly equal frequency of the three topologies is indicative of random sorting of the ancestral alleles. The expected degree of incongruence stemming from incomplete lineage sorting can be modeled using the multispecies coalescent model. Deviations from that model, such as more incongruence than expected, may also be evidence of a past hybridization event (Degnan and Rosenberg 2009).

Hybridization events can also be detected using frequencies of site patterns within a phylogenetic framework (Hibbins and Hahn 2022). For example, the D-statistic (or the ABBA-BABA test) is one pioneering approach in this area that leverages expectations about biallelic site patterns along a phylogeny (Fig. 2A-E) (Green et al. 2010). Specifically, if the ABBA-BABA test detects asymmetric support between ABBA and BABA patterns at biallelic sites, then an introgression/hybridization event is suggested; in contrast, equal proportions of ABBA and BABA site patterns suggest the absence of introgression/hybridization and instead favor incomplete lineage sorting as the primary source of incongruence. Leveraging genome-scale data, the ABBA-BABA test can accurately quantify introgression across a wide parameter space (Zheng and Janke 2018). Variants of this test that leverage five taxa instead of four can further polarize the directionality of past introgression but are limited to symmetrical tree topologies (Eaton et al. 2015; Pease and Hahn 2015). ABBA-BABA and related tests benefit from a wealth of loci and, given that they are restricted to certain numbers of taxa, extensive locus sampling is important to obtain high-resolution.

Analytical factors challenge the detection of ancient hybridization/introgression events using these methods, such as the inherent difficulty of detecting site-wise orthology and saturation by multiple substitutions. Evaluating the limits of these methods to ancient events remains underexplored and is an avenue for future research. Alternatively, new approaches specifically tailored for detecting ancient hybridization may be needed. For example, branch-length tests of hybridization may not work for ancient events due to asymmetric evolutionary rates through time. Researchers may also consider using different data types for evidence of ancient hybridization, such as synteny or ancient linkage groups (Steenwyk and King 2024).

The signatures of introgression may also be masked at shallower evolutionary depths. For example, population subdivision followed by extensive gene flow may result in incomplete speciation events (Huang 2020). This may result in numerous subspecies, not distinct species, such as the case for birds (Mayr 1999). In these cases, ecotypes or geographic morphs may better describe evolutionary processes at play, rather than speciation events (Sterner 2017; Steenwyk et al. 2024 Mar 6). These

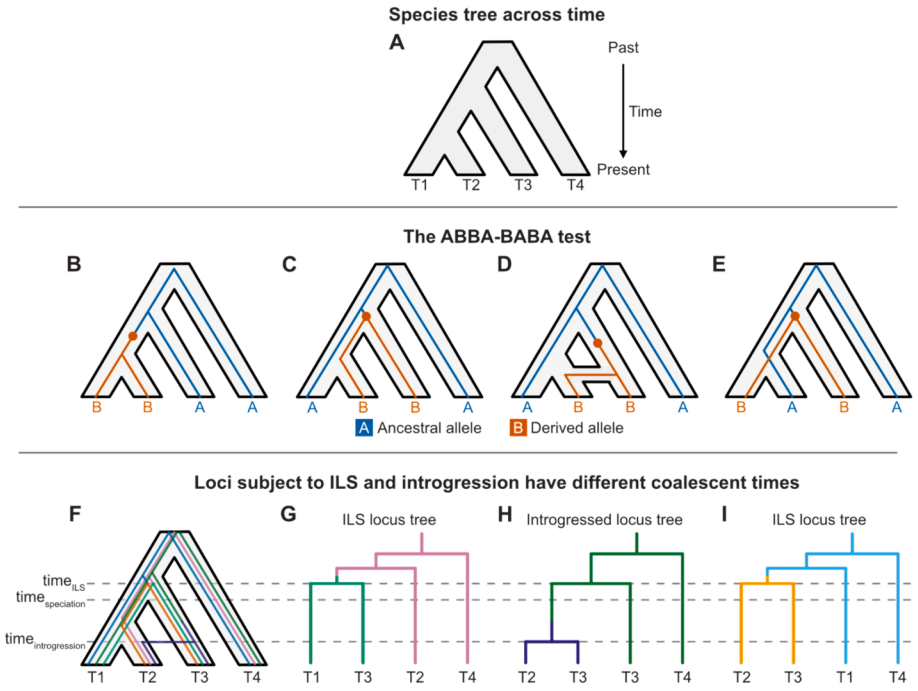

Fig. 2. Detection and differentiation of introgression/hybridization from incomplete lineage sorting. To detect introgression/hybridization in the (A) four-taxon case (represented as T1 through T4 where T4 is the outgroup), (B-E) the D-statistic or ABBA-BABA test can be used. (B) The orange dot represents a mutation from the ancestral allele 'A' (blue) to a derived allele 'B' (orange). The BBAA pattern, which is not directly accounted for in the ABBA-BABA test, is a biallelic site that follows the organismal phylogeny. Asymmetric patterns of ABBA and BABA biallelic site patterns suggest the occurrence of an introgression/hybridization event. The ABBA pattern can arise from (C) incomplete lineage sorting or (D) introgression/hybridization, whereas the (E) BABA pattern can only arise from incomplete lineage sorting; thus, unequal frequencies of ABBA and BABA patterns are suggestive of introgression/hybridization. (F-I) Coalescent times of loci subject to incomplete lineage sorting and introgression will differ. (F) Species tree depicting patterns of single-locus variation. Single locus phylogenies are also shown in panels G through I, wherein G and I depict incomplete lineage sort and H depicts the case of introgression. Of note, loci originating from introgression have a coalescent after speciation, whereas loci subject to incomplete lineage sorting coalesce before speciation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

caveats demonstrate how difficult it is to identify introgression between sister lineages. Sufficient taxon sampling of key (sub)lineages may help determine if introgression has occurred.

3.2. Coalescent times differ between incomplete lineage sorting and introgression

The degree of incomplete lineage sorting can also differ depending on the timing between speciation events. When speciation occurs at a constant tempo, with sufficient time to accumulate mutations between cladogenic events, incongruence stemming from incomplete lineage sorting is expected to be low (Rokas and Carroll 2006). In contrast, when speciation events occur rapidly, such as during radiation events, the proportion of gene trees supporting all three possible topologies of a rooted triplet is expected to be roughly equal (Song et al. 2023). As a result, differentiating between the three topologies is challenging even with genome-scale data, prompting some to represent such divergences as a polytomy (Sayyari and Mirarab 2018). Several polytomies indicative of near-simultaneous radiation events have been identified in fungi and plants (One Thousand Plant Transcriptomes Initiative 2019; Li et al. 2021; Steenwyk et al. 2021), harkening back to what was earlier called a 'star phylogeny' with more limited data (Lara et al. 1996).

Analyses of coalescent times among single loci can help differentiate loci originating from introgression events compared to incomplete lineage sorting. In the case of incomplete lineage sorting, loci will coalesce before speciation, while in the case of hybridization, loci will coalesce after speciation (Song et al. 2023) (Fig. 2F-I). This analysis relies on divergence-time analyses of single loci; however, statistical uncertainty can challenge these analyses due to a lack of information in an alignment, and differences in their underlying mutation rates (Koch and Carmona 2024). It is therefore strongly recommended to evaluate loci according to the rate of evolution and relative phylogenetic usefulness (Mongiardino Koch 2021). The influence of different clock model assumptions and time calibrations should also be systematically evaluated to parameterize the 'chronospace' of a given analysis (Smith et al. 2018; Mongiardino Koch 2021; Koch and Carmona 2024).

3.3. Horizontal gene transfer: high throughput screens and the phylogenetic gold standard

The methods employed for detecting horizontally acquired loci vary in precision and accuracy. Early techniques relied on identifying deviations in gene sequence characteristics. In the case of very recent prokaryote-to-eukaryote horizontal gene transfer, detection could be achieved by observing genes that deviate in guanine-cytosine content, intron content, gene order, and codon usage across the host genome (Friedman and Ely 2012; R. Zhang et al. 2014; Jaramillo et al. 2015; Gonçalves and Gonçalves 2022). In the phylogenomic era, these methods are often employed to support identifying horizontal gene transfer events rather than serving as primary detection tools.

Another approach is to conduct a high throughput screen by calculating the alien index – a score that compares the similarity between sequences within the target group and sequences from outgroup taxa (Gladyshev et al. 2008; Alexander et al. 2016) – of all genes in a host genome. Loci exhibiting alien indices indicative of potential horizontal gene transfer are then selected for further investigation through phylogenetic inference, the gold standard approach for horizontal gene transfer detection. Several software tools have been developed to calculate alien indices or similar metrics for assessing horizontal gene transfer. Examples include AvP, HGTector, and HGTphyloDetect (Zhu

et al. 2014; Koutsovoulos et al. 2022; Yuan et al. 2023; Yuan et al. 2023).

These tools help detect putative horizontal gene transfer events but there are several areas for improvement. For example, there is a relative scarcity of tools that use phylogenetics during high throughput identification of horizontally transferred genes. This may partly be due to the more extensive computational requirements needed and suite of dependencies. However, doing so will help improve overall accuracy and make the approach more amendable to datasets of ever-increasing size. Orchestration of different inputs and outputs between various dependencies may be achieved using workflow management systems like SnakeMake (Köster and Rahmann 2012). Similarly, it is difficult to identify horizontal gene transfer between more closely related lineages (such as between genera from the same class) as opposed to different kingdoms (such as bacteria and fungi). While direct modeling of horizontal gene transfer, duplication, and loss may help distinguish horizontal gene transfer from extensive gene loss, this area is ripe for improvement.

Phylogenetic trees that suggest horizontal gene transfer events are characterized by the confident placement of one or a few sequences within an unexpected taxonomic group (Fig. 3A and B). For instance, in the case of prokaryote-to-eukaryote horizontal gene transfer, sequences in a eukaryotic genome may be nested deep within a prokaryotic lineage (Coelho et al. 2013; Gonçalves et al. 2018; Husnik and McCutcheon 2018; Shen et al. 2018; Zhou et al. 2018; Gonçalves and Gonçalves 2019; Kominek et al. 2019; Van Etten and Bhattacharya 2020; Irwin et al. 2021; Li et al. 2022). The evidence for horizontal gene transfer can be strengthened using topology tests like the Kishino-Hasegawa and Shimodaira-Hasegawa tests (Kishino and Hasegawa 1989; Shimodaira and Hasegawa 1999). These tests compare the likelihood of a phylogeny constrained to reflect a vertical evolutionary scenario (the null hypothesis) with the observed topology, reflecting the occurrence of horizontal gene transfer (the alternative hypothesis) (Gonçalves et al. 2018; Shen et al. 2018).

3.4. Horizontal gene transfer events can inform relative divergences

The timing of divergences plays an important part in understanding the evolutionary history on earth. For example, time-calibrated phylogeneies have been used to identify how plant and fungal symbioses led to radiations in both lineages (Lutzoni et al. 2018). One relatively underexplored method to determine relative divergences is to compare patterns of horizontal gene transfer events (Davín et al. 2018; Davín et al. 2022). Specifically, two competing hypotheses may suggest the origin of one clade preceded or came after the origin of another clade (Fig. 3C concerning clades A and B compared to E and F, which are simplified as clade AB and clade EF, respectively). The robust identification of horizontal gene transfer events between lineages of interest may help support one hypothesis. For example, if transfer events are identified between the ancestor of clade AB into the ancestor of EF, this would support EF diversifying before clade AB (Fig. 3D). In contrast, if a transfer event is identified between taxon A into the ancestor of clade EF, this would suggest that clade AB diversified before clade EF (Fig. 3E). In other words, the expectation that donor clades are older than recipient clades means that careful determining of horizontal gene transfer events across a phylogeny can help determine relative divergence times.

Complex evolutionary histories among horizontally transferred loci may complicate the inference of relative divergences. For example, determining the precise origin of a horizontal gene transfer event in the recipient lineage can be challenging due to differential gene loss or pseudogenization. For example, horizontally acquired loci may be retained in some descendants in a recipient ancestor and lost in others. As a result, it will be difficult to determine at which branch in the organismal phylogeny a gene was acquired, introducing errors in relative divergence time estimates. Specifically, since donor lineages are older than recipient lineages, differential gene loss in a donor lineage may erroneously support a later divergence in the recipient clade. A

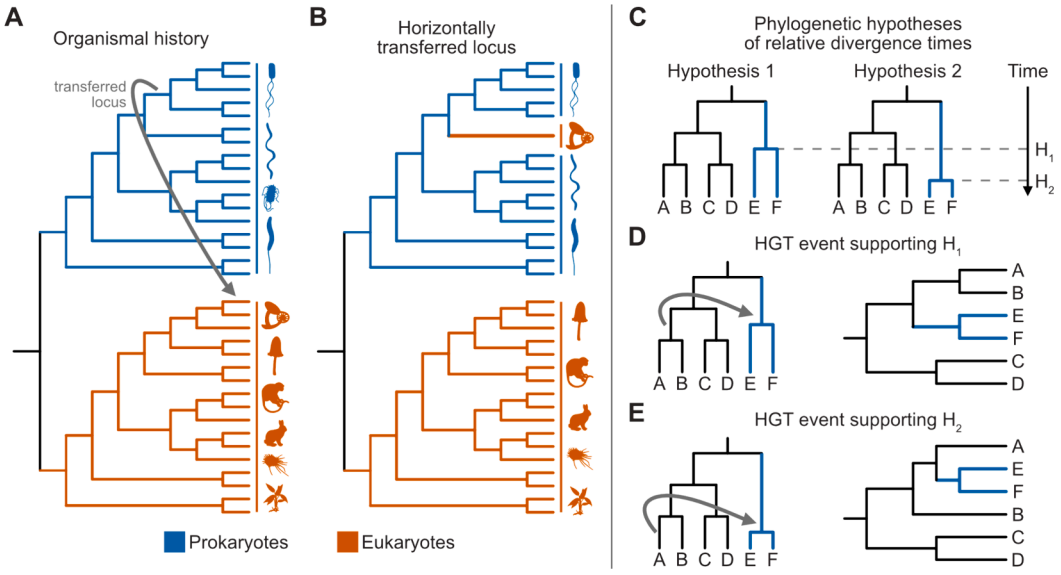

Fig. 3. Signatures of a horizontal gene transfer event and their applicability to relative divergence estimation. To detect horizontal gene transfer, (A) organismal histories are compared to (B) single-locus phylogenies. Horizontal gene transfer is suggested when sequences are placed within an unexpected taxonomic group in single-locus phylogenies. Here, an example of prokaryote-to-eukaryote transfer is depicted wherein an organism from the fungal kingdom (orange) is monophyletic with prokaryotic sequences (blue). The horizontal gene transfer event is depicted as a grey arrow. (C) Similar horizontal gene transfer events can be used to estimate relative divergences, especially in lineages where horizontal gene transfer occurs sufficiently frequently. Specifically, consider the scenario of two competing phylogenetic hypotheses wherein the clade containing taxa E and F diverged before or after the clade with A and B (hypotheses 1 and 2 or H_1 and H_2, respectively). (D) A horizontal gene transfer event that would support H_1 would involve the ancestor of A and B transferring a locus to the ancestor of E and F, whereas (E) a horizontal gene transfer event that would support H_2 would involve the transfer of a locus to E and F from a lineage along the stem branch leading to A. In panels D and E, the left panel depicts the horizontal gene transfer event and the rght panel depicts the phylogenetic tree of the horizontally transferred locus. HGT is an abbreviation for horizontal gene transfer. Silhouette images were obtained from PhyloPic (https://www.phylopic.org/); credit goes to their respective contributors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

similar issue can occur due to pseudogenization. Using the previous example, horizontal transfer into the ancestor of AB followed by the subsequent loss of the horizontally transferred gene in taxon B would erroneously support hypothesis two (Fig. 3C-E).

This method also relies on detecting enough horizontal gene transfer events. Certain lineages are known for having higher rates of horizontal gene transfer events – like cyanobacteria, archaea, and fungi. Among these lineages, transfers have helped determine the relative divergences (Davín et al. 2018). However, other lineages, such as animals, tend to experience fewer horizontal gene transfer events (only from some viruses and transposable elements (Osmanski et al. 2023)), raising the question of how many horizontal gene transfers are needed to overcome detection limits from differential gene loss and other factors. This question raises the need for further methods development.

Nonetheless, relative divergence-time estimation using horizontal gene transfers may be particularly helpful for lineages lacking fossils, such as many soft-bodied fungi and microbes. Numerous examples exist of horizontal gene transfer of microbial loci to lineages with well-established fossils, like animals and plants (Yue et al. 2012; Li et al. 2022). In this case, horizontal gene transfers between microbial lineages and those with well-established fossils can help constrain the evolution of microbial lineages in geologic time. Such analyses may help refine the timing of radiations between symbiotic lineages such as plants and fungi, helping to establish key evolutionary episodes, including how fungi may have helped plants colonize land (Lutzoni et al. 2018).

3.5. Recombination and GC-biased gene conversion

Genomic shuffling by recombination can lead to regions with partially independent evolutionary histories (Schrempf and Szöllősi 2020), which can cause incongruence between locus and species trees (Kroken and Taylor 2001). GC-rich regions typically undergo higher recombination rates compared to AT-rich regions because recombination is GC-based when fixing mutations resulting in increased GC content over time; this phenomenon is termed GC-biased gene conversion (Bossert et al. 2017). Higher levels of recombination tend to increase with incongruence. When combined with selection, phylogenetic signal decreases, leading to even more incongruence (Stott and Bobay 2020). Moreover, loci subject to recombination can also robustly support phylogenies incongruent with the species tree (Retchless and Lawrence 2010). Other evolutionary processes may influence or be confounded by recombination – such as polyploidization events and horizontal gene transfer (Hao and Palmer 2011; Wang and Paterson 2011).

While recombination may cause single loci to differ from the species tree (Hsu et al. 2010; Hao et al. 2012), the influence of recombination on species tree inference seems minimal. For example, a simulation study that allowed all loci in a dataset to evolve under high levels of recombination resulted in a species tree with minimal difference from a species tree inferred from nonrecombining data (Lanier and Knowles 2012). Similarly, in simulated and empirical data of prokaryotes, species trees inferred using core genomic regions (i.e., those found in all species/strains) were generally robust to recombination (Stott and Bobay 2020). Recombination may partly have little impact due to the multispecies coalescent model assuming free recombination among loci (Mirarab et al. 2021).

However, recombination can negatively influence other analyses commonly conducted by phylogenomicists. For example, recombination can influence parameter estimation for Bayesian modeling of ancestral population sizes (Zhu et al. 2022). Similarly, recombination may also negatively influence coalescence time inference among loci (Hein et al. 2004).

Accordingly, researchers may want to identify loci subject to recombination and purge them from datasets. One approach for identifying loci subject to recombination is calculating the pairwise homoplasy index (Phi). The Phi statistic tests if a locus rejects the null hypothesis of being nonrecombinant by examining the similarity between closely linked sites (Lamichhane et al. 2020). The null distribution is generated by permuting sites in an alignment and evaluating the correlation of genealogical support between adjacent sites; in the absence of recombination, all sites have the same history, while recombination will result in variation (Bruen et al. 2006).

3.6. Phylogenetic networks for detection and visualization of reticulation

Rather than a strictly bifurcating tree, reticulate evolution can be represented as network-like evolutionary processes. Numerous approaches now exist for phylogenetic network reconstruction, such as splits networks where nodes do not necessarily correspond to hypothetical ancestors and reticulate networks where internal nodes correspond to ancestral taxa (Huson and Bryant 2006; Wägele and Mayer 2007). Similarly, numerous tools exist that employ diverse methods or ingest different types of data, such as SplitsTree, PhyloNet, SNaQ, and NetRax among others (Huson 1998; Huson et al. 2007; Than et al. 2008; Solís-Lemus and Ané 2016; Solís-Lemus et al. 2017; Wen et al. 2018).

Phylogenetic networks can be inferred from sequences, distances, or phylogenetic trees and often directly account for incomplete lineage sorting (Wen et al. 2018). The resulting network can also be visualized using different approaches. For example, in a consensus network made from single-locus phylogenies, all splits in a fixed number of trees will be depicted (Huson and Bryant 2006). This can help disentangle reticulation stemming from allopolyploidy compared to introgression, since a stronger signal of reticulation is expected for allopolyploids. Reticulation by hybridization can also be more directly tested using a hybridization network (Moret et al. 2004). Here, specific hypotheses of a hybridization event can be defined *a priori* to determine if a set of trees – often locus trees – support the hybridization event (Huson and Bryant 2006). Given the need for pre-defining hypotheses, the sampling of distantly related taxa may not be needed, which can allow for greater locus sampling (Emms and Kelly 2018). While maximizing taxon sampling is generally recommended for species tree inference (Pollock et al. 2002; Steenwyk et al. 2023 Jun 27), extensive taxon sampling may not always be needed for tests of introgression, as long as key lineages for the specific hypotheses being tested are well represented.

In population studies, ancestral recombination graphs (or recombination networks) can be inferred from biallelic sites to detect recombination events (Lyngsø *et al.* 2005). Similarly, explicit hypotheses of recombination events may need to be pre-specified. Future developments may focus on agnostic tests for hybridization/recombination, rather than explicitly defining hypotheses to test. This may help identify heretofore undetected hybridization events.

Like in the reconstruction of bifurcating phylogenies, statistical uncertainty in phylogenomic data can introduce noise, even error, during phylogenetic network construction. One approach to overcome this is to collapse poorly supported branches before network inference from single-locus phylogenies (Kandziora et al. 2022). Bayesian frameworks for network inference provide a robust approach to account for uncertainty by producing posterior distributions of probable networks that can be used for downstream analyses (Lewanski et al. 2023 Oct 18). However, other methods can also be used to determine certainty in network topology network support, such as bootstrapping (Lutteropp et al. 2022).

4. Time-calibration of inferred locus- and species-tree divergences

Divergence times among branches in a phylogenomic analysis can be estimated using fossils, mutation rates, horizontal gene transfers, or other temporal evidence to calibrate a molecular clock model (Ho and Phillips 2009; Dos Reis et al. 2016; Davín et al. 2018; Dos Reis et al. 2018; Tiley et al. 2020). This procedure converts the relative divergences of molecular substitution rates to absolute time, often in units of thousands or millions of years ago. The resulting time-calibrated

phylogenies, which may be referred to as 'timetrees' or 'chronograms', differ from uncalibrated phylogenies ('phylograms') in that the former is comparable to other evidence that is scaled to absolute time. Timetrees can be used to investigate causal eco-evolutionary dynamics relative to a broad array of independent evidence; for example, past changes in global temperature versus rates of lineage divergence (Oliveros et al. 2019; Schubert et al. 2019 May 21; S. Meseguer and Condamine 2020; Feijó et al. 2022), co-diversification among taxa (Sabrina Pankey et al. 2022; Nelsen et al. 2023), and rates of speciation among related clades (Harvey et al. 2020; Upham et al. 2021).

Approaches to estimating divergence times can be divided into node dating, tip dating, and fossil-free dating. Node dating places temporal constraints (i.e., calibrations) on a bifurcating internal node of a phylogeny. In contrast, tip dating places calibrations on terminal taxa that existed at some time in the past (Ho and Phillips 2009; Heath et al. 2014). The ages of serially sampled taxa – usually fossils or viruses and other microbes (Stadler and Yang 2013) – are the most reliable data for calibrating divergence times in phylogenomic datasets. Fossils and their associated ages can calibrate divergence times at either nodes or tips, typically using a probability distribution to incorporate age uncertainty (Ho and Phillips 2009; Stadler and Yang 2013). A fossil's phylogenetic position relative to living members of a given clade must be inferred or assumed based on other data for that fossil to serve as a time calibration (Parham et al. 2012). Viruses and other microbes evolve rapidly enough that samples collected in the last few decades offer valuable tip calibrations analogous to the role of fossils in longer-lived mammals or plants (Volz et al. 2013; Andréoletti et al. 2022). The resulting 'phylodynamic' analyses can help expose the population-dynamic processes that generate the phylogenetic patterns inferred from phylogenomic datasets (Stadler et al. 2021; Andréoletti et al. 2022).

In both node and tip dating, clock models are used to extrapolate species divergence times from temporal constraints. Strict clock models assume a fixed mutation rate in all branches, which is often violated when comparing more distant relatives (e.g., the 2 %-per-million-years rate long used for bird mitochondrial genes; (Ho 2007)). Indeed, strict clocks may lack biological realism, so this assumption is often relaxed, such as in autocorrelated clock models where closely related branches have similar mutation rates or, in uncorrelated models where each branch is given an independent rate (Drummond et al. 2006; Lepage et al. 2007; Steenwyk and Rokas 2023). Relaxed clocks allow greater flexibility for handling the observed molecular-rate variation among lineages, and thus they are in wide use today for all types of time-calibration strategies. Multi-species coalescent dating approaches additionally leverage information about ancestral population sizes to estimate species divergence times (Dos Reis et al. 2016; Dos Reis et al. 2018; Flouri et al. 2022). Such coalescent dating approaches can be quite accurate when mutation rates are known from pedigrees (Tiley et al. 2020), and appear to be robust to small amounts of introgression in phylogenomic datasets (Huang et al. 2020; Tiley et al. 2023).

What if no fossils or other serial samples are available for a particular taxon? Two main options exist to calibrate divergences: use a fixed, strict clock model to project estimates back from tips, or use secondary calibrations derived from previous analyses. Secondary calibrations typically apply the divergence times estimated at a larger phylogenetic scale (from primary fossil or rate calibrations) for a sister taxon or outgroup, which can be used to calibrate the root node for a clade of interest (Shaul and Graur 2002). However, caution is required to avoid specifying overly precise secondary calibrations, given the strong assumptions involved (Schenk 2016).

Choosing which software to use for divergence-time estimation involves a trade-off between available compute resources and the desired level of biological realism. At one extreme, the most realistic models (e.g., BPP and StarBEAST (Flouri et al. 2018; Douglas et al. 2022)) will perform Bayesian inference to estimate multi-species coalescent parameters across thousands of gene genealogies, considering multiple rate priors, and integrating across both phylogenetic and temporal uncertainty to yield a posterior distribution of time-scaled trees. However, these 'full methods' do not scale to large numbers of taxa or distant relatives (Tiley et al. 2020; Jiao et al. 2021).

At the other extreme, concatenated sequence data can be used stepwise to first estimate the phylogenetic tree topology in units of substitutions/site, which can then be calibrated in a second step of divergence-time estimation. Step-wise methods most commonly use maximum-likelihood (e.g., r8s, treePL, RelTime; (Sanderson 2003; Smith and O'Meara 2012; Tao et al. 2020)), but can also be implemented using Bayesian inference in programs like BEAST or MrBayes, which often requires fixing the tree topology. Midway between these extremes is the use of concatenated sequence data to perform simultaneous estimation of topology and divergence times, generally as implemented in a Bayesian framework (e.g., BEAST, MCMCtree, MrBayes, PhyloBayes, RevBayes). This latter approach has been implemented in large datasets (e.g., 800 taxa by 40,000 sites; (Upham et al. 2019)), and continues to be aided by GPU-based computing libraries (Ayres et al. 2019). Strategies for setting node-age priors can strongly impact divergence-time estimation and are thus a further key consideration, particularly since such analyses generally assume the monophyly of all time-constrained nodes (Barba-Montoya et al. 2017).

During divergence time estimation, a range of plausible dates is typically returned under the model's experimental conditions. Thus, divergence-time results are communicated using confidence intervals, often of the middle 95 % (from 2.5 % to 97.5 % of the resultant distribution). Divergence times can also be inferred using a bootstrapping approach for intractably large datasets (Liu et al. 2023). However, any divergence times communicated without a confidence interval should be viewed with caution given the strong assumptions involved in choosing a point estimate (Huelsenbeck et al. 2000). Overall, the choices of node, tip, or fossil-free dating and strict or relaxed clocks depend on the question of interest, available molecular and morphological data, and prevalence of locus-tree-species-tree incongruence.

5. Conclusion

This review explores how to infer a species tree and subsequently detect reticulate evolutionary processes and date divergence events within phylogenomic datasets. We expect that future research avenues will seek to improve upon these methods in five main ways.

First, for detecting horizontal gene transfer, improvements in high-throughput tree-based methods will reduce the number of phylogenetic trees that need to be (semi)manually inspected and pruned from collections of putatively horizontally transferred genes. Currently, the alien index is relied upon for high-throughput screening, but it is prone to false positives and thus does not scale well to phylogenomic data. Methods for detecting horizontal gene transfer that can scale to large phylogenomic datasets of 1,000 + taxa will be especially useful given the current exponential rise in published genomes (Chen et al. 2021).

Second, for detecting introgression, site-based approaches like the ABBA-BABA test will continue to be valuable among recently diverged species or populations, but model-based approaches are needed to test for hybridization at more ancient nodes where substitution saturation is expected (Swofford et al. 2001; Hibbins and Hahn 2022). Building on earlier methods for single loci (Huson et al. 2005), the node-by-node frequency of topologies discordant with the species tree will be skewed to one topology in cases of ancient hybridization whereas incomplete lineage sorting will yield two equally represented discordant topologies. Several studies have generated their own pipelines for analyzing sliding genomic windows to find signatures of ancient hybridization in this way (e.g., in butterflies, fruit flies, and mammals (Edelman et al. 2019; Suvorov et al. 2022; Foley et al. 2023)). However, high-throughput and general-purpose tools for these tests are needed. One promising approach is to examine potential signatures of introgression using synteny-based analyses (e.g., maps of gene order and recombination rate (Bredemeyer et al. 2023)). Developing automated,

high-throughput methods for accurate introgression detection from phylogenomic datasets containing hundreds to thousands of taxa will illuminate the general prevalence of introgression across the Tree of Life.

Fourth, for dating divergence events using single loci, improvements in the accuracy of dates will help differentiate incomplete lineage sorting from introgression, given the expectation that introgressed loci will coalesce more recently than the corresponding species-tree divergence. Doing so will require confident inferences of per-locus substitution rates across genomic windows of different sizes, which is particularly difficult among ancient divergences, due to substitution saturation. Automated divergence estimation – augmented with modeling of the evolutionary process – will help differentiate incomplete lineage sorting and introgression in the Tree of Life. Another potential area for future research is integration divergence time methods into phylogenetic networks.

Fifth, one method to potentially refine molecular clock models is to leverage long-term experimental evolution data, where mutation rates are known to vary (Lenski 2017; Wei et al. 2022). In other taxa, per-species estimates of *de novo* mutation rates can be obtained by trio-based sequencing of genomes from wild-caught mother-father-offspring (Bergeron et al. 2023; Suárez-Menéndez et al. 2023), which could be leveraged to calibrate divergence times more accurately than with external fossils. Such insights may improve models of the complex interrelationships between mutation rate, population size, natural selection, and the divergence of lineages as manifested in locus-tree-species-tree dynamics.

Taken together, we have identified numerous considerations and opportunities for further research to understand how reticulate evolution can inform – and has shaped – our knowledge of the Tree of Life.

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CRediT authorship contribution statement

Saelin Bjornson: Writing – review & editing, Conceptualization. **Heroen Verbruggen:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Nathan S. Upham:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Jacob L. Steenwyk:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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