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# Conflict and complementarity of paleontological and molecular chronologies?

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*Abstract*.—Evolutionary history studies depend on having reliable chronologies of macroevolutionary processes. Construction of such chronologies often yields discrepancies between paleontological and molecular dates, which are sometimes viewed as conflicting. Nevertheless, each macroevolutionary process is composed of two main phases: emergence of a trait or clade and success of that trait or clade, which differ in mechanisms, drivers, and types of evidence. Moreover, emergence may be observed as gene divergence (which may be trait-coding or trait-unrelated genes), trait emergence, and clade emergence; whereas success can be observed as increase in abundance, diffusion, and/or diversity or as overall persistence over geologic time. Therefore, to fully and correctly understand any macroevolutionary process, it is of paramount importance to understand what event each date refers to, and how dates of various events and their integration reveal the complexity of macroevolutionary processes. I demonstrate this through three examples: the chronological gap between oxygenic photosynthesis emergence and the Great Oxidation Event, the chronological gap between paleontological and molecular dates of angiosperm emergence, and the evolution of plant silicon accumulation.

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## Introduction

A key requirement in studying evolutionary history is to have reliable chronologies of macroevolutionary processes such as the evolution of new clades (monophyletic groups) and traits (character states). Reliable chronologies enable us to study whether and how organismal traits and forms coevolve and whether and how macroevolutionary processes affect and are affected by environmental changes. Acquiring reliable chronologies and correctly interpreting them requires reliable dating methods and good understanding of *what* component of the macroevolutionary process is dated. Modern biostratigraphic, radiometric, and molecular techniques allow us to accurately date genes, proteins, fossils, and strata. Nevertheless, the paleontological and molecular records can provide considerably different chronologies (Fig. 1), with dates obtained from fossils tending to be younger than dates obtained from molecular techniques (e.g., Rodriguez-Trelles et al. 2002; Marjanovic and Laurin 2007; Quental and Marshall 2010; Erwin et al. 2011; Herendeen et al. 2017). This difference stems from some principal and technical differences between paleontological dating and molecular dating (see following section), which means that scholars from the two schools do not always date the same components of the macroevolutionary process (Fig. 2).

It is therefore important to first understand *what* is actually dated (e.g., Nichols 2001; Pulquerio and Nichols 2007; Jablonski 2008a; Pennell et al. 2014; Herendeen et al. 2017). Each macroevolutionary process is inherently composed of two main phases: emergence of a trait or clade (divergence of a derived form from an ancestral one) and success (a trait or clade becoming quantitatively significant). While emergence usually takes place in lower organizational levels and at small temporal and spatial scales (genes to communities, days to millions of years, local to regional), success usually reflects larger scales (communities to ecosphere, decades to hundreds of millions of years, local to global) (Table 1). The study of macroevolutionary processes therefore requires an understanding of what component of the macroevolutionary process is dated and how the dates of these components can complement each other to reveal the more complete,

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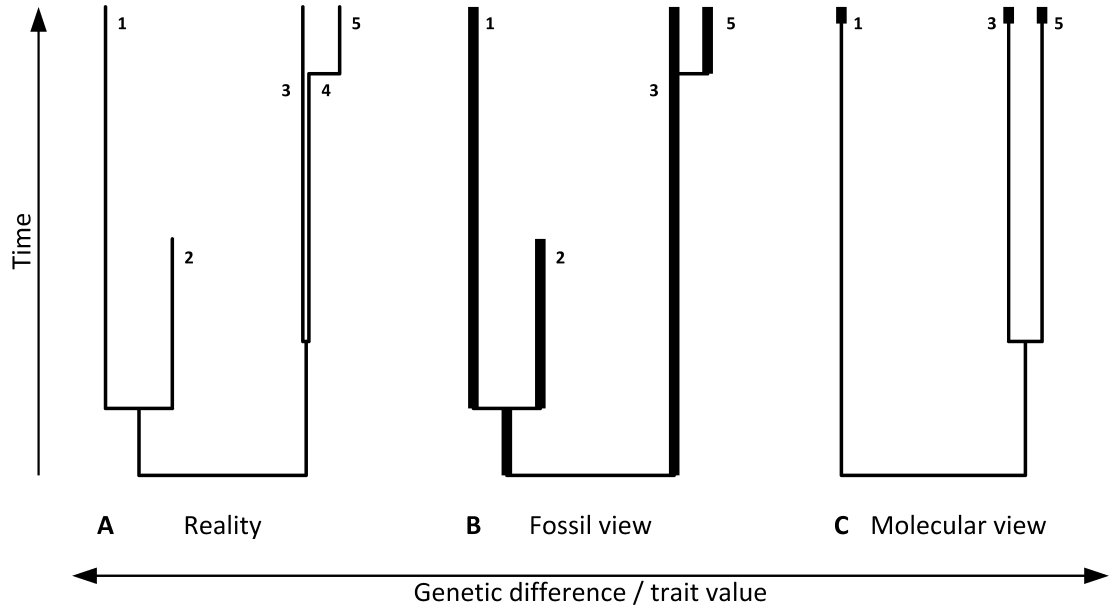


FIGURE 1. Complex macroevolutionary processes may be viewed differently by paleontologists and phylogeneticists, neither of whom is able to see the full true picture. In this example, paleobiological reality (A) consists of two major clades. One includes sibling extant (1) and extinct (2) clades. The second diverged early into two clades (3 and 4) that cannot be distinguished morphologically (i.e., are paleontologically cryptic) but are genetically separate (e.g., have distinctly different organellar DNA sequences), with clade 4 more recently acquiring apomorphies and shifted into a distinctive clade 5. A paleontologist with a full fossil record (B) will not be able to distinguish 4 as a clade separate from 3, and will conclude that clade 5 recently diverged from clade 3. A molecular phylogeneticist with access to extant species only (C) will construct a phylogenetic tree consisting of clades 1, 3, and 5, but will suggest that clades 3 and 5 separated a long time ago. Bold lines denote available fossils (B) and molecular data (C).

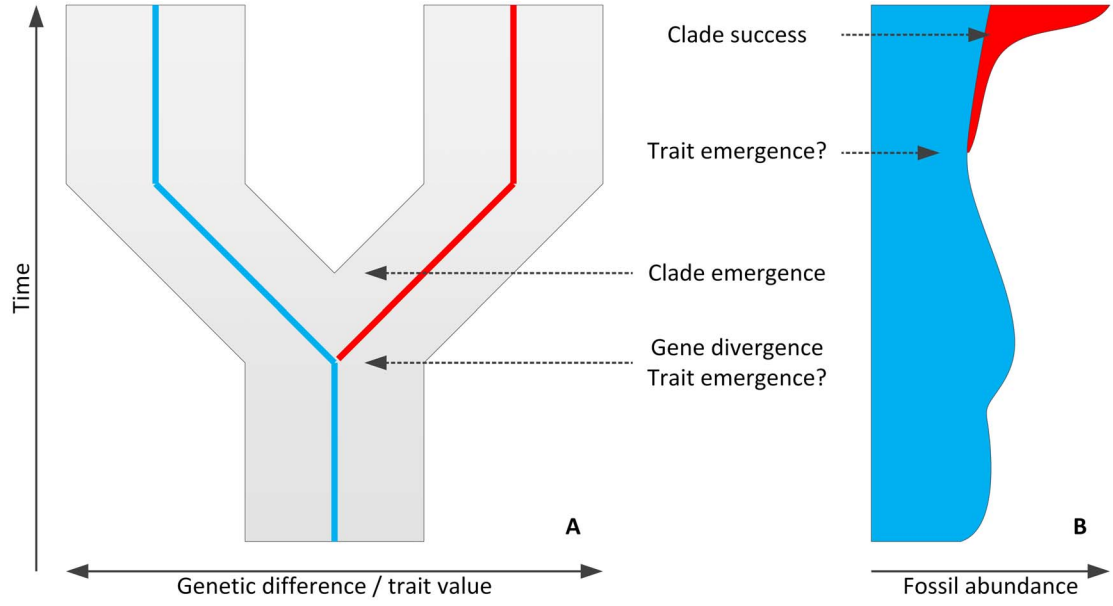


FIGURE 2. Molecular (A) and fossil (B) chronologies provide information on different phenomena of a macroevolutionary change (here, divergence of a dark/red trait clade form from a pale/blue one) or provide different evidence for these events, often resulting in disparities among gene, trait, and clade divergence times and between emergence and success.

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TABLE 1. The three main components of success differ in the main factors that can enhance them and in the types of fossil and molecular information that can be used to identify and date them. Key to taxonomic levels at which each any factor or dating method is relevant: I, individual; S, species; H, above species.

| Characteristic | Abundance | Diffusion | Diversity |
|---|---|---|---|
| Type of intrinsic organismal attributes that enhance component values | Fecundity,[I,S] fitness[S] | Mobility,[I] range[S] | Genetic change,[S] plasticity[S] |
| Type of ecological processes and attributes that enhance component values | Competitive superiority,[S] facilitation[S] | Niche size and range[S] | Niche partitioning[S,H] |
| Type of geographic relations between populations or genotypes that enhance component values (all taxonomic levels) | Connectivity?[S,H] | Connectivity?[S,H] | Isolation[S,H] |
| Fossil information that can be used to measure component (all taxonomic levels) | Frequency[S,H] | Distribution[S,H] | Morphological species number[H] |
| Molecular information that can be used to measure components | Effective population size estimates[S] | Phylogeography[S,H] | Within-clade variance[S?,H] |
| Possibility of assigning a date to changes and trends in a component's value using molecular techniques | Weak or impossible | Possible | Possible |

complex, and real story. Here, I describe the variation among date types and how different dates may refer to different components of the macroevolutionary process, and how being aware of these differences allows us to better understand macroevolutionary processes and events.

## Sources of Chronological Information

Fossils of all kinds are the most tangible evidence for past organisms' existence and attributes and are therefore considered by many to be the least disputed sources of paleobiological information (e.g., Herendeen et al. 2017). Nonetheless, the fossil record is neither complete nor unbiased. Fossil morphologies and anatomies are open to subjective interpretations to some degree, which may result in dubious assignment of fossils to clades (e.g., Rutschmann et al. 2004; Forest 2009; Sansom 2015; Baron et al. 2017). Morphometric methods (e.g., Roth-Nebelsick et al. 2000; Hughes and Chapman 2001; Goswami et al. 2010) and multiple-trait phylogenetic analyses (e.g., Hughes and Chapman 2001; Baron et al. 2017), for example, have been able to reduce such biases but not to resolve them altogether. Moreover, the fossil record suffers from inherent incompleteness and representational biases due to uneven preservation, for which solutions are also being developed at appreciable rates (e.g., Crampton et al. 2003; Crepet et al. 2004; Forest 2009; Sansom et al. 2010; Sansom 2015). Therefore, fossil dating can provide valuable information on the occurrence of clades and traits over geologic time, and fossils remain—and are likely to remain—the most reliable source of information about organismal traits; but fossils alone cannot always reliably attest to clade or trait abundance, diversity, and geographic distribution, nor can they always provide undisputed dates for trait or clade emergence (Magallon 2004; Erwin et al. 2011; Fig. 2).

The use of molecular dating (i.e., molecular phylogenetic trees with molecular clocks) in addition to the fossil record is becoming increasingly common, although its reliability is still disputed, especially due to confidence intervals tending to be larger than for fossil dating (Rodriguez-Trelles et al. 2002; Graur and Martin 2004; Hedges and Kumar 2004; Pulquerio and Nichols 2007; Ho and Phillips 2009; Parham et al. 2012). The main methodological shortcoming of molecular dating is the inability to extract molecular information from extinct species. Despite some methodological advances in extracting DNA and other organics from fossils (Woodward et al. 1994; Li et al. 2010), fossil preservation is rarely sufficient to provide molecular data of the quality required for phylogenetic analyses. Until recently, a common practice was to use noncoding, mitochondrial, and plastid DNA sequences—or genes that code organellar structures (e.g., ribosomal DNA)—over sequences that code specific proteins and traits, because

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the former have more consistent nucleotide substitution rates and are less affected by natural selection. However, nuclear DNA sequences tend to be more informative in deeper geologic time (e.g., Brower and DeSalle 1998), and if they code traits of interest, they are more appropriate for understanding the evolutionary history of these traits (e.g., Xiong et al. 2000; Trembath-Reichert et al. 2015). It is therefore unsurprising that the choice of molecular data source is a matter of much debate and can substantially affect results and interpretations (Brower and DeSalle 1998; Soltis and Soltis 1998; Heckman et al. 2001; Shaw 2002; Small et al. 2004; Sole-Cava and Wörheide 2007).

Regardless of the type of molecular data source and specific method, molecular dating requires reliable estimates of nucleotide substitution rates (Graur and Martin 2004; Hedges and Kumar 2004; Rutschmann 2006; Pulquerio and Nichols 2007; Ho and Phillips 2009). This is usually achieved by calibrating the molecular phylogenetic tree with fossil evidence (Parham et al. 2012). This calibration can be done in two ways. More traditional node-dating approaches use the date of the oldest known fossil as a minimum age constraint on internal nodes among which the relationships are predefined (e.g., Magallon 2004; Rutschmann et al. 2004; Hug and Roger 2007; Marjanovic and Laurin 2007; Gandolfo et al. 2008; Ho and Phillips 2009; Quental and Marshall 2010). However, the oldest fossils to bear a trait are almost never the remains of the first bearers of the trait and thus cannot directly attest to the time of gene or clade divergence (Magallon 2004). More recently, tip-dating approaches have been introduced, which simultaneously assign fossils to nodes and date node branching without pre-assuming the relationships among fossils (e.g., Pyron 2011; Bapst et al. 2016). Others calibrate phylogenetic trees using tectonic events that explain vicariance (e.g., Rutschmann et al. 2004; Ho and Phillips 2009), which comes with its own set of potential errors and risk of circular argumentation (Rutschmann et al. 2004; Kodandaramaiah 2011; De Baets et al. 2016).

Therefore, having reliable molecular clocks and molecular dates is in itself not an easy task, and the uncertainty around the reliability of molecular dating techniques is a major challenge for constructing correct chronologies, and there is (rightfully) much debate over how to construct evolutionary chronologies using paleontological and molecular dating techniques. In extreme cases, scholars may categorically dismiss dates that are retrieved from one type of method in favor of another (e.g., Herendeen et al. 2017). In addition to these methodological challenges, I wish to bring forward another set of challenges in interpretation of chronologies. Eventually, even if we are able to resolve all methodological challenges and achieve near-perfect dating methods (from both fossil and molecular data), it is unlikely that fossil and molecular chronologies will be in full agreement, for the simple reason that different methods date different macroevolutionary events. In this paper, I explain and discuss the challenge of chronological discrepancies and how this challenge may be harnessed to improve our understanding of the macroevolutionary process.

## Emergence: Genes, Traits, and Clades

Trait emergence begins with genetic or developmental changes within an individual organism or a small number of organisms and is therefore driven by intrinsic forces. Nevertheless, one cannot simply equate gene divergence times with trait emergence times (Fig. 2). First, genotypes do not always reflect phenotypes, due to phenotypic plasticity or genotype by environment interactions (Pigliucci 2005; Whitman and Agrawal 2009). Phenotypic plasticity can also initiate trait shifts that are later canalized through genetic assimilation (Pigliucci et al. 2006). Conversely, some complex traits are composed of several interacting components (developmental, physiological, biochemical, etc.) that are coded by networks of polygenes, quantitative trait loci, or master genes (McKay 2001). Because such complex traits truly emerge only when all their genotypic and phenotypic components are coordinated (cf. Donoghue 2005), the prerequisites to take any gene divergence time as a trait emergence time are to construct the underlying genetic network and identify the genes whose

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changes are the critical turning points. These challenges are exacerbated as trait complexity and diversity increases and as its origins lie deeper in geologic time, as has been demonstrated by the limited success in the attempts to trace the evolutionary history of photosynthesis (Xiong et al. 2000; Hohmann-Marriott and Blankenship 2011). Traits and clades should also not be equated, and thus neither should trait and clade phylogenetic trees and divergence times (Figs. 1 and 2). Trait trees differ from clade trees, because the former are constructed from specific trait-coding genes and the latter from whole genome sequences (e.g., Xiong et al. 2000) or from noncoding, mitochondrial, and plastid sequences (e.g., Bowe et al. 2000).

A key question is, therefore, what roles traits and trait emergence play in speciation, if any, and whether and how trait and clade divergence times can be used to understand macroevolutionary processes. To avoid an overly exhausting discussion that is outside the focus of this paper and is extensively present in the literature (e.g., Wiens 2004; Hansen and Orzack 2005; Jablonski 2008a; Schluter 2009; Butlin et al. 2012; Pennell et al. 2014), I will briefly claim that trait variations and emergence of novel traits do not necessarily lead to speciation and that, conversely, speciation does not necessarily arise from trait variations. First, the roles of sexual and natural selection and of genetic drift in speciation are still an open question (Butlin et al. 2012). Second, trait variations are not always subjected to sexual or natural selection to a degree that can result in reproductive isolation. Third, that different traits or trait states imply different fitness is an assumption rather than a rule, and speciation is sometimes decoupled from adaptation and natural selection (e.g., Wiens 2004; Pennell et al. 2014). Fourth, reproductive isolation can precede trait divergence, for example, in allopatric speciation, so one cannot simply assume that trait emergence precedes clade divergence or that chronological relationships between the two can provide clear patterns (Fig. 1; see also section on angiosperm origins below). Finally, speciation may be independent of trait change altogether, and may even be a result of phylogenetic niche conservatism that hinders species from maintaining reproductive connectivity following habitat fragmentation (Wiens 2004).

Therefore, gene trees and clade trees are also not the same, and hence neither are gene divergence times and clade divergence times (Edwards and Beerli 2000; Nichols 2001; Wall 2003; Fig. 2A). This disparity is not so much a result of complex interactions between genes and traits, as it is a result of disparity between traits and clades, as manifested in the multiple ways by which traits and speciation may be linked. Furthermore, molecular phylogenetics "skips over" traits to directly associate certain genes with clades (e.g., Fig. 1C). Put together, the complexities of gene–trait and trait–clade relationships result in "the threads connecting genes and selection [being] still few" (Schluter 2009) and the question of "speciation genes" remaining unresolved (Butlin et al. 2012). Therefore, one must ask oneself what is dated (genes, traits, or clades?), and how any one date should be inferred as a stand-alone and in conjunction with other dates.

## What Is "Success" and How Can We Quantify It?

The term "success" appears to follow the descriptive form of "I know one when I see one," an attribute shared with other terms like "key innovations" (Hunter 1998), "niches" (Godsoe 2010), and "novelty" (Pigliucci 2008). Different scholars use and interpret the term "success" in various ways, and thus also translate it to operational terms differently. Success is usually used to denote that a trait or clade is abundant, dominant, geographically widespread, morphologically diverse, or persistent through geologic time (Wilson 1987; Hunter 1998; Poulin et al. 2002; Gheerbrandt and Rage 2006; Erwin et al. 2011; Katz 2015, 2018). Following these past uses of the term, I suggest that three readily quantifiable criteria to determine the degree of success are abundance (number of individuals), diffusion (realized geographic range), and diversity (variance) (Fig. 3; Table 1). These three criteria are measurable at any discrete point or interval in geologic time, assuming that the fossil record for this point or interval is sufficiently complete and unbiased.

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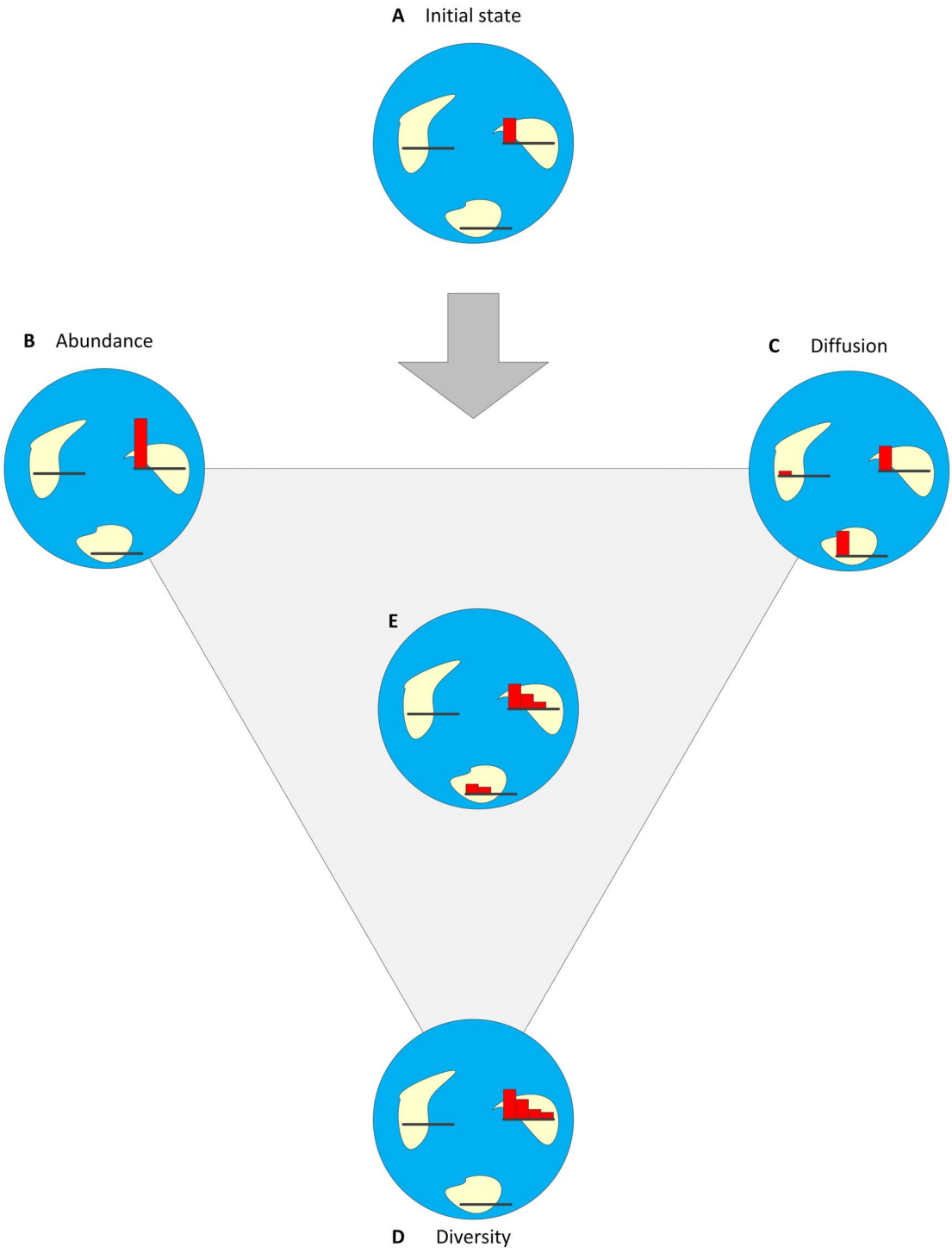


FIGURE 3. Success has three components and can be described as a combination of the degrees of abundance, diversity, and diffusion through geologic time. In this example, a trait/clade that emerged on one island and has reached a certain level of abundance (A) can become more successful if it becomes more abundant (B), diffused (C), diversified (D), or some combination of the three (E). For each island, a small histogram describes the abundances of up to four variants (species/phenotypes) from the clade.

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To these three, I suggest adding Wilson's (1987) criterion of persistence through geologic time, which is likely a strong outcome of the three. Persistence through geologic time is also potentially quantifiable by measuring the duration a clade existed through geologic time. However, devising a quantitative universal persistence index is hindered by several issues regarding the end date of a clade's existence. One challenge is how to treat mass extinctions that can nonselectively wipe out multiple clades, regardless of their success before the event (Lockwood 2003). Another challenge is a bias with regard to extant clades: we simply do not have end dates for them, and thus older extant clades will seem more persistent than younger ones. Regarding these two challenges, it appears that the number of genera that persist more than 45 Myr is higher in more recent geologic time and less affected by mass extinctions (Rohde and Muller 2005; Jablonski 2008b), which suggests further bias in using persistence over geologic time as a measure of success. Moreover, persistence through geologic time is cumulative, so unlike the other three criteria, for which we can potentially identify changes over time (e.g., an increase in diversification rate can be taken as the time of a clade becoming diverse), a clade does not become persistent at any point in time.

The four proposed criteria are often linked (Wilson 1987; Heard and Hauser 1995). Net diversification rate is calculated by subtracting extinction rate from diversification rate. However, because high abundance may reduce extinction probability, it can indirectly be positively linked with net diversification rate. Successful diffusion (i.e., establishment of a population) also depends on size (abundance). If diffusion leads to geographic isolation, genetic isolation, and speciation, it increases diversity. Finally, diffused and diverse clades have higher probabilities to persist through geologic time (Wilson 1987; McKinney 1997), while the effects of abundance on extinction risk are yet unclear (Harnik 2011; Harnik et al. 2012).

Taxon geographic range is negatively correlated with extinction probability (Payne and Finnegan 2007; Jablonski 2008b; Harnik 2011; Harnik et al. 2012), a correlation that is stronger for background extinctions than for mass extinction events (Payne and Finnegan 2007; Jablonski 2008b). If the extinction risk of any species is equal to that of others, it is less likely that all species within a larger clade become extinct. If a clade is not only more taxonomically diverse (i.e., has a larger species number) but is also more functionally diverse (i.e., its species differ more from one another), then it is more likely that at least one species bears a trait (or traits) that reduce its extinction risk. Kolbe et al. (2011), for example, found that more morphologically diverse bivalve taxa were more likely to survive the Plio-Pleistocene extinction. Extant animal species in some clades are at higher extinction risks than species in other clades (Purvis et al. 2000), with higher extinction risks found in more species-poor genera (Russell et al. 2008). In contrast, more species-rich plant families are more likely to have rare species (Dominguez Lozano and Schwartz 2005), and young and rapidly diversifying plant clades are at greater risk of extinction (Davies et al. 2011). This difference between plants and animals may be explained if speciation among plants is driven more by reproductive isolation than by functional disparity.

The degree of overall success is a combination of the four criteria but does not require a high degree of any single one of them (Fig. 3). Developing a success index will require first devising good measurements of each criterion and then modeling the relationship among the four criteria. However, the usefulness of a success index is probably very limited: one will not be able to simply determine that one clade is more successful than another using such an index, because any clade's success index value may be driven by another criterion. How can we tell what degree of abundance is equivalent to what degree of diversity, or how can we equate an abundant but nondiffused clade to a rare but diffused clade? I will therefore discuss each of the three first criteria (abundance, diffusion, and diversity) separately, focusing on how it can be made quantifiable and how we can detect changes in abundance, diffusion and diversity over geologic time.

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## Dating Abundance, Diffusion, and Diversity

Local increase in abundance (Fig. 3B) is first and foremost the result of individualistic properties: fecundity, fitness, and life span. For a species' abundance to increase, it needs to reproduce and not have traits that drastically reduce survival rates in a given environment, and if individuals live longer, there is greater overlap among generations. Being measured relative to others, fitness inherently encompasses the ecological perspective of how individuals perform and their ability to outperform competitors or benefit from facilitation by others. Geographic connectivity may also contribute to abundance if it provides refuge from abiotic and biotic stressors or more opportunities to reproduce; nevertheless, these processes are more likely to prevent local extinction or inbreeding depression than to effectively increase abundance per se (Wilson 1987). Increase or decrease in abundance can be observed in the fossil record if it is sufficiently continuous and accounts for representational biases (e.g., Wignall and Benton 1999). The use of molecular methods to identify and date increases in abundance is more limited, mostly because it relies on extant or very recently extinct species rather than on remains of ones that may have perished millions of years ago. Ancestral effective population sizes can be estimated from molecular data (e.g., Rannala and Yang 2003; Wall 2003; Schiffels and Durbin 2014, and references therein), but cannot be equated with population size, and are still constrained by the inability to sample extinct clades.

Diffusion (Fig. 3C) demonstrates the ability of a trait or clade to exceed the confines of its initial range and to expand in physical space. Because such spatial expansion often requires expanding beyond the initial niche or crossing geographic and ecological barriers, diffusion often encompasses not only expansion and flexibility in physical space but also in niche space, and can be taken as a measure of wide-range adaptedness or fitness. Diffusion depends on factors such as physical mobility, niche size, and niche range, which are translatable to geographic range (Wiens and Donoghue 2004; Sen 2013; Godsoe 2010). Although geographic connectivity can contribute to increased diffusion, it can also be a confounding factor if a clade diffuses simply because geographic connectivity exists (or becomes possible due to tectonic changes), rather than because of its intrinsic traits. Diffusion due to a trait that overcomes geographic fragmentation or ecological limitations often makes a more convincing case for success (e.g., Gheerbrandt and Rage 2006; Godsoe 2010). Diffusion can be observed in the fossil record as the expansion of geographic and niche spaces in which fossils are found. Phylogeography can contribute to reconstructing the chronology of diffusion by indicating when and how a clade diffused in physical space (e.g., Bouchenak-Khelladi et al. 2010; Prieto-Marquez 2010). Nevertheless, phylogeographic analyses are less effective in identifying diffusion, because conducting such analyses requires a wide geographic range of extant clade members that is by itself evidence of diffusion, and because such analyses are unable to identify areas that clades have occupied in the past but abandoned since then.

Diversity (Fig. 3D) is probably the most commonly used measure of success (e.g., Heard and Hauser 1995; Donoghue 2005), for three main reasons. First, diversification takes time and is therefore likely to be positively correlated with persistence through geologic time. However, some clades can persist for hundreds of millions of years without being extremely diverse at any time throughout their long history or well after their diversity decreased, as exemplified by the 445 Myr history of horseshoe crabs (Rudkin and Young 2009; Lamsdell 2015). Second, the existence of many forms sharing a trait increases the probability that the trait survives over time (Wilson 1987). Third, diversity is often conceived as demonstrating that a shared trait confers an ecological advantage to a variety of organismal forms and niches (Heard and Hauser 1995; Hunter 1998; but see Donoghue [2005] and Pigliucci [2008], who present a more pessimistic view of what key innovations mean for diversification). Notwithstanding this, diversity differs from abundance and diffusion in several aspects (Table 1). Reflecting genotypic and/or phenotypic variance within a derived clade (or

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group of clades sharing a common key trait), diversity mirrors emergence is certain ways. It is more strongly affected by genetic processes than by processes more closely associated with population ecology and is probably driven more by niche partitioning than by competitive superiority or niche range. While abundance and diffusion are often increased by geographic connectivity, diversification may require geographic isolation. Finally, both the fossil and the molecular records strongly attest to periods of high diversification rates. The fossil record provides information on morphological species numbers (e.g., Crepet et al. 2004; Benton 2010; Prieto-Marquez 2010; Herenden et al. 2017), whereas molecular data can directly attest only to current within-clade variance but can indicate the time most of this variance stems from (e.g., Magallon and Castillo 2009; Erwin et al. 2011; Magallon et al. 2015).

The criteria for success differ in the abiotic, ecological, and geographic variables and processes that drive their dynamics (Table 1). Therefore, defining and quantifying the components that contribute to success at different points in geologic time can improve our understanding of macroevolutionary processes and the external factors that may have contributed to a trait's or clade's success. The fossil record can be especially important in such analyses, because each criterion of success is potentially identifiable and datable by a different type of fossil information (Table 1). Molecular methods also hold great potential for quantifying and dating different stages in the rise to success, albeit possibly to a lesser extent than and with some reliance on the fossil record.

## Three Examples

*Oxygenic Photosynthesis and the Great Oxidation Event.*—Approximately 2.4–2.2 Ga, atmospheric $O_2$ concentrations increased from 0.1% to nearly 10%. This increase, the Great Oxidation Event (GOE), is thought to have been caused by intense activity of oxygenic photosynthesizing cyanobacteria (Lyons et al. 2014), and it is often taken as evidence for a great cyanobacterial increase in abundance. Nevertheless, we now have mounting evidence from fossils (Wacey 2010; Schopf 2012), geochemistry (Planavsky et al. 2014), and phylogenetics (Schirrmeister et al. 2015) that oxygenic photosynthesizing cyanobacteria had already existed as far back as 0.3–1 Gyr before the GOE (see reviews in Buick [2008], Hohmann-Marriott and Blankenship [2011], and Schopf [2012]; and critique of some of this evidence in Rasmussen et al. [2008]). This is possibly one of the largest chronological gaps between trait emergence and evidence for its success. One explanation is that cyanobacterial oxygenation before the GOE was absorbed and buffered by the oceans (Goldblatt et al. 2006). Another explanation is that early cyanobacterial oxygenation limited cyanobacterial nitrogen-fixing ability (an anaerobic process) and that cyanobacteria evolved the ability to segregate nitrogen fixation from oxygenation only shortly before the GOE (Berman-Frank et al. 2003; Schirrmeister et al. 2015). It was only once these adaptations evolved that oxygenizing cyanobacteria's fitness increased, leading to them outcompeting non-oxygenic photosynthesizing species (Schopf 2012), increasing in abundance, and eventually causing the GOE.

This example demonstrates that differences in emergence and success times (Fig. 2) can be evidence for complex macroevolutionary processes and for the complex reciprocity that can exist among traits. It also demonstrates the impaired ability to clearly define key innovations as phenotypic "game changers" (Donoghue 2005). In this example, it appears that it is not oxygenic photosynthesis itself that caused an increase in abundance and eventually the GOE, but the subsequent adaptations to the high intracellular oxygen concentrations. So what is, if any, the key innovation?

*Angiosperm Origins.*—A large body of fossil evidence shows that the key morphological and anatomical traits that define angiosperms (e.g., double fertilization, dense leaf-vein systems, and advanced durable vascular tissues) all emerged approximately 200–150 Ma, with no earlier fossil evidence for these traits (Crepet et al. 2004; Herendeen et al. 2017). However, molecular analyses of mitochondrial, plastid, and nuclear sequences suggest that the angiosperm clade and its sibling gymnosperm clade had diverged at least 250 Ma, with

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some studies even suggesting 350 Ma (Qiu et al. 1999; Bowe et al. 2000; Magallon and Castillo 2009; Magallon et al. 2015; and see supporting pollen evidence in Zavada [2007]). Molecular dating of crown angiosperms' emergence, however, agrees with the fossil record, setting dates of approximately 141–135 Ma (Magallon and Castillo 2009; Magallon et al. 2015). Zavada's (2007) report of angiosperm-like pollen in the Triassic suggests that some angiosperm-like or angiosperm ancestral plants did exist at least 250 Ma, but there is no mesofossil or macrofossil evidence for plants with other angiosperm-like traits until 200 Ma. These lines of evidence suggest a 50–200 Myr stasis, in which the ancestral angiosperm and the gymnosperm clades were separated genetically but had indistinguishable morphologies (Sanderson 2015; Katz 2018); that is, ancestral angiosperms were a paleontologically cryptic clade (Sanderson 2015; Struck et al. 2018; Fig. 1).

This possible chronological gap raises questions like how such a long stasis was maintained, or whether distinguishing features exist but are yet invisible to us (Katz 2018). A further question is how quickly after acquiring their distinct traits did true angiosperms diversify and become dominant in various ecosystems (e.g., Krassilov and Silantieva 2005; Magallon and Castillo 2009; Magallon et al. 2015; but see conflicting pollen evidence in Zavada [2007]). Was there a reason that after a long stasis, all angiosperms' key defining traits emerged in such a short time and led to their success? Moreover, it is still disputed whether and which of these traits were the key innovations responsible for angiosperm success (Berendse and Scheffer 2009; Katz 2018), and morphological and anatomical innovations long thought to be key may be abandoned in favor of life cycle traits (Berendse and Scheffer 2009).

*Plant Silicon*.—Silicon confers various benefits to plants that can accumulate it in large amounts, including defense from herbivores and improved resistance and tolerance to aridity (Katz 2014). Trembath-Reichert et al.'s (2015) analysis of plant silicon transporters' phylogeny revealed that the genetic infrastructure for silicon accumulation is shared by all land plants and may precede the invasion of the land. Strömberg et al. (2016) found that despite the shared genetic infrastructure (Trembath-Reichert et al. 2015), active silicon accumulation evolved independently several times among land plants and angiosperms, but found no temporal coalescences with possible environmental drivers (e.g., aridity or herbivory). Finally, Katz (2015) found that silicon-rich angiosperms' early success (reflected by the diversification of angiosperm orders with silicon-rich species compared with clades with only silicon-poor species) is possibly contemporaneous with the evolution of abrasion-adapted dentition in several dinosaur and mammalian clades, suggesting a possible coevolution of the two traits. These three studies allegedly tell three different stories.

The contradiction between Strömberg et al.'s (2016) failure to identify external drivers and Katz's (2015) suggested coalescence can be explained by Katz (2015) referring to success time, which reflects increased fitness that can more strongly be related to external drivers than Strömberg et al.'s (2016) emergence times (Fig. 2). The difference between Trembath-Reichert et al.'s (2015) and Strömberg et al.'s (2016) emergence times can be explained by silicon accumulation being a complex trait that involves several transporters (Ma and Yamaji 2015), whose physiology and ecology vary among plant clades (Katz 2014). The shared genetic infrastructure for silicon accumulation that Trembath-Reichert et al. (2015) studied is only partial, so the trait's later independent emergences possibly follow the emergence of other components of the complete silicon-accumulation system or the removal of certain physiological barriers (Fig. 1). Therefore, each of the three studies or research approaches tells only a part of the full story: the emergence of genetic and physiological infrastructure (Trembath-Reichert et al. 2015), the emergence of the trait and the clades bearing it (Strömberg et al. 2016; Fig. 2), and its ecological success (Katz 2015; Fig. 3).

## Concluding Notes

Genes, traits, and clades; fitness, diversity, and biogeography—each is a part of the macroevolutionary process. The mechanistic and

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chronological linkages among these turn macroevolution from a series of events into a process. Therefore, a correct reading of the full story relies on our ability to distinguish the various components that make a macroevolutionary process and how they are mechanistically and chronologically linked. Any new date assigned to a part of the macroevolutionary process—whether it is obtained from a newly discovered fossil or from analyses of the fossil and molecular record—needs to be examined by asking and answering the fundamental question of what component is actually being dated. Then the new date needs to be compared with other dates (again, considering which components of the macroevolutionary process they date). Conflicts exist if dates for the same component (e.g., the emergence of a gene or a trait) differ greatly or if the chronological order of two or more components is highly improbable (e.g., a trait emerging before the genes that code it). Such conflicts most likely indicate a methodological problem.

However, other cases, such as the ones described in the three examples presented earlier, do not reflect real conflicts. Such chronological gaps can potentially exist because of real biological phenomena (e.g., the cases of cyanobacteria and angiosperm ancestry) or because of differences in data sources (e.g., the cases of cyanobacteria and plant silicon). Such chronological gaps may also not exist—or at least may be undetectable—if gene emergence, trait emergence, clade emergence, and rise to success all take place in a tight time frame. However, when such gaps exist, they present new questions and new avenues of research. The ecology of early cyanobacterial oxygenation and the possibility of ancestral angiosperm crypticity are only two examples. Hence, looking into these gaps can increase our understanding of macroevolution itself, and even raise principal questions, for example, how traits and clades evolve, or how and what we perceive as key innovations.

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