



Biogeographic Dating of Phylogenetic Divergence Times Using Priors and Processes

9

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Abstract

Historical biogeographic processes shaped the distribution of life throughout space and time. A species range might expand, contract, or subdivide throughout its evolutionary history, during which extrinsic factors such as the palaeogeographic arrangement of land masses can influence how a species range evolves. Phylogenetic studies can therefore benefit from incorporating biogeographic and palaeogeographic evidence into their analyses in order to better estimate species divergence times and species relationships. This chapter begins by outlining a conceptual framework for using biogeography to date phylogenies, with some emphasis on the inherent uncertainty of reconstructing past events. Following this, the chapter explores two methods (prior- and process-based methods) for estimating divergence times using biogeographic evidence and discusses their applications and merits.

Keywords

Phylogenetic inference · Time-calibration · Dating · Biogeography · Palaeogeography

9.1 Introduction

How have the evolutionary lineages of life diversified during Earth's history? Phylogenetic inference seeks to answer this question in two principal ways: with topological estimates that explain relationships among lineages and with dating estimates to bracket when lineages diverged in geological time (in millions of years). Today, tree topology is readily estimated from molecular sequence data thanks to nearly 50 years of parallel advancements in the fields of molecular evolution, genetic sequencing, and phylogenetic inference. But even with this bounty of molecular sequences, those data alone are incapable of dating geological divergence times under existing models of molecular evolution. For now and for the foreseeable future, extrinsic information is needed to time-calibrate (or date) the ages of phylogenetic lineages, information such as that from the fossil record or from the lasting impression of palaeogeographical scenarios upon biogeographic patterns (see Chap. 5). Fossils have been, and remain, indispensable in how biologists understand evolution. In the current era of phylogenetic inference, the fossil record is unquestionably the preferred source of evidence for time-calibrating molecular phylogenies (see Chap. 8). Under the best conditions, a fossil specimen preserves the ancient presence of an evolutionary lineage through its morphological features and its age. With palaeontological expertise, that morphology can be used to diagnose the fossil

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taxon's phylogenetic relationship to extinct and extant taxa. If the phylogenetic hypothesis places the fossil within a clade of extant taxa (a crown group), then that clade must be at least as old as the fossil, i.e., a crown-group fossil constrains the minimum age for that clade (Marshall 1990).

For many, this line of reasoning is quite direct and intuitive. But, in practice, fossil dating is complicated by a range of challenges, spanning the theoretical to the empirical. Researchers are actively advancing how we understand fossil dating in topics as varied as its application (Donoghue and Moore 2003; Parham et al. 2012), its robustness (Warnock et al. 2015; Brown and Smith 2017), and how to explicitly incorporate fossil morphology into the model of divergence-time estimation (Pyron 2011; Ronquist et al. 2012), with diversification processes that allow for the preservation of fossil-taxon occurrences (Heath et al. 2014) and fossil-taxon time series (Stadler et al. 2018), with fossilization processes under the multispecies coalescent (Ogilvie et al. 2018), and more (see Chap. 11).

While many theoretical obstacles in fossil dating are likely to surrender to human creativity (and computational muscle) over time, some empirical obstacles appear to be immutable properties of our natural world. Perhaps the largest empirical complication is the paucity of known fossils for many groups of organisms. To make this concern concrete, take the turtles (order Testudines), a clade with a fossil record so exquisite that turtles serve as a model clade for experimenting with fossil dating strategies (Joyce et al. 2013; Warnock et al. 2015). In contrast, consider the daisy family (Asteraceae), where new fossil discoveries are rare and when found rewrite our understanding of their diversification (Barreda et al. 2015). While the Paleobiology Database is not a perfect reflection of the fossil record itself, Asteraceae is represented by far less than one-thousandth as many described fossil specimens per living species when compared with Testudines ($\frac{100}{26000} \div \frac{8000}{350} \approx 0.00017$) on the database (Turtle Taxonomy Working Group 2017; Paleobiology Database 2018;

Angiosperm Phylogeny Website 2018). Many plant, fungus, and insect clades lack fossils useful for dating, creating widespread demand for dating methods that do not directly depend on the fossil record.

Biogeographic dating is one possible alternative. Biogeographic evidence, like the fossil record, is fundamentally linked to our understanding of how evolution has generated and maintained biodiversity over geological time. Since the earliest days of evolutionary thinking, biogeographic disjunctions have been viewed as both intriguing and perplexing patterns (Wallace 1855; Darwin 1859; Wallace 1876). In particular, how is it that closely related lineages come to inhabit distinct regions that are separated today by a geographical barrier? One lineage must have either dispersed over the barrier after it was formed, or dispersed into the new region before the barrier existed. Studying disjunctions from an evolutionary perspective makes it clear that dispersal opportunities are shaped by palaeogeographical dynamics that play a central role in shaping biogeographic processes and patterns: the opening and closing of ancient seaways, the formation of mountains, and the surfacing of volcanic islands.

It follows that palaeogeography and biogeography, together, can serve as a valuable source of dating information. Take, for instance, a clade of species that is endemic to a young oceanic island, far from its mainland relatives (Fleischer et al. 1998). The endemics did not spontaneously originate on the island, so what sequence of biogeographic events can explain the clade's geographical distribution? At one extreme, all lineages within the clade might have first originated on the mainland before the new island formed, then independently colonized the island only after its origination, followed by any necessary extirpation and/or extinction of mainland lineages. In this case, the clade might be older than the island. A second, more plausible scenario is that one lineage colonized the new island and then radiated upon it (Baldwin and Sanderson 1998). If this second scenario were true, the clade would be younger than the island. Time-calibrating phylogenies with biogeography and

palaeogeography operates by this reasoning: that some biogeographic scenarios are more likely than alternatives for a given palaeogeographical context, and that likelihood should influence what ages we estimate for the lineages involved (Ho et al. 2015; de Baets et al. 2016).

Although historical biogeography and palaeogeography are each fascinating in isolation, I will only focus on how they serve to inform divergence times in this chapter. Translating possible biogeographic histories into statistical information, specifically, to inform or date divergence times in a tree, is the exercise of dating phylogenies using historical biogeography. I will begin this chapter by reviewing several examples of how palaeogeography, biogeography, and diversification together generate information to date phylogenies. Then, I will discuss two Bayesian frameworks for biogeographic time-calibration, and illustrate the utility of both with empirical examples. First, I will consider biogeographic node calibrations that date key divergence events using expert-defined prior node densities. Second, I will explore a newer class of likelihood-based biogeographic dating methods, which explicitly model and probabilistically weight alternative biogeographic histories. This chapter concludes by characterizing general views of the utility of biogeographic dating in the field, its uses, its shortcomings, and its future.

9.2 Linking Phylogeny, Biogeography, and Palaeogeography

In its simplest form, biogeographic dating relies on combined evidence from palaeogeographic, biogeographic, and molecular phylogenetic data (Renner 2005; Ho et al. 2015; de Baets et al. 2016). What dating information can be extracted from these data depends entirely on what clade, what regions, and what timescales are under study. Rather than speaking in generalities, this section will examine several idealized scenarios portrayed in Fig. 9.1 to develop guidelines for identifying what biogeographic scenarios might enrich a phylogenetic dating analysis.

For clarity, we will consider geography in a discrete setting, with two regions, a northern region (N) and a southern region (S). The palaeogeographic context, which describes features such as the availability of and connectivity between regions, changes at the time labelled T . Figure 9.1 shows three alternative palaeogeographic scenarios: the new availability of a region where the initial existence of region S begins only after time T (Fig. 9.1a); the new connectivity between the regions N and S after time T (Fig. 9.1b); and the lost connectivity between the regions N and S after time T (Fig. 9.1c).

Three biogeographic and phylogenetic scenarios are shown in Fig. 9.1 and these are explained in more detail below. In each biogeographic scenario, I assume that we know precisely when and how the palaeogeographic context changed, how that influenced species range evolution, and how that relates to lineage diversification. Note that the examples assume identical statements of phylogenetic topology and species ranges across scenarios, highlighting how node-age distributions (in red) should respond to alternative palaeogeographic histories. All scenarios require at least one dispersal event from region N into region S. Multiple dispersals could also explain the observed biogeographic patterns, but those explanations would generally be eliminated by parsimony or penalized by probability: all else being equal, the probability of one dispersal, p , is greater than or equal to the probability of two dispersals, $0 \leq p^2 \leq p \leq 1$.

The first biogeographic scenario describes the recent colonization of and radiation within a newly accessible region (Fig. 9.1d). One example of a newly available region is the birth of an oceanic island through volcanic activity (Fig. 9.1a; Clague and Sherrod 2014). Regional availability provides a strong maximum age constraint for divergence times, since the region could not have been inhabited before it existed. New interregional connectivity generates a related, but weaker, source of dating information. Connectivity between regions increases following events such as the merging of two continents or the erosion of an intermediate mountain range

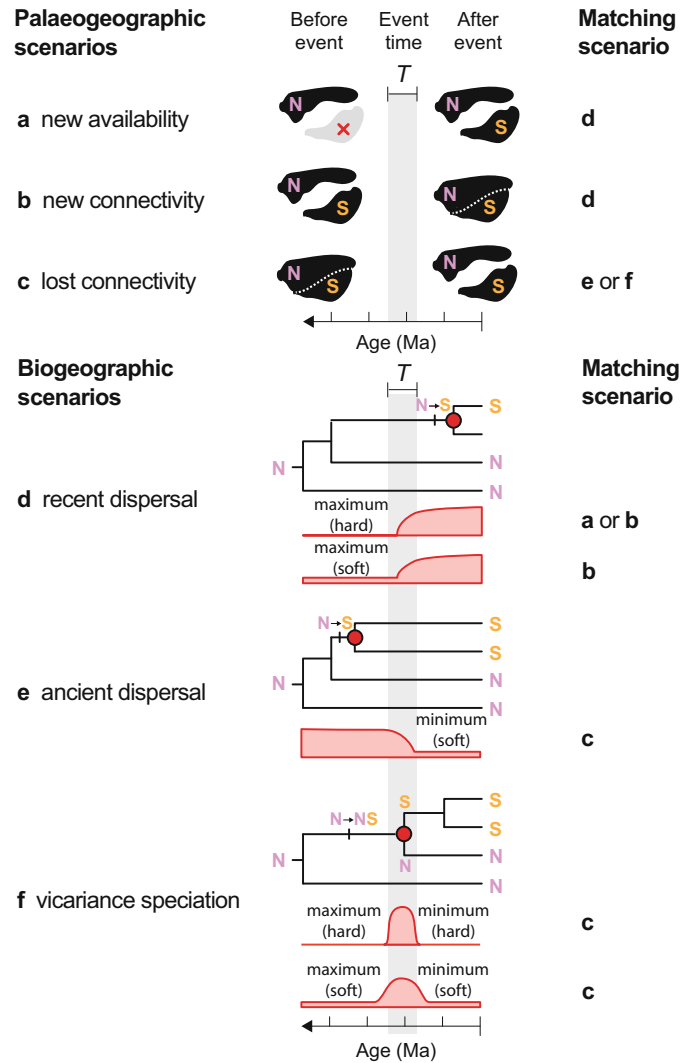


Fig. 9.1 Cartoon of biogeographic dating scenarios. Node-age distributions (red) by combining evidence that supports particular palaeogeographic scenarios (top) and biogeographic scenarios (bottom), either with prior- or process-based methods (further details are given in Sect. 9.3 of the main text). The three palaeogeographic scenarios show how connectivity and availability between two regions, N and S, changed during the time interval T (grey bar): **(a)** region S originates; **(b)** regions N and S

merge; and **(c)** regions N and S split. The three biogeographic scenarios show various timings for biogeographic and lineage splitting events and whether those timings are consistent or not with the proposed palaeogeographic scenarios **(a–c)**: **(d)** a recent dispersal scenario; **(e)** an ancient dispersal scenario; and **(f)** a vicariance scenario. Panels **(d–f)** all show the same topology and species ranges, differing only in the ages of biogeographic and lineage splitting events

(Fig. 9.1b). In this scenario, colonization events can precede the formation of the barrier, but they occur at a much lower rate (i.e., with lower probability per unit time).

The second biogeographic scenario describes ancient dispersal (Fig. 9.1e). Ancient dispersal involves a lineage colonizing a region before a geographical barrier is formed. Interregional connectivity is lost with the emergence of mountains,

the splitting of continents, the submergence of a land bridge (Fig. 9.1c), or the loss of an intermediate connecting region (absent in Fig. 9.1 since it requires >2 regions). Lineages can freely disperse between regions before the barrier forms, but they do so at a much lower rate afterwards (i.e., with lower probability per unit time). For the example shown in Fig. 9.1e, dispersal into region S occurs before the barrier forms, with the

lineages diverging for unspecified reasons well before regions N and S separate.

The third biogeographic scenario describes vicariance (Fig. 9.1f). Vicariance speciation involves two phases. First, a new geographical barrier interrupts the gene flow within a widespread species range. Widespread is a relative term, which operationally means that the species range spans multiple regions; in Fig. 9.1f, one lineage becomes widespread when it expands from region N into both regions N and S. Second, while this new barrier stands, subdivided populations in the species range develop heritable incompatibilities that establish one or both isolates as new lineages. Note that vicariance requires that the split lineage is ancestrally widespread, implying that vicariance scenarios involve an ancient dispersal event at some point in the clade's ancestry. While an ancient dispersal scenario prefers clade ages that predate the age of the new geographical barrier (Fig. 9.1e), a vicariance scenario constrains both the minimum and maximum clade ages to follow the age of the new barrier.

To reiterate, the biogeographic scenarios presented in Fig. 9.1 are simplified in order to introduce three categories of biogeographic dating evidence. When appropriate, each biogeographic scenario generates its own set of divergence-time constraints: recent dispersal scenarios are used to constrain the maximum age of a divergence, ancient dispersal scenarios provide a minimum age constraint, and vicariance scenarios provide both maximum and minimum age constraints. But how do we know when it is appropriate to invoke biogeographic evidence to date a phylogeny? And how much influence should biogeography and palaeogeography have on clade-age estimates? After all, in standard phylogenetic analyses, we do not precisely know the relationships among lineages, their divergence times, and the biogeographic history of the clade (which depends on phylogenetic knowledge), not to mention our poor knowledge of the exact sequence and timing of many palaeogeographic events. The next section discusses these matters in more detail.

9.3 Time-Calibrating Trees with Biogeography

A central premise of biogeographic dating is that palaeogeography informs phylogenetic node ages through the clade's biogeographic history. But how do we translate palaeogeographic events and biogeographic patterns into information about clade ages in practice? To begin, I will reintroduce several familiar modelling components used in molecular phylogenetics that were detailed in Chaps. 5 and 6. Here, and for the rest of the chapter, we will assume that we are interested in estimating phylogeny by modelling a molecular substitution process (Felsenstein 1981) where lineages diversify following a branching process (Nee et al. 1994) and molecular rates along branches vary according to a relaxed-clock model (Thorne et al. 1998). By fitting such a phylogenetic model to molecular data, we can simultaneously estimate the parameters for the tree topology, the node ages, the substitution process, the relaxed molecular clock, and the diversification process.

Without calibrations, the node ages can be estimated in units of relative time at best (Thorne et al. 1998). To estimate geological divergence times, researchers have typically relied on fossil evidence, secondary calibrations from backbone phylogenies, or biogeographic hypotheses. Regardless of the dating method, the exact relationship between any line of extrinsic evidence and the timing of one (or several) divergence events is not known with absolute certainty. Because they readily accommodate this inherent source of uncertainty, Bayesian phylogenetic approaches have proven extremely effective for divergence-time estimation (Drummond et al. 2006; Yang and Rannala 2006; Ronquist et al. 2012; Chaps. 6 and 13).

Briefly reviewing Bayesian phylogenetics will help frame how we survey biogeographic dating methods. The chief aim of Bayesian phylogenetics is to estimate the distribution of evolutionary parameters that have a high probability of generating the data that we observe in nature, such as the observed data being the

molecular sequences and geographic ranges of the species being compared. This estimated distribution is called the posterior distribution, and it is defined as being proportional to the product of the likelihood function and the prior distribution.

$$P(\tau, a, \theta|X) = \frac{1}{Z} \times \underset{\text{likelihood}}{P(X|\tau, a, \theta)} \times \underset{\text{prior}}{P(\tau, a, \theta)} \quad (9.1)$$

In the above formulation, the posterior distribution defines the joint probability over the possible tree topologies, τ , divergence times, a , and other model parameters, θ , such as various rates of evolution and diversification-process parameters, conditional upon the observed data collected from nature, X . The normalization term, $\frac{1}{Z}$, is the reciprocal of the marginal likelihood, which is not directly relevant to the topic of dating discussed here. What is important to recognize here is that the likelihood function, $P(X|\tau, a, \theta)$, is a function of the observed data, X , while the prior distribution, $P(\tau, a, \theta)$, is not. The likelihood function defines a model of evolution that can generate our observed data, X , that we use to fit the model parameters, θ . This means that if our observations of the natural world for X changed, so would our parameter estimates for θ . In contrast, the prior distribution θ remains constant regardless of the value of X . In this sense, the prior density is data-independent and the likelihood function is data-dependent, which has consequences for the dating estimates that are discussed later. The next two sections introduce Bayesian strategies for time-calibrating phylogenies: prior-based node calibration methods and process-based dating methods. In these sections, I will discuss some of the strengths and sensitivities of each approach.

9.3.1 Prior-Based Node Calibrations

Prior-based node calibrations, often called node calibrations or node priors for short, are used to

constrain the range of divergence times for targeted nodes in phylogenies. During inference, the prior probability of the calibrated node's age is taken into account when computing the joint probability of all node ages in the phylogeny. Dated phylogenies with node ages that do not conform to all specified node calibrations are scored with low probabilities, and are thus disfavoured during estimation. In practice, node calibrations are most often applied using fossil evidence. Over decades, palaeontologists and evolutionary biologists have developed a rich literature of techniques and best practices (Parham and Irmis 2007; Parham et al. 2012; Joyce et al. 2013; Warnock et al. 2015) that we can extend to frame principles for biogeographic node calibrations here.

Applying fossil-based node calibrations involves two major steps: the calibration must first be justified, then the age constraints must be specified. Justification involves determining that a fossil specimen is a valid representative of early-diverging stem or crown lineages of the target node that is present in an explicitly stated phylogenetic hypothesis. Parham et al. (2012) advocate for the placement of fossils through the cladistic analysis of morphology of fossil and extant taxa. During justification, the biologist defines the prior probability for the distribution of possible ages relating to the calibrated node. Some aspects of specification are considered standard practice, particularly that fossil specimens represent the minimum age of the split, so the calibrated lineage must be at least as old as the fossil representative (Marshall 1990). Yet other aspects of the prior are not so easily specified. In particular, when did a lineage first originate, i.e., what is its maximum age? The clade could lack early fossil representation because of taphonomy or simply because the lineage had not yet originated (Jaanusson 1976), rendering the true maximum age unknowable. While models exist to estimate origin times under fossil sampling distributions (Strauss and Sadler 1989; Marshall 2008), assigning maximum age constraints to calibrations is, to some, a dubious exercise (Heads 2012). Nonetheless, explicitly or

implicitly, all sources of calibration uncertainty are encoded in the phylogenetic position and the prior age density.

Superficially, biogeographic node calibrations resemble fossil node calibrations in that they both assert an evolutionary hypothesis to justify the prior preference for certain node-age estimates. To justify, specify, and validate a biogeographic node calibration, however, requires principles that are distinct from what fossil-based methods use (Kodandaramaiah 2011; Ho et al. 2015; de Baets et al. 2016). I have outlined these principles below and diagrammed them in Fig. 9.2.

An overview of prior-based biogeographic dating

(I) Justification

- (a) Declare the phylogenetic hypothesis of lineage relationships.
- (b) Record the biogeographic distributions for the taxa.
- (c) Indicate which node will be calibrated by identifying a biogeographic disjunction between one clade and its close relatives.
- (d) Assert the hypothesis that a (dated) palaeogeographic event facilitated or maintained the biogeographic disjunction that is represented by the calibrated node.

(II) Specification

- (a) Record the range of possible dates for the palaeogeographic event named in Step I-d.
- (b) Define a prior to constrain the range of plausible ages for the node specified in Step I-c as influenced by the dated palaeogeographic event of Step II-a.
- (c) Define standard models of molecular evolution and lineage diversification.

(III) Estimation

- (a) Estimate the posterior of dated phylogenies under the chosen biogeographic prior.
- (b) Confirm that dated phylogenies do not imply internal inconsistencies, i.e., no resulting biogeographic scenarios that contradict premises for justifying the calibration.

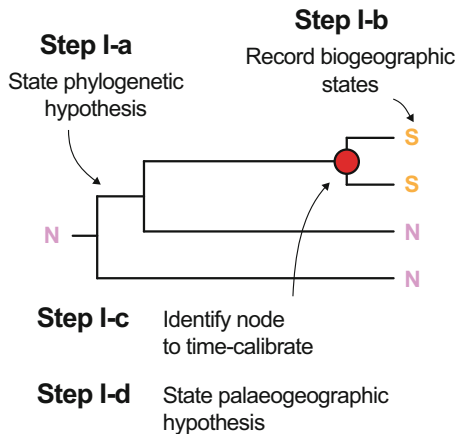
- (c) Assess prior sensitivity of posterior estimates.

Justifying a biogeographic node calibration leverages a combination of palaeogeographic, biogeographic, and phylogenetic evidence. Typically, the researcher begins with a phylogenetic hypothesis, such as the topology estimated from a molecular phylogeny. Next, biogeographic disjunctions are identified from species range data mapped to the tips of the phylogenetic hypothesis. Lastly, the researcher identifies and asserts that a particular palaeogeographic event influenced the age of the proposed biogeographic scenario. For example, take the phylogenetic hypothesis (Step I-a) and range data (Step I-b) of the biogeographic scenario in Fig. 9.1d. In this case, we assert that a dispersal event into region S followed by in situ speciation in region S explains the biogeographic disjunction between regions N and S today (Step I-c), where the dispersal event must have occurred after region S came into existence (Step I-d).

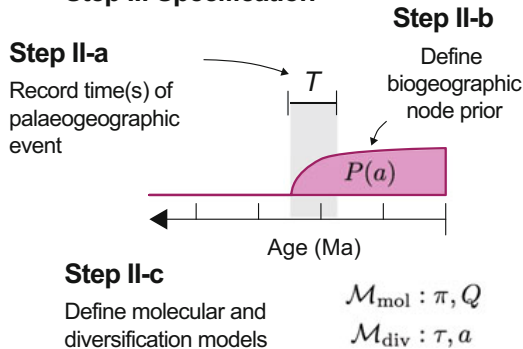
Justifying biogeographic node calibrations is often challenging for purely practical reasons: small and recent radiations often lack sufficient molecular variation to claim strong phylogenetic hypotheses, while backbone phylogenies built from, for example, genera as taxa generally represent deeper timescales, making it difficult to assert specific historical biogeographic scenarios with certainty. Perhaps more troublingly, several researchers (Renner 2005; Kodandaramaiah 2011) hold that circular reasoning is sometimes required to justify biogeographic node calibrations: to assert that a biogeographic event should favour a certain phylogenetic hypothesis (i.e., a range of node ages for a divergence event), the practitioner must first assume a phylogenetic hypothesis (i.e., that biogeographic change induced the divergence event).

Once the calibrated node has been justified, specifying the calibration density requires two main considerations: When was the palaeogeographic event and, relative to it, when might the calibrated divergence event have occurred? Depending on the event, the palaeogeographic event might have occurred

Step I: Justification



Step II: Specification



Step III: Estimation

Step III-a

Estimate posterior ages from molecular data and node prior

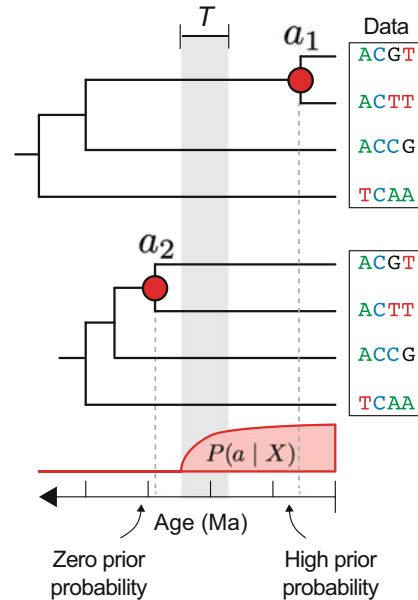


Fig. 9.2 Diagram of prior-based biogeographic dating. Node calibration involves three major steps. Justification (Step I) asserts a divergence scenario by interpreting evidence from a phylogenetic hypothesis (I-a) and the biogeographic states of the taxa (I-b) to identify a divergence event (I-c) whose biogeographic disjunction was hypothetically caused by a palaeogeographic event (I-d). Specification (Step II) designs a model to estimate divergence times by recording the time of the divergence-causing palaeogeographic event (II-a) then assigning a node prior

of divergence times relative to the palaeogeographic event time (II-b), along with specifying standard molecular and diversification model components (II-c). Estimation (Step III) fits the model with the node prior to the molecular data to estimate a posterior density of dated phylogenies. The prior density (purple; Step II-b) has zero probability for ages older than T , which is reflected in the posterior density (red). Thus, the posterior density prefers young ages (a_1) rather than old ages (a_2). Steps III-b and III-c are not shown. See Sect. 9.3.1 for additional details

instantaneously or gradually, and its date (or duration) might be known precisely or not (Step II-a). When in doubt, conservative times that minimize the dating information are preferred, e.g., using an island age that is slightly too old reduces the influence of a young-dispersal node calibration. To define the offset between the calibrated divergence time and the

palaeogeographic event, the shape of the calibration density should reflect whatever scenario was used for its justification (Step II-b). The divergence event might have preceded, coincided with, or followed the palaeogeographic event (Fig. 9.1). For example, the young-dispersal scenario acts as a hard maximum age constraint for the crown node of a subclade's radiation, so the

prior probability should be zero for all subclade ages that are older than the newly available region (Fig. 9.1d). Ancient-dispersal scenarios include only a minimum age constraint (Fig. 9.1e). Vicariance speciation scenarios apply both minimum and maximum age constraints (Fig. 9.1f). Node ages that do not conform to the asserted biogeographic scenario can be assigned zero prior probability (hard constraints) or small nonzero probabilities (soft constraints). Typical node prior densities are simple univariate densities (e.g., uniform, exponential, gamma, and lognormal) with shapes that reflect the asserted biogeographic hypothesis. In addition to the node prior, a standard model of molecular evolution and lineage diversification is specified (Step II-c).

The final step, estimation, first estimates the posterior of time-calibrated phylogenies (Step III-a), then validates those estimates in two ways. One type of validation re-examines whether the initial justification for the calibration is compatible with the subsequent estimates for all nodes in the phylogeny (Step III-b). A vicariance-based node calibration, for example, will assert that a conspicuous biogeographic disjunction resulted from, say, continental rifting that subdivided an ancestor's range. This justification excludes long-distance dispersal as an explanation, but if a vicariance-based calibration inadvertently induces long-distance dispersal events elsewhere in the phylogeny, then the justification itself is questionable (discussed by Kodandaramaiah 2011). It is also crucial to validate that the specified calibrations do not interact negatively with other model priors and with the data (Step IV-b). Though choosing well-behaved priors in Bayesian phylogenetics is often difficult (Alfaro and Holder 2006), misbehaviour can be detected through prior-sensitivity analyses in which the prior and posterior divergence-time estimates are compared under a variety of calibration hypotheses (Warnock et al. 2015; Brown and Smith 2017).

Practical details aside, hundreds of studies have employed prior-based node calibrations based on biogeographic evidence over the past two decades. Listed below is a sample of biogeographic node-calibration analyses applied to a

diversity of clades and historical scenarios (Fig. 9.1). Pioneering examples include the work of Fleischer et al. (1998), who calibrated the Hawaiian honeycreeper radiation using the ages of the modern High Islands while being careful to explicate what they assumed to justify the calibrations. That same year, Baldwin and Sanderson (1998) dated the Hawaiian silversword radiation, not using the island ages themselves, but rather the date of dry-summer conditions that appeared in the western North American continent during the mid-Miocene (15 Myr ago). Under the assumption that the arid climate predated the radiation of the silverswords' arid-adapted ancestors (crown Madiinae), this palaeoclimatic shift was used to impose maximum age constraints to calibrate the tree. Hawaiian palaeogeography has been subsequently used to date numerous clades, including *Megalagrion* damselflies (Jordan et al. 2003) and *Hyposmocoma* moths (Haines et al. 2014).

Island palaeogeography outside of Hawaii has also proven useful for node calibration. Studying Sapotaceae, Swenson et al. (2014) used the age when New Caledonia last surfaced from the sea to date five independent colonizations of New Caledonia, shifting crown node ages to be younger by 15–20% (up to 5 million years) relative to when palaeogeography was ignored. Plana et al. (2004) took the formation of two volcanic islands to time-calibrate the radiation of African begonias, a clade with no described fossils. From 16 possible biogeographic calibrations dependent on volcanic and continental island ages, Andújar et al. (2014) computed Bayes factors to select eight biogeographic scenarios that yielded congruent divergence times for *Carabus* beetle diversification.

To marine organisms, the appearance of new land in the ocean acts as a geographical barrier that potentially limits, rather than facilitates, new dispersal opportunities. To this end, many biogeographic calibration studies have focused on the closure of the Isthmus of Panama during the Pliocene: Cowman and Bellwood (2011) used this event, along with fossil calibrations, to date four families of coral reef fishes; Thacker (2017) dated two fish families, Elotridae and

Apogonidae, and showed that using biogeographic calibrations reduced mean divergence times by roughly 30–35%; Swart et al. (2015) also used the isthmus to date Carangidae fishes, which, during validation, revealed that an ancient divergence event and biogeographic disjunction was incidentally consistent with the closure of the Tethys Sea. Yet, as a land bridge, the isthmus simultaneously facilitates terrestrial dispersal: Fuchs et al. (2007) calibrated the basal node of a North-South American disjunction in woodpeckers (Picidae), arguing that dispersal was improbable before the isthmus began to form.

Gondwanan vicariance has been proposed extensively to date clades distributed throughout the Southern Hemisphere, with mixed results in studies of terrestrial invertebrates. Allwood et al. (2010) invoked Gondwanan vicariance to date the evolution of velvet worms (Onychophora), a monophyletic phylum with no inferred transoceanic dispersals. If it is true that New Zealand was entirely below sea level during the late Oligocene (Mildenhall et al. 2014), then this vicariance calibration would imply that velvet worms somehow survived the island's submersion. Allegrucci et al. (2010) examined the Gondwanan distribution of cave crickets (Raphidophoridae), finding that while many vicariance calibrations appear justified, other biogeographic disjunctions can only be explained by invoking long-distance dispersal or with exceedingly ancient (Precambrian) crown-node ages (also see Beasley-Hall et al. 2018). McCulloch et al. (2016) studied the effect of various fossil and tectonic calibrations on the date estimates of Gondwanan stoneflies (Plecoptera). Examining 17 uncalibrated nodes that corresponded to Gondwanan disjunctions, McCulloch et al. found that five of those nodes had age estimates consistent with tectonic events: vicariance sufficiently explained some, but not all, divergence events.

Mountain-building episodes have also been used to calibrate divergence times. On one hand, mountains can serve as geographical barriers between regions: Mansion and Zeltner (2004) used the dates of uplift of the Sierra mountains and various Mexican mountains to calibrate nodes of the *Zeltnera* (Gentianaceae) phylogeny.

Mountains also resemble islands to high-altitude specialists: Chaves et al. (2011) dated the serial expansion of *Adelomyia* hummingbirds, a clade of cloud forest endemics, using calibrations based on the south-to-north uplift of the Andean mountains.

Like many fossil-based node calibrations, biogeographic node calibrations are often contentious. Node calibrations should be, and are, subject to measured scientific scrutiny. For example, efforts to date the plant clade Crypteroniaceae stoked discourse among phytogeographers about if, when, and how one might use biogeographic calibrations. Conti et al. (2002) applied tectonic calibrations for Crypteroniaceae, including its migration from the African to Asian continent aboard India as it drifted northwards following the breakup of Gondwana. Moyle (2004) proposed an alternative phylogenetic hypothesis that undermined the justification of Africa-India vicariance calibrations and questioned the range of dates used to represent Gondwanan rifting (see response by Conti et al. 2004), but a comprehensive effort to validate the calibrations by Rutschmann et al. (2004) supported the original conclusions of Conti et al. (2002).

There are important cases where the fossil record undermines the justification of key calibrations. Gibb et al. (2015) questioned the use of Gondwanan vicariance to time-calibrate several passerine phylogenies in the literature. The calibration depended on the rifting of Zealandia from Australia throughout the Late Cretaceous (~82 Myr ago) to date the split between a clade composed of two species of flightless wrens that are endemic to New Zealand from all remaining passerines. Gibb et al. (2015) took two issues with the justification of this calibration. First, the wrens might have arrived in Zealandia after the rifting event if their ancestors could fly. Second, flightless wrens would have been extirpated from New Zealand if and when the island was inundated in the late Oligocene (22–25 Myr ago). Gibb et al. (2015) also took one issue with the specification: that the Australia-Zealandia rift might not have completed until much later (~55 Myr ago). In another example, Goswami and Upchurch

(2010) found that the vicariance calibrations used by Heads (2010) were unjustified in explaining the disjunction between New World monkeys and Old World monkeys. The calibrations require that early primate lineages were globally distributed, first diverging during the breakup of Pangaea in the Jurassic (~160 Myr ago). It would be unprecedented, Goswami and Upchurch argued, for primates to be sufficiently ancient and widely distributed, yet leave no appearances in the fossil record until the late Paleocene (~56 Myr ago). Moreover, no eutherian mammal fossils were known prior to 125 Myr ago (Goswami and Upchurch 2010). If primates were so ancient, per the Pangaeian vicariance hypothesis, that fact would radically alter our understanding of evolutionary processes, vicariance speciation, and the fossil record.

In other cases, sole reliance on fossils for dating can result in node-age estimates that are unusual when viewed in light of biogeographic and palaeogeographic evidence. Ali (2020) identified that the fossil-calibrated phylogeny of *Kurixalus* frogs (Lv et al. 2018) implies that Taiwan was colonized at least 10 Myr before the island had originated. Román-Palacios et al. (2018) detected a similar issue in a fossil-dated phylogeny of Caribbean anoles that they estimated. In it, a clade of island endemics appeared to predate the emergence of the island itself. The quality of a dating analysis is improved by examining where complementary lines of evidence agree or disagree.

To summarize this section, biogeographic node calibrations encode expert knowledge and diversification hypotheses as prior probabilities to constrain when key lineage-splitting events occurred. Biogeographers and evolutionary biologists are developing new conceptual frameworks for how to justify and specify palaeogeographic node calibrations (Kodandaramaiah 2011; Ho et al. 2015; de Baets et al. 2016). Two dominant themes emerge from the few examples of biogeographic node calibration listed above. First, biogeographic node calibrations tend to be used to date clades with little or no representation in the fossil record, including plants, insects, fish, and birds. And,

second, the justification for some biogeographic calibrations, particularly vicariance calibrations, wither away when assessed critically, while others remain firm.

Beyond their application in the literature, it is important to recognize that node priors are only as good as their justification and specification. With justification, how certain is it that a particular biogeographic event influenced the phylogenetic split of interest? If this scenario is unlikely, then any dates estimated under its premise are equally questionable. If one could confidently state the probability, p , of a key biogeographic scenario informing the age of the calibrated node, a_n , then the node prior could be treated as a mixture of priors where a_n follows the calibration prior with probability p and an uninformative uniform prior with probability $1 - p$. This is a calibration with soft bounds (Yang and Rannala 2006). What complicates this strategy is that the value of p should depend on the biogeographic states at the tips of the tree, the tree topology and distribution of divergence times, the tempo and mode of the biogeographic process, and the unknown interactions between biogeography and palaeogeography: that is, p needs to be inferred from the data with a biogeographic model.

Specifying node prior calibration densities is also challenging. What probability density represents all of the uncertainty concerning the age of the divergence event relative to the palaeogeographic event? This depends a great deal on the palaeogeography, biogeography, and phylogeny of the system in question. For example, a prior density for a lineage from the mainland colonizing and radiating in an island system might be constructed as a compound prior

$$a_n = a_i - t_c - t_d \quad (9.2)$$

where a_n is the age of the first divergence event among a clade of island endemics, a_i is the age of the island, t_c is the waiting time for a mainland lineage to colonize the new island, and t_d is the waiting time until divergence following genetic isolation. Decomposing the prior in this manner clarifies some of the assumptions made to specify it. For example, we might define a_n as the age of a

uniformly distributed island age minus two exponentially distributed waiting times: this would be fairly consistent with the definition of a gamma distribution centred on a random age away from zero. While it might be straightforward to acquire a radiometric date (with error terms) for the island age component, a_i , it is less clear what the expected waiting times until colonization, t_c , and until lineage splitting, t_d , should be. Like the justification probability, p , the values of t_c and t_d are quantities that one typically estimates from data phylogenetically, rather than what one asserts a priori.

Despite the many conceptual challenges, prior-based calibration methods are easy to apply, computationally speaking. Most prior densities are standard univariate parametric distributions, so it is simple and fast to compute the node-age probability under the calibration. That said, multiple node calibrations can induce a joint prior density that behaves in unpredictable ways, making it imperative to assess the prior sensitivity of the calibration model: see Warnock et al. (2015) for an excellent overview of this subject. Biogeographic node calibrations can be specified in any phylogenetic software that supports node priors, such as MrBayes (Ronquist et al. 2012), RevBayes (Höhna et al. 2016), BEAST (Bouckaert et al. 2014), and MCMCTree (Yang and Rannala 2006).

9.3.2 Process-Based Biogeographic Dating

The previous section explored how prior-based methods date phylogenies that reflect hypothetical biogeographic scenarios. This section introduces a second class of dating methods, called process-based methods, that instead rely on data-dependent biogeographic inference. Process-based dating methods estimate posterior node-age densities that are shaped through the likelihood function rather than through the prior. The distinction between prior- and process-based approaches is important to many researchers, because process-based inference means that node-age estimates result from the

palaeogeographic, biogeographic, and phylogenetic evidence provided, rather than as an interpretation of the evidence that one asserts on the inference problem through the prior. The two biogeographic dating strategies are directly analogous to prior-based (Donoghue and Moore 2003; Yang and Rannala 2006; Parham et al. 2012) and process-based (Pyron 2011; Ronquist et al. 2012; Heath et al. 2014; Gavryushkina et al. 2017) fossil dating strategies.

As the name suggests, process-based biogeographic dating methods require that we define a biogeographic process of range evolution. Much like any process of molecular evolution, biogeographic processes are used to compute transition probabilities for biogeographic change over time, for example to compute the probability that a lineage dispersed from a continent into an island within 1 million years of the lineage's existence. To compute this probability, again similar to molecular processes, biogeographic processes probabilistically average (integrate) over all possible histories that are compatible with the biogeographical data observed at the tips of the tree, weighing each history by its probability. Biogeographic models come in a variety of forms, with special attention paid to discrete regions (Ree et al. 2005; Sanmartín et al. 2008), continuous regions (Lemmon and Lemmon 2008; Lemey et al. 2009; Quintero et al. 2015), range-dependent speciation-extinction rate variation (Goldberg et al. 2011; Caetano et al. 2018), cladogenetic range-inheritance events (Matzke 2014), and factors including geography (Landis et al. 2013; Tagliacollo et al. 2015), ecology (Meseguer et al. 2015; Landis et al. 2021), morphology (Sukumaran et al. 2016), and interspecific competition (Quintero and Landis 2020).

Unlike molecular processes, however, biogeographic processes can readily incorporate palaeogeographic information to structure their transition rates (and thus their transition probabilities) between regions so that they depend on the geological age of a possible range-evolution event. These models are often called time-stratified (Ree et al. 2005; Ree and Smith 2008) or epoch models (Bielejec et al. 2014). As an example, a dispersal event from a

continent into a 5-million-year-old island at any time during a 1 Myr interval would have zero probability before the island surfaced (e.g., 10 Myr ago) and nonzero probability only after it originated (e.g., just 1 Myr ago). Although evolutionary rate and geological time are non-identifiable from one another under standard molecular models (Zuckerlandl and Pauling 1962; Thorne et al. 1998), the parameters can be separately identified under biogeographical models that are palaeogeographically structured (Landis 2017).

A major strength of process-based dating methods is their ability to model the uncertainty that is inherent to biogeographic dating approaches. Rather than justifying and specifying individual biogeographic node calibrations as one does in a prior-based approach, process-based methods assess the likelihood of observed biogeographic disjunctions by fitting models with historical interactions between palaeogeographic, biogeographic, and phylogenetic components. By integrating over hypothetical scenarios involving palaeogeographic, biogeographic, and phylogenetic interactions that compete to explain the observed molecular and biogeographic variation, process-based dating methods generate posterior distributions of node-age densities through the model's likelihood function. A brief overview of how to design a process-based analysis is given below (Fig. 9.3).

An overview of process-based biogeographic dating

(I) Specification

- (a) Define a set of discrete regions.
- (b) Define a model of palaeogeographical dynamics.
- (c) Define a palaeogeography-dependent model of biogeographic evolution.
- (d) Define standard models of molecular evolution and lineage diversification.

(II) Estimation

- (a) Estimate the posterior of divergence times from molecular and biogeographic data.
- (b) Assess prior sensitivity of posterior estimates.

- (c) Conduct simulation experiments to assess confidence in empirical results.

Process-based dating relies on two major steps: specification and estimation. Unlike prior-based dating, there is no justification step because the specified model averages over possible biogeographic and palaeogeographic justifications (hypotheses). Specification, however, is more involved. The first step is to define the set of regions that will adequately portray the relevant palaeogeographic dynamics and biogeographic disjunctions in the analysis (Step I-a). For example, two regions are sufficient to capture the dynamics in Fig. 9.1. Further dividing region S into regions SW and SE would not expose any new dating information. Next, characterize the palaeogeographic dynamics in terms of the availability and connectivity between regions with respect to time (Step I-b). In practice, this can be done by defining a vector of adjacency graphs, where nodes correspond to regions, edges correspond to dispersal routes, and each graph in the vector is indexed by the timing of a palaeogeographic event (Buerki et al. 2011; Landis 2017). The time-stratified biogeographic model of Step I-c will then be defined to condition on the palaeogeographic structure defined in Step I-b by, for example, declaring that dispersal rates between two regions are greater than zero only if the regions are connected. To estimate the topology and branch-length parameters, standard molecular phylogenetic models are used (Step I-d).

Once the molecular, biogeographic, and palaeogeographical models are specified, all model components are simultaneously fitted to the molecular and biogeographic data in a joint Bayesian analysis (Step II-a). The estimates are then validated in two ways. Prior sensitivity experiments or simulation experiments can be used to validate process-derived age estimates. Prior sensitivity analyses for process-based methods behave similarly to those for prior-based methods (see previous section), except that the priors applied to the biogeographic process parameters should also be tested for sensitivity. Sensitivity analyses are useful to assess the

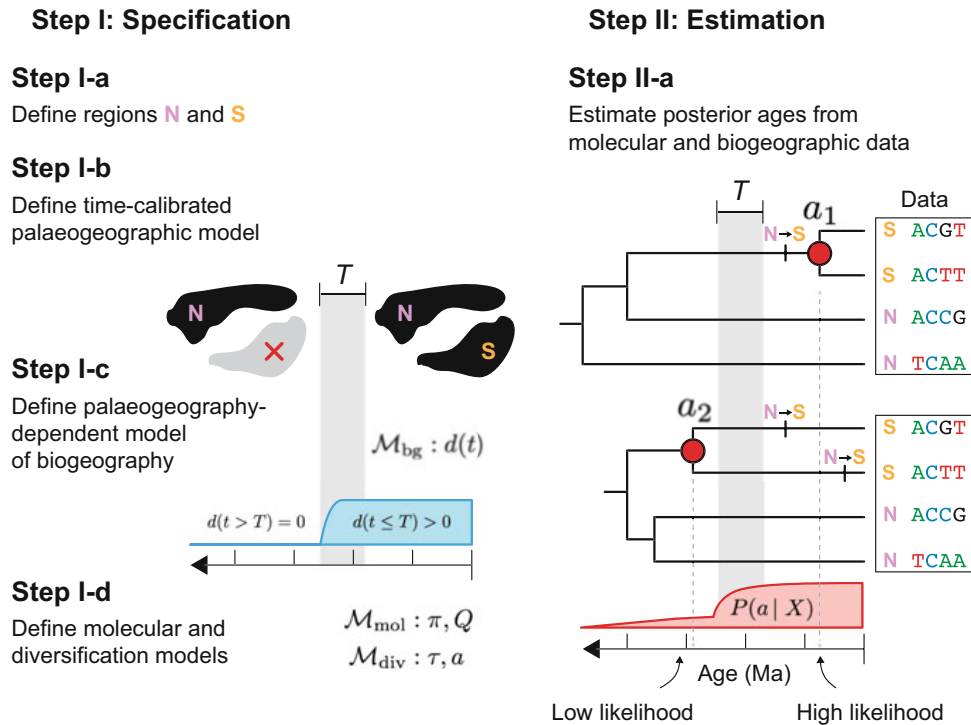


Fig. 9.3 Diagram of process-based biogeographic dating. Node calibration involves two major steps. Specification (Step I) first defines a set of biogeographic regions (I-a), then defines a dated palaeogeographic model for the availability and connectivity of those regions (I-b) that structures a time-stratified biogeographic model (I-c). Here, the biogeographic model, \mathcal{M}_{bg} , defines palaeogeography-dependent dispersal rates, $d(t)$, that are zero before region S appears at time T and positive afterwards (blue density). Simple molecular and diversification

models (\mathcal{M}_{mol} and \mathcal{M}_{div}) are also defined (I-d). Estimation (Step II) fits the model to the molecular and biogeographic data to estimate a posterior density of dated phylogenies (II-a). The model likelihood favours few, young dispersal events over many, (young or ancient) dispersal events, which is reflected in the posterior density (red). Thus, the posterior density prefers young ages (a_1) rather than old ages (a_2). Steps II-b and II-c are not shown. See main text for details

accuracy of divergence-time estimates under a variety of controlled settings, such as under the assignment of alternative prior densities to model parameters. Simulation experiments involve simulating many (≥ 100) phylogenetic data sets under the model defined in Steps I-b, I-c, and I-d, then estimating divergence times for those simulated data. If the estimated ages agree with the true simulated ages, that instils confidence that the process-based method behaves well under controlled conditions. But if the method grossly misestimates divergence times, then it is likely that any empirical estimates are incorrect or worse. Simulation experiments cannot be conducted naturally using prior-based dating methods, since priors do not generate

biogeographic data, making this form of validation somewhat unique to process-based methods.

Process-based biogeographic dating methods are quite young relative to prior-based methods, with only two examples in the literature at this time. In the study that introduced the method, Landis (2017) used the process-based techniques to date the phylogeny of crown turtles (Testudines). Testudines has received excellent taxonomic and phylogenetic treatment for decades (Crawford et al. 2015), and possesses a superbly documented fossil record that spans the Mesozoic and Cenozoic. These data have been used to generate numerous fossil-based estimates of the clade's age (Near et al. 2004; Hugall et al. 2007; Joyce et al. 2013), which are valuable to

validate whether alternative dating methods find similar ages. Biogeographically speaking, Testudines exhibits an ‘out-of-Gondwana’ distribution (Joyce et al. 2016) that remains imprinted in extant ranges thanks to their tendency for slow-and-steady dispersal. Together, these natural and scientific conditions made Testudines ideal for studying the behaviour of process-based biogeographic dating methods.

Landis (2017) dated the global expansion of Testudines lineages by jointly modelling interactions between processes of diversification, molecular evolution, biogeographic change, and palaeogeography while assuming a fixed topology. To do this, I introduced a global empirical model of continental drift for 25 regions and 26 time intervals, stretching from the Cambrian (540 Myr ago) to the present. The continental drift model defined connectivity between regions as strong, weak, or absent with three sets of graphs, defining ~ 200 connections per time interval, with over 1000 changes to interregional connectivity in total. It is not obvious how important geographic connectivity is to any particular clade: birds might disperse freely across mountains, but turtles might not. Rather than asserting the importance of connectivity a priori, as one must do when justifying a prior-based node calibration, the combined importance of strong, weak, and/or absent connectivity on biogeographic change was estimated from the data. Fitting the model to the Testudines data set estimated a mean posterior root age of 205 Myr (95% highest posterior density of 135–358 Myr), a result that was congruent with the fossil-based estimates from the literature, which reported estimates as low as 150 Myr (Joyce 2007) and as high as 325 Myr (Dornburg et al. 2011).

In the second study, Landis et al. (2018) estimated divergence times for the silversword alliance, an iconic adaptive radiation of plants that dispersed throughout the Hawaiian Islands (Carlquist 1966). Like many island plant endemics, silverswords lack any described fossils, so estimating the age of this clade has been consequently difficult (Baldwin and Sanderson 1998). To complicate matters, the topology within the silversword clade is not

completely resolved, making it difficult to justify calibrations for a specific phylogenetic hypothesis. Although there was likely to have been only one long-distance dispersal event from the North American continent into the Hawaiian archipelago (Baldwin et al. 1991), silverswords are found only throughout the High Islands, the set of younger islands that are not more than 6 million years old (Clague and Sherrod 2014). The exact sequence and timing of island colonization events within the archipelago must inform the divergence times, but no single biogeographic scenario is suitable for justifying or specifying node calibrations, further limiting the applicability of prior-based methods.

Similar to the approach taken by Landis (2017), Landis et al. (2018) estimated what combination of evolutionary histories for silverswords with divergence times, tree topologies, biogeographic histories, and island origination times had a high probability of generating the observed molecular and biogeographical data. The silversword crown age was dated to be roughly 3.5 Myr, and at most 5.1 Myr, a date that is consistent with the maximum age estimate of Baldwin and Sanderson (1998) that disregarded island ages to date the clade. Standard practice for using prior-based methods would assign the maximum age of the clade as equal to the oldest inhabited island (Kauai), while potential dating information from younger islands would be disregarded because it cannot easily be justified. But process-based dating applied to the silverswords extracted additional information for subclade ages when using all islands’ ages rather than only the oldest island’s age. For example, when testing prior sensitivity of the age estimates, one subclade (*Argyroxiphium*) age was estimated to be twice as old when only using the age of Kauai in comparison with an analysis using all islands’ ages.

Keep in mind that evolutionary biologists and biogeographers are often interested in dating phylogenies for the purposes of estimating ancestral states. Dated phylogenies that rely on biogeographic node calibrations generally cannot be used to later reconstruct ancestral species ranges: prior-based calibrations are justified through the assertion of a historical biogeographic scenario,

so subsequent ancestral range estimates would be biased towards scenarios that conform to the prior hypothesis (de Jong 2007). As part of the process-based dating analysis, Landis et al. (2018) estimated distributions of possible biogeographic scenarios, then used those estimated histories to test various biogeographic hypotheses, such as which island silverswords first colonized and whether dispersal and speciation processes favoured young or old islands. Because process-based dating methods do not involve a justification step, they avoid many such forms of circular reasoning ascribed to prior-based methods (Renner 2005; Kodandaramaiah 2011; de Jong 2007).

In summary, process-based biogeographic dating methods measure the probabilities of competing node-age distributions by averaging (integrating) over all possible palaeogeographic, biogeographic, and phylogenetic histories that are defined by the likelihood model. Because process-based dating methods fit models to palaeogeographic and biogeographic data, they are more data-intensive than prior-based methods. This makes process-based methods more sensitive to data errors, such as errors in coding species ranges or island ages, which could skew first arrival times to islands. In addition, process-based methods are more computationally intensive than prior-based methods. Estimating divergence times using a process-based approach requires repeatedly computing the biogeography model's likelihood function, which can be as slow as computing the molecular likelihood function or worse. Most biogeographic models scale abysmally with increasing numbers of regions (Ree and Sanmartín 2009), and current methods designed to circumvent this issue cannot treat phylogenies as random variables (Landis et al. 2013).

Biogeographic model adequacy is also a major concern. Models that neglect major features of range evolution will assign inaccurate probabilities in support of alternative biogeographic scenarios. For example, an extremely inadequate model might treat all geographical barriers as entirely impermeable, assigning zero probability to any dated phylogeny that requires

long-distance dispersal to explain biogeographic disjunctions. But, in reality, long-distance dispersal always has a nonzero probability, however small. At the moment, phylogenetic models of biogeography are still in their infancy (Albert and Antonelli 2017), but are maturing steadily (Sanmartín et al. 2008; Webb and Ree 2012; Matzke 2014; Meseguer et al. 2015; Quintero et al. 2015; Tagliacollo et al. 2015; Sukumaran et al. 2016). Not only are the biogeographic models young, but so are the methods that apply them to divergence-time estimation problems (Landis 2017; Landis et al. 2018), meaning the properties of those methods are poorly understood relative to prior-based methods. Further limiting the method's use, the computational framework needed to jointly model phylogenetic, biogeographic, and palaeogeographic interactions is specialized and only currently available in RevBayes (Höhna et al. 2016).

9.4 Conclusions

Recounting the biological history of Earth requires knowledge of the order and timing of the constituent events. Our record of historical events is incomplete, meaning that we rely on inference to retrace the past. But it is no trivial matter to locate key phylogenetic events, such as when or where lineages diverged, throughout most of the tree of life. Advances in phylogenetic inference let us establish a geological timescale for lineage divergences by recruiting extrinsic evidence: for example, the age and morphology of a fossil specimen can indicate the early origins of a particular clade. Palaeogeographic events, such as the birth of islands, the building of mountains, or the separation of continents, have also proven useful for dating evolutionary lineages, particularly lineages in clades with poor fossil representation. That framework, biogeographic dating, works by adopting a phylogenetic perspective to disentangle how a clade's age and biogeographic pattern might have been influenced by one or several palaeogeographic events.

In this chapter, I reviewed the conceptual basis of biogeographic dating under two methodological frameworks: prior-based biogeographic node-calibration methods and process-based biogeographic dating methods. Although prior- and process-based methods both convert biogeographic hypotheses into information to estimate divergence times, they do so in different ways. Prior-based methods require that the researcher first justifies that a particular biogeographic scenario resulted from a palaeogeographic event and, second, specifies a range of plausible origination times for the newly diverged lineage(s). Process-based methods specify a model of palaeogeography-dependent biogeographic evolution that is fitted to the observed species ranges by probabilistically averaging over the distribution of possible historical scenarios.

Prior-based dating is extremely flexible. Part of this flexibility emerges from the conceptual foundation of biogeographic node calibrations, which has been regarded as somewhat murky (Renner 2005; Kodandaramaiah 2011; de Baets et al. 2016). But being murky comes with advantages and disadvantages. Prior-based dating affords the biologist complete control to set the precision and accuracy of the dating estimates in such a way that comports with their expert description of the system's evolutionary history. From the computational perspective, prior-based node calibrations tend to be fairly easy to design and evaluate in phylogenetic analyses. But it is not uncommon to hear experts disagree about whether a calibration has a correct justification or specification. While those disagreements are not easily settled quantitatively because the justification and specification are, ultimately, related to prior model design, they can be settled logically (Goswami and Upchurch 2010; Kodandaramaiah 2011). Several researchers have also voiced concern that justifying a biogeographic node calibration often requires circular reasoning, or at least the assertion of an unfalsifiable hypothesis (Renner 2005; Kodandaramaiah 2011; de Baets et al. 2016). One last consequence of prior-based dating is that the biogeographically dated trees cannot later be used to estimate ancestral species ranges without improperly 'double

counting' the biogeographic evidence (de Jong 2007). Despite any complications, prior-based methods are still the most popular and widely used biogeographic dating strategy.

Process-based methods extract calibration information from the joint distribution of palaeogeographic data, biogeographic data, and molecular data. When compared with prior-based methods, the biologist is required to make fewer strong assertions about specific biogeographic scenarios, such as exactly how species are related, how completely a geographic barrier disrupts geodispersal, and the exact choreography of a clade's spatial radiation. Rather than supposing a particular scenario a priori, process-based dating approaches average over all historical biogeographic scenarios that are defined by the model, weighing each scenario by its probability of having occurred. While process-based approaches have some features that are theoretically appealing, they depend entirely on the adequacy of our biogeographic models, which are still quite simple despite ongoing developments. Process-based methods are fundamentally more complex than prior-based methods, with a computational burden that might limit their application in practice.

Regardless of whether one uses prior-based or process-based methods, the most satisfying divergence-time estimates are those that are correct (high accuracy) and confident (high precision). Precise results without accuracy are especially disturbing, leading one to draw the wrong conclusions from the evidence at hand. Seeking highly precise dating estimates should not be a goal at the expense of all else (Graur and Martin 2004). How do we extract that dating information from biogeography without introducing bias? When applying biogeographic prior-based calibrations, first, be critical of whether the calibration is truly justified and defensible. What empirical evidence or computational experiment could render the justification invalid? Second, avoid recycling densities that were previously published in the literature. Instead, the biologist should define a new density that represents her prior beliefs for when a divergence event occurred after reviewing the phylogenetic, biogeographic, and palaeogeographic

evidence. Experiment with densities with higher variance or soft tails during validation. For example, if it is not certain that a vicariance scenario occurred, consider the use of a ‘soft’ vicariance prior (Fig. 9.1f, bottom), or instead use the less constrained ancient dispersal prior (Fig. 9.1e). Process-based methods are also prone to giving biased estimates when the biogeographic data contain coding errors, when the palaeogeographic model is too restrictive or contains inaccurate dates, and when the biogeographic model is severely inadequate. Simulation experiments might help to detect and protect against such biases.

We do not know the exact limits for when we can accurately or precisely date nodes using biogeography. It is worth mentioning that fossil-based estimates are generally deemed superior to biogeography-based estimates for many good reasons. The timing of biogeographic scenarios contains many uncertainties: the timing of many palaeogeological events is not known precisely, the actual palaeogeographical event might be prolonged over many millions of years, or the relationship between the palaeogeographic event and the biogeographic event is itself unclear. Fossil specimens are often dated with fairly high precision when compared with biogeographic scenarios, and fossilization and divergence scenarios involve fewer contingent events to describe patterns than do biogeographic scenarios. This ultimately makes it easier to model fossilization scenarios (with a prior or a process). Despite the superiority of fossil-based dating in these respects, the fossil record varies in reliability: some groups (such as carnivorans and cetaceans) have exceptional records, while many groups are poorly represented (bacteria, plants, fungi, soft-bodied invertebrates, and small vertebrates). Fossil and biogeographic dating methods, however, should be regarded as complementary, not competing, strategies. Applying the two strategies simultaneously will, in principle, improve dating estimates beyond what might be learned using only one half of the available evidence.

Our understanding of evolution draws from diverse lines of evidence, and so our attempts to chronicle evolutionary history will require similarly diverse evidence and methods. No matter what method is used to time-calibrate a phylogeny, it is a delicate and often difficult practice. But biologists, in exercising care, curiosity, and patience, are making steady progress towards a richer portrait of when, where, and how life diversified.

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