Bayesian transmogrification of clade divergence dates: a critique

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ABSTRACT

The crucial step in Bayesian dating of phylogenies is the selection of prior probability curves for clade ages. In studies on regions derived from Gondwana, many authors have used steep priors, stipulating that clades can only be a little older than their oldest known fossil. These studies have ruled out vicariance associated with Gondwana breakup, but only because of the particular priors that were adopted. The use of non-flat priors for fossil-based ages is not justified and is unnecessary. Tectonic calibrations can be integrated with fossil calibrations that are used to give minimum clade ages only.

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CALIBRATING THE TIME-COURSE OF EVOLUTION: THE FOSSIL RECORD

Recent studies have endorsed the long-held idea that fossil age does not equal clade age. The youngest fossils of an extinct clade pre-date the extinction (Signor & Lipps, 1982). Likewise, the oldest known fossils of a clade only give a minimum age for the origin of the clade. This is termed the Jaanusson effect (after Jaanusson, 1976) or the Sppil–Rongis effect (the converse of the Signor–Lipps effect). Dornburg *et al.* (2011, p. 519) wrote: 'the taphonomic bias in the fossil record (Sppil–Rongis effect) increases the probability of fossil preservation toward the present, with large gaps often artificially truncating the distribution of lineages at deeper time scales'.

Despite this limitation, the authors of the modern synthesis accepted that the fossil record provides the best source of information on evolutionary chronology, or even the only source (Simpson, 1944). Recent authors have agreed: 'molecular clocks require fossil calibration… directly or indirectly, all molecular clock analyses rely on palaeontological data for calibration' (Donoghue & Benton, 2007, p. 424); 'Fossil calibrations are essential when dating evolutionary events' (Wilkinson *et al.*, 2011, p. 17).

Nevertheless, other molecular biologists are starting to acknowledge serious problems in relying on the fossil record to date lineages and are instead using tectonic calibrations (e.g. Azuma *et al.*, 2008, on cichlid fishes; Irestedt *et al.*, 2009, on birds of paradise; Allwood *et al.*, 2010, on Onychophora; Jønsson *et al.*, 2012, on crows). In this approach, phylogenetic and distributional breaks in molecular variation are related to dated tectonic events in the same location (Heads, 2011, 2012). Fossil calibrations might work well in some marine groups but there is excellent fossil evidence, supplemented by molecular studies, of huge gaps in the fossil record of terrestrial groups. The tectonic approach does not reject the fossil record, but uses it only to provide minimum, not maximum, clade ages.

In addition to sampling error and the Sppil–Rongis effect, identification of fossils can present serious difficulties. Molecular work has rejected many long-established groups that were based on traditional morphology. For example, in plants, dicots are now thought to include monocots, while in birds, ratites now include tinamous, and in mammals, Artiodactyla now include Cetacea. Many other cases are known at lower taxonomic levels. Yet fossil-calibrated molecular biogeographical studies rely on assigning fossils to a correct position in a phylogeny and this is done using traditional morphological homologies. If morphological analyses of living taxa have been wrong so often, it seems strange to base the molecular clock calibration entirely on morphological interpretation of fossil material, a much more difficult task.

Biologists have often assumed that fossil taxa must be primitive and basal with respect to living relatives. Thus, 'appropriate' characters may be selected for phylogeny reconstruction. Pennington *et al.* (2004) noted a tendency in many studies to assign fossils to the stem of the clade that they belong to and, as they emphasized, this will lead to underestimates of divergence times. Smith *et al.* (2010, p. 5897) also criticized 'the default practice of assigning fossils to the stem of the most inclusive crown clade to which they probably

belong, thereby possibly biasing estimated ages (possibly throughout the tree) to be younger'. A typical example concerns the geckos (Gekkota) and their oldest known fossil, the mid-Cretaceous *Cretaceogekko*. Studies of geckos (Nielsen *et al.*, 2011; Pepper *et al.*, 2011) have used this fossil to calibrate the base of the gecko tree. Nevertheless, while *Cretaceogekko* is the oldest gecko fossil, the only analysis of the genus (Arnold & Poinar, 2008) gave no indication that it is basal in the group.

TRANSMOGRIFICATION OF MINIMUM (FOSSIL-CALIBRATED) CLADE AGES INTO MAXIMUM CLADE AGES

For many years, fossil ages – estimates of *minimum* clade age – were converted, implicitly, into estimates of *maximum* clade age. There was no discussion or even mention of this process, and so I have referred to it as a transmogrification (Heads, 2012). In earlier studies the transmogrification was informal. Authors read the record literally and equated the age of a *clade* with the age of its earliest known *fossil*, 'perhaps adding a safety margin of a few million years' (Soligo *et al.*, 2007, p. 30). In this approach, groups that have their oldest known fossil in, for example, the Eocene, such as bats or modern primates (not including plesiadapiforms) could, at a stretch, have evolved in the Palaeocene, but a Cretaceous origin would be ruled out. One literalist study estimated that the probability of primates existing at 80 Ma (Late Cretaceous) was one in 200 million (Gingerich & Uhen, 1994).

Horses are another group with oldest known fossils in the Eocene (55 Ma), and the oldest known fossils of their sister group, the rhino–tapir lineage, date to about the same time. Waddell *et al.* (1999, p. 125) wrote:

> This is about as good as fossil calibration points get, in that there exist multiple good fossils representing both sister lineages, which appear in appropriate chronological order… To account for the *already differentiated fossils of the two lineages appearing rather suddenly* (probably from migration to the fossil sites), we consider the split could be as much as 58 mybp (a conservative estimate; e.g., D. Archibald, pers. comm.). So we have a conservative 55 mybp calibration point (SE ~1.5) [italics added].

The use of such a small standard error reflects the assumption that oldest known fossil age is more or less equivalent to clade age.

Although Benton & Donoghue (2007, p. 26) agreed that 'paleontological data can provide good estimates only for minimum constraints on the timing of lineage divergence events', they also proposed transmogrified maximum ages for a selection of clades and these were also based on the fossil record. They were derived simply by 'bracketing' (based on the maximum ages of sister groups – established with fossils) and 'bounding' (based on the age of the youngest fossiliferous formation that lacks a fossil of the clade) (Donoghue & Benton, 2007). In a similar way, Goswami & Upchurch (2010) argued that: A. Fossil dates gave minimum ages. B. The oldest known fossil of true primates is dated at 56 Ma,

the oldest known eutherian mammal at 125 Ma. Therefore, C.: 'it seems probable that the first true primate originated somewhere between 56 and 125 Ma' (p. 407). Yet this is not logical; C does not follow from A and B.

Wagstaff *et al.* (2006) accepted that 'The first appearance in the fossil record imposes only minimum age constraints'. Nevertheless, they transmogrified their fossil-calibrated dates for *Abrotanella* into maximum ages, concluding that the genus 'initially diverged during [not before] the Miocene' (p. 100), with secondary species radiations 'about [not "before about"] 3.1 million years ago' (p. 100). Using these dates as maximum possible ages they were able to rule out earlier vicariance and conclude that the disjunct distributions 'undoubtedly reflect long-distance dispersal…' (p. 95).

HIDING TRANSMOGRIFICATION BEHIND A BAYESIAN CURTAIN

Many papers now annotate fossil-calibrated phylogenies with minimum and maximum estimates of clade ages, given in the form of 95% credibility intervals. In other words, fossil-calibrated ages have been converted from minimum into maximum estimates, with statistical support. How exactly is this achieved? In these studies, the transmogrification is carried out in a Bayesian framework, using programs such as BEAST (Drummond & Rambaut, 2007). The key point is that specific prior probability distributions (priors) are assigned to the calibrations before any analysis is carried out.

An oldest known fossil from, say, 10 Ma may be used to calibrate the phylogeny of a clade. The actual age of the clade, or at least the probabilities of different actual ages, are specified in Bayesian analysis. Given the 10 Ma fossil, possible clade ages and their probabilities could be specified as, say, 10 Ma (90%), 20 Ma (50%) and 30 Ma (10%). As an alternative, a steeper probability/age curve could be set, prior to any analysis, with clade ages of 10 Ma (99%), 11 Ma (10%) and 12 Ma (0.5%).

After adopting these constructs, Bayesian analyses provide estimates of the maximum possible age of a fossil-calibrated clade, with statistical support. Clade ages are usually given as 95% Bayesian credibility intervals, or highest posterior density (HPD) intervals. These intervals incorporate information from the priors, in contrast with traditional confidence intervals which are based only on the data.

Drummond & Rambaut (2007) wrote that the priors 'may represent other sources of knowledge such as expert interpretation of the fossil record'. Yet they may also introduce error, for example, by incorporating traditional, literalist interpretations of the fossil record. If appropriate priors are selected, young clade ages with narrow credibility intervals can be calculated. In their study of *Abrotanella*, Swenson *et al.* (2012) transmogrified fossil-calibrated dates (minimum ages) into maximum clade ages using BEAST and specifying appropriate priors for the calibrations. The authors suggested that the method has the 'advantage' that it will always

provide maximum clade ages (with 95% credibility) and that it moves beyond 'the simplistic use of a minimum age constraint'. Assigning only minimum ages to fossils gives no constraint to maximum ages, and so it is seen either as a problem (or 'simplistic') in the traditional approach. The question for Bayesian analysis is: how are the priors selected?

For a given fossil age, normal, lognormal, gamma, or exponential curves are often specified as priors for probability/age curves and these give rapidly decreasing probabilities for older clade ages. An exponential prior is especially useful for generating young ages. It assigns the highest probability to a clade age that is the same as that of its oldest known fossil age, with the decreasing probabilities for older ages following an exponential curve. Ho & Phillips (2009, p. 372) warned that exponential priors should be used only 'when there is strong expectation that the oldest fossil lies very close to the divergence event'. Nevertheless, the traditional approach – a literal reading of the fossil record – *always* expects clade age to reflect oldest known fossil age (although this has been refuted in many individual cases) and so, as shown below, many authors now adopt exponential priors.

A few authors have recognized the problem with the priors. Parham *et al.* (2012, p. 352) observed: 'Most studies use a Bayesian framework for estimating divergence dates with probability curves between minimum and maximum bounds… but there is presently no practical way to estimate curve parameters'. A review of recent studies shows that the parameters are usually not justified (Warnock *et al.*, 2011). Lee & Skinner (2011, p. 540) noted that 'current practice often consists of little more than educated guesswork'. Parham *et al.* (2012) wrote: 'the fact that a widely applied methodology is subjected to such ambiguous assumptions that have a major impact on results… is a major limitation of molecular divergence dating studies' (p. 352). As these authors concluded, authors should adopt maximum bounds that are 'soft and liberal…' (p. 352), and the failure of many studies to do so is the topic of the present critique.

Wilkinson *et al.* (2011, p. 28) also criticized the whole current approach as seen in studies on primates (Chatterjee *et al.*, 2009) and wrote:

> [Their] young age estimate may be due to the use of two exponential distributions… These distributions… implicitly assume that the true age is close to the minima and unlikely to be much older than those minima. This assumption, we feel, is unlikely to be warranted, as it does not take account of the sizable gaps that exist in the primate fossil record.

The gaps are probably not infinite though and possible maximum ages can be suggested, based on tectonics. For example in the primates, the oldest known fossils are from the Palaeogene, and molecular clocks suggest a Cretaceous origin, but, assuming the Madagascar and the South/Central America endemic clades are due to rifting, the group could have evolved in the Jurassic (Heads, 2012).

Bayesian analyses that stipulate appropriate priors will 'validate' young ages for clades, a key component of modern synthesis biogeography. These clade ages can then be used to 'rule out' earlier vicariance. This whole process is then said to provide 'evidence' supporting a centre of origin/dispersal model. As in traditional transmogrification, the age of the oldest known fossil in a clade is converted from a *minimum* clade age into an estimate of *maximum* clade age, and the Bayesian framework adds a gloss of respectability to the process. The HPD intervals provide a false illusion of statistical support, and the calibrations, together with the maximum clade ages based on them, are likely to be gross underestimates of clade age.

The rest of this paper addresses the questions: which priors have been adopted in recent dating studies, and what were the results?

CASE STUDIES

The following studies provide typical examples of Bayesian transmogrification from the recent literature. The details of the methods differ but all studies used non-flat priors and transmogrified dates to rule out vicariance associated with Gondwana breakup.

Asteraceae

Swenson *et al.* (2012) calibrated a phylogeny for Asteraceae using a fossil dated as 47.5 Ma and placed on the stem above *Dasyphyllum*, a member of Barnadesioideae. Stipulating different priors (exponential, lognormal and normal) for the clade age of the fossil, the authors calculated median ages for the basal node of Asteraceae between 31 and 55 Ma (95% HPD) and so ruled out any vicariance in the family associated with the breakup of Gondwana.

Annonaceae

The Annonaceae are a pantropical plant family, widespread in both wetter and drier lowland habitats. Su & Saunders (2009) emphasized the scarcity of unequivocal fossils and wrote that 'only two fossils, *Archaeanthus* and *Futabanthus*, were regarded as sufficiently reliable [for calibration]'. They used *Archaeanthus*, from 98 Ma, to date the Magnoliaceae, and *Futabanthus*, 89.9 Ma, to date the Annonaceae (except *Anaxagorea*). Based on morphology, *Futabanthus* was allocated a position as sister or near the base of all extant taxa except *Anaxagorea* (Takahashi *et al.*, 2008).

Although the fossil record of Annonaceae is so scanty and is bound to have large gaps, Su & Saunders (2009) selected exponential priors and stipulated that the age of the group's oldest known fossil, *Futabanthus*, 89.9 Ma, was an estimate of its clade age, 89–90.4 Ma (95% HPD). This age was then used to calibrate the phylogeny. All the other clades were estimated to have a maximum age of less than 85 Ma (Late Cretaceous) (95% HPD), meaning that vicariance could be ruled out. The many transoceanic connections in this diverse, pantropical group could only have occurred after Gondwana breakup, therefore they were all attributed to chance,

transoceanic dispersal. One genus of Annonaceae, *Pseuduvaria*, is widespread in forests from Burma to Australia, with maximum species diversity in New Guinea. Transmogrification gave a Neogene age for *Pseuduvaria* (10–20 Ma, 95% HPD). Based on this date and a DIVA analysis (Ronquist, 1997), the authors supported the traditional model of a centre of origin in mainland Asia/Sumatra, followed by eastward dispersal through Malesia to New Guinea and Queensland. DIVA and similar programs using divergence–extinction–cladogenesis (DEC) models (Ree & Smith, 2008) stipulate a priori that the location of a basal, paraphyletic group represents a centre of origin, rather than, say, a centre of differentiation in a widespread ancestor. For example, given an area phylogeny: A (A (A (B))) a centre of origin is proposed in A. Instead, the pattern could have been caused by repeated vicariance in an ancestor in A + B, at a break in A, followed by local overlap in A, and without any dispersal between A and B (Heads, 2009).

In a study of an African–Asian–Australasian genus of Annonaceae, *Uvaria*, Zhou *et al.* (2012) used similar methods to those of Su & Saunders (2009) on *Pseuduvaria*, including exponential priors, and found similar results.

Calceolariaceae

In a fossil-calibrated study of the genus *Jovellana* (Calceolariaceae), distributed in Australasia–Chile, Nylinder *et al.* (2012) calculated a Neogene age and ruled out vicariance. Yet they reached this conclusion only because they stipulated that clade age could be no more than 5 Myr older than the fossil age.

Campanulaceae

Prebble *et al.* (2011) calibrated a phylogeny for the genus *Wahlenbergia*, with an emphasis on the New Zealand species. Three calibration points were used. The oldest known fossil of *Wahlenbergia* in New Zealand is pollen from the Waipipian Stage (3.6–3.0 Ma). The prior for the Waipipian fossil's New Zealand–Australia–South Africa clade was assigned a mean value of 3.3 Ma, a standard deviation of 0.2 Myr, and a normal distribution. These settings gave a 95% credibility interval of 3.0–3.6 Ma for the actual clade age. Here, the fossil age or minimum clade age was transmogrified into an estimate of maximum clade age that coincides exactly with that of the geological stage from which the fossil is known.

Prebble *et al.* (2011) incorporated two other fossil calibrations in the same way. A third node was based on the split between the Campanulaceae and the Lobeliaceae, dated in a previous fossil-calibrated study at 52 Ma (Wikström *et al.*, 2001). The priors for the node were assigned a normal distribution, a mean age of 52 Ma, and a standard deviation of 3 Myr. This gave an actual age for the family of 47.1–56.93 Ma (95% HPD), young enough to rule out a vicariance origin for the genus. The authors suggested Pliocene dispersal from Africa to Australia (c. 8000 km).

Malvaceae

Wagstaff & Tate (2011) calibrated the time-course of evolution in Australasian Malvaceae by assuming that clades in eastern and western Australia diverged in the Miocene, and that endemic forms on the Chatham Islands could be no older than proposed ages for the modern islands (1–3 Ma). Both of these assumptions can be questioned (Heads, 2012). For their third calibration point Wagstaff & Tate (2011) used the oldest known fossils of the tribe Malveae in Australasia and South America, dated as Eocene. They transmogrified this date into an estimate of most likely maximum clade age, specifying an exponential prior. Using these three dubious calibrations the authors deduced a Miocene age for the New Zealand Malveae, ruled out a vicariance origin for the group, and supported the traditional centre of origin/chance dispersal model.

Begoniaceae

Thomas *et al.* (2011) studied the pantropical *Begonia* (Begoniaceae) in Asia and Malesia. They used fossil calibrations and treated the age of the oldest eudicot fossils as a maximum clade age. Clade ages based on other fossils, such as the oldest Fagales fossil, were assigned exponential priors, 'reflecting the assumption that, based on the good fossil record… the age of the oldest relevant fossils is relatively close to the actual divergence date' (p. 1002). Using the calculated clade ages and results from centre of origin analyses (DIVA, Ronquist, 1997; DEC, Ree & Smith, 2008), the authors supported the standard model of an Asian centre of origin followed by eastward dispersal into Malesia and New Guinea in the Late Miocene to Pleistocene.

Monimiaceae

Based on the oldest known fossils of Monimiaceae, dated at 87–83 Ma and 83–71 Ma, Renner *et al.* (2010) placed a normally distributed prior of 83 Ma with a standard deviation of 1.5 Myr on the crown group node. This gave an age for the group (95% HPD interval) of 80.5–85.5 Ma. Based on fossils dated at 34–28 Ma they also placed a normally distributed prior of 30 Ma on the divergence of *Xymalos*, with a standard deviation of 1.5 Myr. This gave an age (95% HPD interval) of 33–28 Ma (Oligocene). Using these priors the authors calculated, for example, that 'The South American *Mollinedia* clade is only 28–16 Myr old [i.e. long after Gondwanan rifting], and appears to have arrived via trans-Pacific dispersal from Australasia' (Renner *et al.*, 2010, p. 1227).

Hernandiaceae

In studies on Hernandiaceae, Michalak *et al.* (2010) assigned two priors. One, applied to the Monimiaceae crown group, was a lognormal distribution with a minimal age of 71 Ma and a 95% confidence interval (CI) that allowed the node to be up to 83 Myr old. This was based on the age of oldest

known fossil Monimiaceae, wood dated as 83–71 Ma. The second prior, applied to the Hernandiaceae/Lauraceae/Monimiaceae trichotomy, was a normal distribution with a mean of 121 Ma and SD of 6. This was applied so that the 95% interval extended between 109 Ma, the age of the oldest lauraceous fossils, and 133 Ma, 'the minimal age of angiosperms' (specified by Michalak *et al.*, 2010, p. 1216, as a maximum age). Use of these priors meant that six intercontinental disjunctions in Hernandiaceae were all dated as Oligocene to Miocene (maximum age) and Gondwanan vicariance was ruled out.

Orchidaceae

In Orchidaceae, fossils of *Dendrobium* (23 Ma) and *Earina* (25 Ma) occur in the New Zealand Miocene. Instead of treating these as minimum clade ages, Gustafsson *et al.* (2010) assigned priors for these fossils and another orchid fossil that gave a date for the *Earina–Dendrobium* break at 25–40 Ma (95% HPD). These young dates falsified a vicariance explanation for New Zealand members of the genera. The authors stipulated a maximum age constraint of 120 Ma for monocots, corresponding to the oldest known monocot fossils. Gustafsson *et al.* (2010) acknowledged that this constraint 'may be questionable since fossils generally provide minimal ages, but in absence of further evidence such upper bounds are technically advantageous'. Unambiguous orchid fossils are very rare (only three are known), but there is a vast amount of other evidence that can be used to calibrate the time course of evolution in the family. Every clade of orchids has a distribution that is defined by phylogenetic and spatial breaks, and these can be correlated with tectonic or climatic events, giving tens of thousands of potential calibrations.

Bees

The bee family Colletidae shows many phylogenetic connections among the southern continents. A Bayesian study ruled out vicariance due to Gondwana breakup and instead supported transoceanic dispersal in the Cenozoic (Almeida *et al.*, 2012). Nevertheless, this result was determined by the use of lognormal priors stipulating that clades could be no more than 10–15 Myr older than their earliest fossils.

Primates

In their Bayesian analysis of ape evolution, Rannala & Yang (2007) used two calibrations, both based on fossil age. The first, for *Homo/Pan* divergence, was assumed to be between (not before) 6 and 8 Ma, with a most likely date of 7 Ma. The second calibration, for the divergence of *Homo + Pan* from *Pongo*, assumed this was between (not before) 12 and 16 Ma, with a most likely date of 14 Ma. Gamma priors were assigned. The primate fossil record is notorious for its paucity and Fleagle (2002) described it as 'frighteningly incomplete'.

Accepting the fossil dates as indications of absolute clade age rather than minimum clade age is not justified.

Hodgson *et al.* (2009) calibrated primate phylogenies and wrote: 'Lower constraints cannot be definitively set, so we have chosen to place lower bounds at or beyond what most authorities consider possible' (p. 5536). Their calibrations included the *Homo/Pan* split, based on a fossil dated at 5 Ma and a stipulated maximum clade age of 8 Ma; the *Homo + Pan/Pongo* split, with fossil age 12.5 Ma and stipulated clade age 18 Ma; the *Papio/Theropithecus* break, with the fossil and clade dates at 3.5 and 6.5 Ma; and the Hominoidea/Cercopithecoidea break, with dates at 21.0 and 30.0 Ma. Thus small differences were proposed between the oldest known fossil ages and the maximum possible clade ages, as in the study of apes by Rannala & Yang (2007). In their Bayesian transmogrification, Hodgson *et al.* (2009) proposed a maximum age for platyrrhines (New World monkeys) of 52 Ma (95% CI), long after the rifting open of the Atlantic Ocean in the Cretaceous. Studies based on similar allocation of priors have stipulated maximum ages for platyrrhines at 59 Ma (95% CI) (Wilkinson *et al.*, 2011) and 48 Ma (95% CI) (Perelman *et al.*, 2011).

Other widespread groups

In studies of many other global or pantropical groups, Bayesian transmogrifications have led to fossil-calibrated maximum ages (95% HPD) for the groups that are younger than the Atlantic, Indian and Southern Oceans. The intercontinental disjunctions have therefore been attributed to chance, transoceanic dispersal. Clades treated in this way include the pantropical groups Sapotaceae subfamily Chrysophylloideae (Bartish *et al.*, 2011), *Ficus* (Xu *et al.*, 2011), and *Mimosa* (Simon *et al.*, 2009, 2011), the global tribe Ranunculeae (Emadzade & Hörandl, 2011), and the global family Bufonidae (Pramuk *et al.*, 2008). Trans-Pacific clades interpreted in the same way include Alstroemeriaceae (Chacón *et al.*, 2012) and *Leptinella* (Himmelreich *et al.*, 2012).

Studies of biogeography on a continental scale that have used Bayesian transmogrification of fossil dates include work on the New World monkey *Cebus* (Lynch Alfaro *et al.*, 2012). In another, Särkinen *et al.* (2012) dated eight Andean clades in the legume family with fossil calibrations and assigned normal probability/age curves with small standard deviations (average 3.9 Myr) as priors. This meant that the initial uplift of the Andes in the Cretaceous, related to the opening of the Atlantic, was ruled out a priori as a causative factor in the evolution of the groups. For alternative treatments of pantropical and New World groups, including *Cebus*, based on both tectonic and fossil calibrations, see Heads (2012).

SPECIFYING BAYESIAN PRIORS AND THEIR PARAMETERS (THE HYPERPARAMETERS)

Huelsenbeck *et al.* (2002, p. 684) wrote that:

the use of a prior probability distribution on trees can be viewed as either a strength or a weakness of the method. It seems a strength when the systematist has prior information about the phylogeny of a group. Why not incorporate such information when it is available? However, when the systematist does not have strong prior beliefs, specifying a prior seems more difficult.

Even more serious problems can arise when the systematist does have strong prior beliefs, as these can be imposed as priors even if they are wrong. Beliefs of the mid-20th century 'modern synthesis' are often used as priors. In Bayesian analyses, the specification of exponential, lognormal and normal priors, and the use of small standard deviations, incorporates the modern synthesis view that the terrestrial fossil record gives a more or less accurate representation of maximum clade ages.

Anyone reviewing the work on Hernandiaceae, Monimiaceae and other groups cited above would conclude that few, if any, geographical disjunctions date back to the breakup of Gondwana, at least for genera and tribes. Nevertheless, this remarkable consensus, which is also supported in papers on vertebrates and invertebrates, is not due to any new data or analysis. Instead, it simply reflects the imposition of a prior belief – that fossil age more or less equals clade age. In these recent studies, fossil-calibrated minimum clade ages are converted into maximum ages (with good statistical support), but only by decree, not by science, and the potential magnitude of the Sppil–Rongis effect is swept under the carpet. The alternative method advocated here instead integrates data from tectonics, biogeography, and the fossil record; fossil data are used to provide minimum ages.

This critique is not meant as a rejection of Bayesian analysis per se, but of the selection of priors in many recent biogeographical analyses. Treating fossil ages only as minimum clade ages, as suggested here, is equivalent to using flat priors. The imposition of steep, non-flat priors for fossil-based clade ages is not justified, is unnecessary, and leads to erroneous conclusions about the formation of biogeographical patterns. The impact of these conclusions on ecological and evolutionary interpretations has been profound. Authors have felt obliged to reject simple tectonic explanations for general distribution patterns and instead invoke chance processes and unknown ecological factors.

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