

## The Great American Biotic Interchange revisited

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The “Great American Biotic Interchange” (GABI) is regarded as a defining event in the biogeography of the Americas. It is hypothesized to have occurred when the Isthmus of Panama closed ca three million years ago (Ma), ending the isolation of South America and permitting the mixing of its biota with that of North America. This view of the GABI is based largely upon the animal fossil record, but recent molecular biogeographic studies of plants that show repeated instances of long-distance dispersal over major oceanic barriers suggest that perhaps the land bridge provided by the isthmus may have been less necessary for plant migration. Here we show that plants have significantly earlier divergence time estimates than animals for historical migration events across the Isthmus of Panama region. This difference in timing indicates that plants had a greater propensity for dispersal over the isthmus before its closure compared with animals. The GABI was therefore asynchronous for plants and animals, which has fundamental implications for the historical assembly of tropical biomes in the most species-rich forests on the planet.

The Isthmus of Panama exists today as a narrow strip of land that separates the Pacific Ocean and the Caribbean Sea, linking together South and Central America. Coates and Obando (1996) suggested that early in its formation, ca 15 Ma, the nascent isthmus consisted of a series of volcanic islands, arranged in an arc between South and Central America, which were formed as a result of the subduction of the Pacific plate under the Caribbean plate. The deposition of water-borne sediment filled in the gaps between them and complete closure of the isthmus occurred around three Ma. An alternative view suggests that the Isthmus of Panama existed initially as a peninsula of southern Central America, as early as 19 Ma, rather than as an island chain (Kirby et al. 2008). The peninsula was, however, separated from South America by a deep marine channel before connecting with it three Ma. Both models estimate that the completion of the land bridge occurred approximately three Ma, so if organisms used the land-bridge to move between South and Central America, we estimate that migration must have occurred after this date.

The predominant biogeographic paradigm regarding the Panama Isthmus is that its closure ended the “splendid” isolation of South America (Simpson 1980), causing an exchange of biota regarded as so fundamental that it has become termed the “Great American Biotic Interchange” (GABI; Stehli and Webb 1985). The original view of the GABI was based largely upon the mammalian fossil record

(e.g. reviews by Simpson 1980, Stehli and Webb 1985, Webb and Rancy 1996, Burnham and Graham 1999), which indicates few migrations before the late Pliocene and the Pleistocene (Burnham and Graham 1999). The palaeobotanical record, which is poorer than the animal fossil record and based principally on pollen (Burnham and Graham 1999), upholds this view of the GABI. Evidence derived from similarities in palynomorphs indicates that, like the mammalian faunas, North and South American floras were distinct until the late Tertiary, with greater similarities developing in the Plio-Pleistocene and especially in the Pleistocene (Graham 1992, Burnham and Graham 1999). The closure of the Panama Isthmus is therefore considered to be a defining event in the neotropical biogeography of both plants and animals (Gentry 1982, Wendt 1993, Burnham and Graham 1999).

Dated molecular phylogenies allow us to determine the times at which sister lineages split from each other. The conventional view of the GABI, implying a special role for a continuous terrestrial corridor for migration of biota, is called into question since numerous recently published dated molecular biogeographic studies have shown that historical long-distance dispersal over major oceanic barriers has to be repeatedly invoked to explain plant distributions (Richardson et al. 2004, Lavin et al. 2005; reviewed by Pennington et al. 2006). Related to this, an intriguing result that has emerged from two biogeographic meta-analyses of

multiple lineages in temperate and subtropical biomes (Sanmartín et al. 2001, Donoghue and Smith 2004, Sanmartín and Ronquist 2004) is a possible difference in the relative frequency of dispersal in the biogeographic history of animals and plants. In a study of dated phylogenies of 18 plant and 54 animal clades from the southern hemisphere, Sanmartín and Ronquist (2004) discovered that dates for the same geographic divergences were older for animals than for plants. In general, tectonic events better explained the animal patterns, and greater amounts of dispersal had to be invoked to explain the plant patterns. A similar result was reported for dated phylogenies of 66 plant and 39 animal clades containing disjunctions between the temperate forests of north America and eastern Asia (Sanmartín et al. 2001, Donoghue and Smith 2004), which was interpreted as the outcome of more recent overwater dispersal for plants compared to overland migration by animals.

In this paper we carry out a meta-analysis of dated molecular phylogenies of animal and plant clades that are distributed in both South and Central America in order to examine whether migrations coincided with the formation of the Isthmus of Panama. In these phylogenies, we searched for instances in which the geographic structure of sister lineages are such that we can infer an unambiguous migration between South and Central America or vice-versa (Fig. 1). Our principal goal was to investigate whether the timing of migration across the Isthmus region differed in plants and animals, and whether both depended upon the completion of a terrestrial migration corridor as the conventional model of the GABI implies.

## Materials and methods

We compiled information from 40 published and three unpublished dated molecular phylogenetic studies of terrestrial plant and animal lineages (Supplementary material Table S1), mostly drawn from a recent review paper by Rull (2008). Of these 16 were plant studies and the rest were of animals. Parsimony optimization of a two state

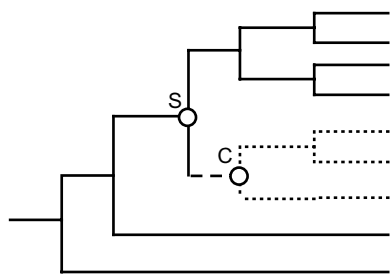


Figure 1. Hypothetical phylogeny of plant species endemic to South (black branches) and Central America (dotted branches) showing geographical structure around the Panama Isthmus. Branch lengths are proportional to time. The Central American clade nested within a South American group indicates migration from south to north. “S” and “C” indicate stem and crown nodes of the Central American clade. The movement from South to Central America could have occurred at any time between the stem and crown nodes (along the dashed line) and therefore the date of the stem node is the earliest possible time of south–north movement.

geographic character (Central America vs South America) was used to infer unambiguous migration events across the Isthmus of Panama region. Where optimization was ambiguous, nodes were not considered in the analysis.

In determining the timing of migration the distinction between stem and crown nodes needs to be highlighted (Fig. 1) because the date of the stem node is the earliest possible time of migration (i.e. a maximum estimate) and the date of the crown node the latest (i.e. a minimum estimate; see Fig. 1 and caption for more details). Because in some cases the difference in age between the stem and crown node is large, there is considerable uncertainty of the exact timing of the dispersal event. Therefore, where possible, both the minimum and maximum divergence times of both stem and crown nodes that indicate transcontinental migration were recorded along with the genes used and the methods of calibration and dating (Supplementary material Table S1 and associated list of references).

Methods commonly used to date phylogenies are reviewed in Renner (2005) and Rutschmann (2006). It is evident from studies that date their phylogenies using more than one approach that different age estimates for the same node on the topology can be obtained (Benton and Ayala 2003, Bromham and Penny 2003). We therefore developed criteria for choosing amongst alternative options. Studies that used the Isthmus of Panama as a calibration to date the phylogeny were discarded since they already assume the effects of the closure rather than testing it. Studies that did not produce a phylogeny but dated lineage divergence through the conversion of genetic distance into ages using a substitution rate calculated from other taxa (a “borrowed” rate) were dismissed because clear identification of “isthmus nodes” was lacking. Explicitly phylogenetic studies that used a borrowed rate were considered acceptable, but dated phylogenies calibrated using external evidence were preferred. In such dated phylogenies, where possible the date chosen was the one that was calibrated using fossils rather than geological events because of the possibility of dispersal (Renner 2005). In dated phylogenies calibrated using external evidence, in the face of different dates resulting from different methods (penalized likelihood (Sanderson 2002), Bayesian (Thorne and Kishino 2002), non-parametric rate smoothing (Sanderson 1997)) we favoured dates calculated by penalized likelihood and Bayesian methods because NPRS has been shown to over-estimate dates (Lavin et al. 2005). Supplementary material Table S1 gives information concerning taxa, mode of calibration, analytical approach, and dates of stem and crown nodes (with confidence intervals).

We assessed the influence of the completion of the Isthmus of Panama land bridge on plant and animal migration events by calculating the probability that each transcontinental crossing occurred before the closure of the Isthmus of Panama using two different measures, both of which pose the question: what is the probability of migration from Central to South America, or vice versa, before three Ma when the isthmus closed? The first approach, “raw probability”, determines the probability ( $p=0-1$ ) of migration over the isthmus before its closure (Fig. 2 and 3). The second approach, “accumulated likelihood”, is a function of the time elapsed between the

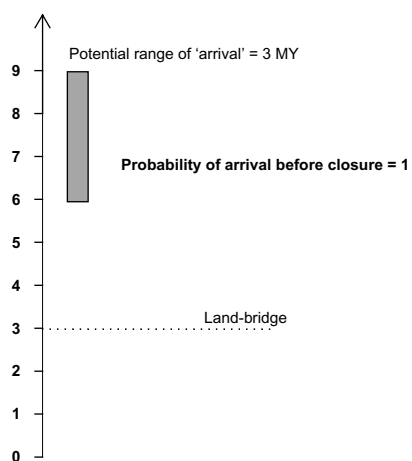


Figure 2. Calculation of raw probability values. Taxa with a range of divergence times that are older than three Ma will receive a raw probability value of one.

migration of a species and closure of the isthmus land-bridge, relative to phylogenetic uncertainty expressed as the estimated age range between minimum and maximum divergence times (Fig. 4).

In addition to these approaches, differences in the estimated divergence times were statistically compared for both stem and crown node data between animal and plant taxa. For each taxon, a mid-point was calculated between the maximum and minimum estimated divergence; mid-points were compared between plants and animals using a nonparametric Mann-Whitney U test.

### Raw probability

This method assigns a probability of one to those taxa that have minimum node values that are greater than three Ma and so indicate migration over the isthmus before its closure (Fig. 2). Conversely, those taxa with maximum node values

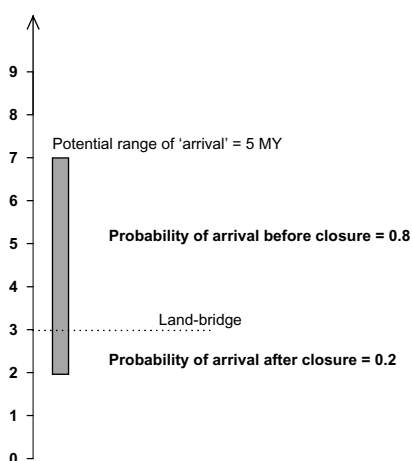


Figure 3. Calculation of raw probability values. Taxa with a range of divergence time estimates that extend both before and after three Ma will receive a raw probability between zero and one. The precise figure will depend on the proportion of the range that is older than three Ma. In the case illustrated the taxon will receive a raw probability of 0.8.

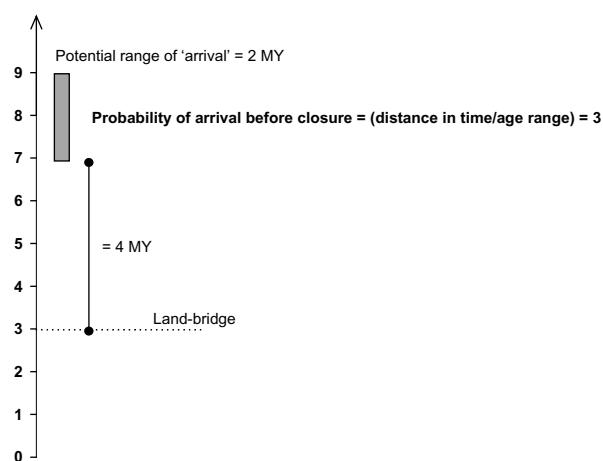


Figure 4. Calculation of accumulated likelihood values. Accumulated likelihood values take into account how much earlier or later than the closure of the Isthmus of Panama migration occurred.

that are less than three Ma, receive a probability value of zero because these divergence time estimates indicate migration over the isthmus after its closure. Taxa that have a range of node values that intersect the three Ma mark have scores calculated by assuming an equal probability of trans-isthmian crossing throughout this range of dates and then estimating the probability of migration before land bridge closure. These probabilities will lie between zero and one (Fig. 3).

For example, taxa with a minimum divergence time of two Ma and a maximum divergence time of seven Ma could have crossed the isthmus before it closed at three Ma, or they could have crossed the isthmus after it closed. The raw probability of crossing before isthmus closure ( $P_r$ ) is the proportion of the age range that lies before three Ma:

$$P_r = (Mx - I) / (Mx - Mn) \quad (1)$$

where  $Mx$  is the maximum divergence time (earliest potential age of arrival),  $Mn$  is the minimum divergence time (latest potential age of arrival) and  $I$  is the age of closure (three Ma). In our worked example,  $Mx=7$  and  $Mn=2$  Ma, giving a  $P_r$  value of 0.8: which is the raw probability that this taxon crossed the isthmus before three Ma. To compare between plants (with fewer studies) and animals (with a greater range of available study data), values of  $P_r$  were plotted along a standardized axis of rank position (standardized between zero and 1).

### Accumulated likelihood values

Raw probabilities are constrained to values between zero and 1, and do not take into consideration how much time before or after the closure of the isthmus migration occurred. For example, taxa exhibiting minimum divergence times that indicate trans-continental crossing 45 Ma are given the same raw probability score ( $P_r=1$ ) as those taxa exhibiting minimum divergence times that correspond to a crossing 3.5 Ma. Given the potential broad time-frame in the dating process it is quite conceivable that the taxon with a divergence time of 45 Ma is more likely to have crossed the isthmus before it had closed, compared to a

taxon with a divergence time of 3.5 Ma. For this reason, we also used an “accumulated likelihood value” ( $P_c$ ) that assigns higher scores to taxa that indicate migration much before isthmus closure and lower scores to taxa with divergence time estimates that indicate a crossing much closer to the timing of the closure of the isthmus. These scores are calculated by determining the distance between maximum or minimum node values and the three Ma closure date, and then dividing this value by the range between the extreme node values (reflecting uncertainty in the phylogenetic time-frame). This calculation estimates the number of times the node age range fits into the distance between the date of migration and the date of isthmus closure (Fig. 4).

$$P_{c(p)} = (Mx - I) / (Mx - Mn) \quad (2)$$

$$P_{c(n)} = (Mn - I) / (Mx - Mn) \quad (3)$$

$$P_{c(i)} = \{ [Mn + (Mx - Mn) / 2] - I \} / [(Mx - Mn) / 2] \quad (4)$$

Accordingly, we used eq. 2 ( $P_{c(p)}$ ) where the minimum node value is greater than three Ma, eq. 3 ( $P_{c(n)}$ ) where the maximum node value is less than three Ma, and eq. 4 ( $P_{c(i)}$ ) where the maximum node value is greater than three Ma and the minimum node value is less than three Ma. Note that eq. 2 is functionally equivalent to eq. 1, and that  $P_c$  scores are in fact a cumulative measure of  $P_r$ . For example, using eq. 3, taxa exhibiting divergence time estimates that indicate migration soon after the closure of the isthmus are given lower (i.e. near zero) negative probability values than those taxa that crossed a long time after the closure of the isthmus. The more negative the probability, the less likely that migration occurred before closure of the isthmus. Where maximum and minimum node data are identical (i.e.  $Mx - Mn = 0$ ) we used a default value of 0.3 Ma (equivalent to the 10th percentile for all differences between values of  $Mx$  and  $Mn$ ). To compare between plants (with fewer studies) and animals (with a greater range of available study data), values of  $P_c$  were

plotted along a standardized axis of rank position (standardized between zero and 1).

## Results

We identified 58 unambiguous migration events across the Isthmus of Panama region in 16 phylogenies for plants and 27 for animals. Figure 5 indicates that plants generally have older stem node ages than animals. Eight of the 25 plant migrations (32%) have stem node divergence dates that are over 20 Ma whereas all animals have stem node divergence dates that are below 20 Ma. The entire range of stem node divergence times for plants spans nearly 50 Ma compared with less than 20 Ma for animals. Based on minimum stem node values, plants have been making cross-continental migrations between South and Central America for the past 50 Ma whereas the majority of animals (31/33; 94%) did not embark on this journey until after ten Ma. Only 19 (33%) plant and animal taxa out of 58 have stem node age ranges that indicate crossing after the closure of the isthmus. Of these, 13 are animals and six are plants. Crown node data in Fig. 6 reveal the same distinction between plant and animal divergence times, albeit somewhat less clearly. Of the 46% of crown node taxa that crossed after closure, six are plants, and 11 are animals. Of those taxa that have divergence times indicating migration across the seaway before ten Ma (Fig. 5 and 6), the majority are plants with the exception of eels (Synbranchidae), rodents (Sigmodontinae) and bats (*Balantiopteryx*). Of these animals with divergence dates over ten Ma, a bat may potentially fly across and the eel has been shown to tolerate salt water.

Our analyses indicate that plants are more likely to have migrated over the isthmus prior to its closure three Ma (Fig. 7 and 8). The left-skewed plant data in Fig. 7 indicates a greater likelihood that plant taxa crossed the isthmus before it closed. Figure 8 shows that accumulated likelihood scores for plants lie above the trend of animals; this is particularly

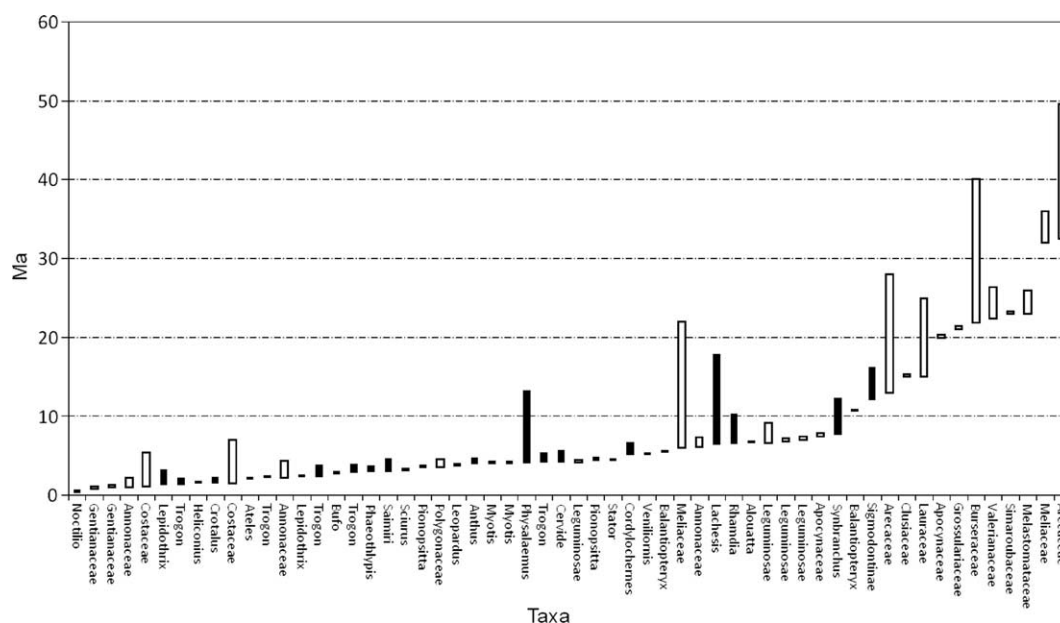


Figure 5. Chronologically arranged stem node divergence times for animals (filled bars) and plants (unfilled bars).

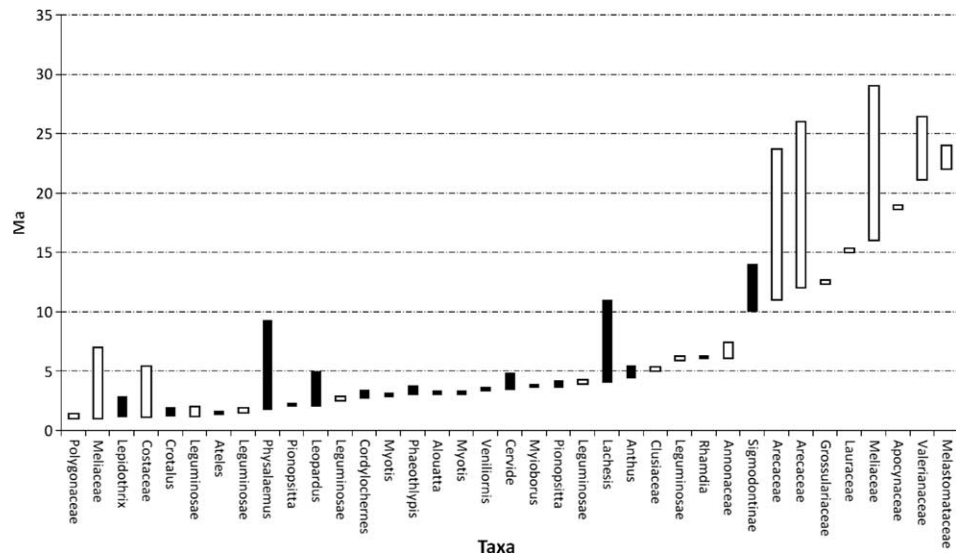


Figure 6. Chronologically arranged crown node divergence time estimates for animals (filled bars) and plants (unfilled bars).

apparent towards the right hand side of the graph where divergence dates tend towards the older end of the spectrum.

The non-parametric Mann-Whitney U test is consistent with the results of all other analyses. For both stem and

crown node data, the estimated plant divergence times occur significantly earlier than for equivalent animal taxa:  $U = 215.5$ ,  $p = 0.002$  (stem node data) and  $U = 101.1$ ,  $p = 0.033$  (crown node data).

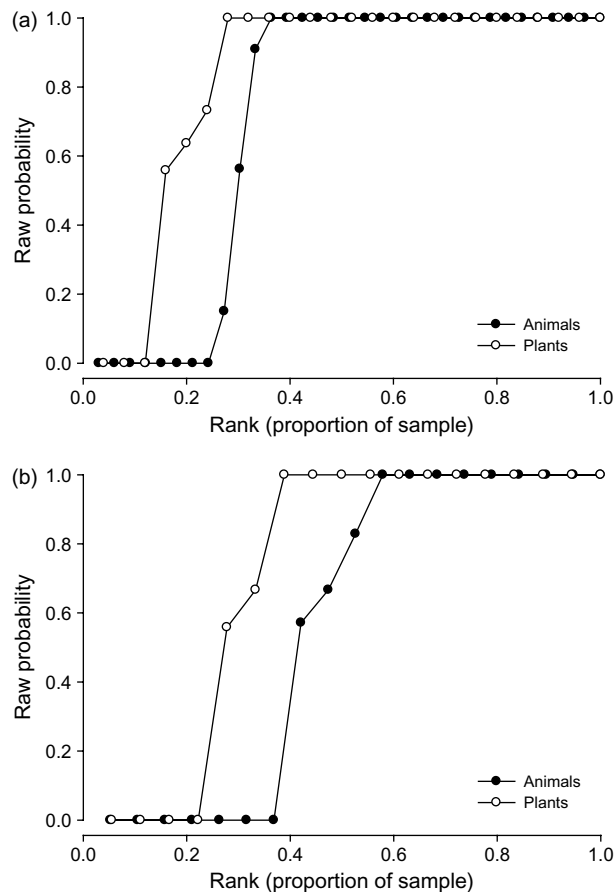


Figure 7. Raw probability scores based on plant and animal stem node (a) and crown node data (b) indicating the probability of migration over the isthmus before its closure.

## Discussion

Our results show clearly that lineages of plants had a greater overall likelihood of crossing the Isthmus of Panama region before it closed, implying a new view for the GABI – that plants tended to move first. Interestingly, the majority of plant and animal phylogenies indicate trans-continental migration prior to the closure of the isthmus (39 plant and animal taxa with minimum stem node ages that are older than three Ma out of 58 plant and animal taxa in the stem node data set, i.e. 67%). These findings indicate one of two things: either both plants and animals had a greater than expected ability to disperse over water between South and Central America before three Ma; or alternatively, an earlier land connection, such as the one hypothesized by Bermingham and Martin (1998) may be plausible. Bermingham and Martin (1998) used divergence time estimates from freshwater fish that were intolerant of salt water to postulate that a land bridge must have existed between South and Central America three to seven Ma. Because no geological evidence has been found to support the Bermingham-Martin hypothesis, we suggest that our results indicate that both plants and animals commonly crossed the narrowing isthmus region before its final closure.

A statistically significant difference in timing of migration between plants and animals is evident from both stem and crown node ages (Fig. 5, 6, 7, 8). That the crown node data display essentially the same pattern is important with regard to migration in relation to the specific date of the closure of the Isthmus of Panama because the crown node dates are minimum estimates and therefore a more conservative test of whether migration occurred before the Isthmus closed.

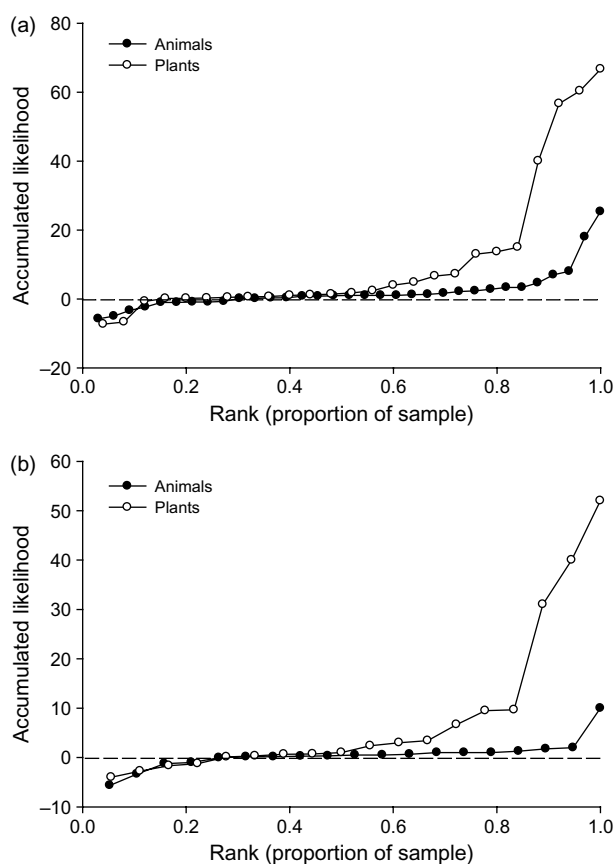


Figure 8. Accumulated likelihood values based on stem node (a) and crown node data (b). Scores greater than zero indicate a balanced migration probability before the isthmus closed and scores below zero indicate a migration probability after the isthmus closed. The greater the positive score, the earlier the minimum divergence date is before three Ma, and the narrower the estimated range in phylogenetic divergence dates. The greater the negative score, the later the maximum divergence date is after three Ma.

We acknowledge several possible sources of error, including inadequate sampling of taxa, varying dating methodology and different means of calibration when drawing comparisons between phylogenetic dates reported in literature (Renner 2005, Rutschmann 2006). In particular, our animal dataset is dominated by vertebrates, especially birds, and in future could be improved by the addition of more invertebrates. In this context, it is interesting to note that the animal dataset of Sanmartín et al. (2001), which was dominated by studies of insects and lacking in studies of vertebrates, still showed evidence for less historical dispersal than a corresponding plant dataset for the same disjunction in the northern hemisphere (Donoghue and Smith 2004, Pennington et al. 2006). This lends support to the conclusion of the present study, which is clearly consistent with plants having a greater capacity than animals for dispersal, and subsequent establishment of founder populations in new territories. Earlier over-water migration by plants is likely to reflect the ability of their propagules to traverse large distances and to establish founder populations successfully. Seeds are often produced in great numbers and some are particularly well adapted to wind or water dispersal. Seed dormancy means

that they can remain viable even after a long journey and need not germinate until conditions are favorable. Perhaps more crucially, flexibility of reproduction either via vegetative propagation or self-fertilization means that some plants can colonize without needing a sexual partner.

The few meta-analyses contrasting the biogeographic patterns of plants and animals (this paper, Sanmartín et al. 2001, Donoghue and Smith 2004, Sanmartín and Ronquist 2004) are limited in their taxonomic scope and suffer methodological problems such as phylogenetic dates calculated using a variety of methods (Pennington et al. 2006). Despite these shortcomings, they indicate that in the temperate and subtropical northern (Sanmartín et al. 2001, Donoghue and Smith 2004) and southern hemispheres (Sanmartín and Ronquist 2004), and in the tropics (this paper), that plants show a greater tendency for dispersal than animals and have geographic disjunctions that occurred at times not correlated with specific geological events. If this pattern is general it has substantial implications for models of community assembly over evolutionary time (Donoghue and Smith 2004), envisaging resident faunas needing to be resilient to more dynamic floras. In the case of the Isthmus of Panama, the different biogeographies of plants and animals across this region has major implications for our understanding of biome assembly in the Neotropics, the most species-rich region in the world. The better ability of plants to disperse and establish means that forests such as in Amazonia, even when South America was an isolated continental island prior to its land connection with Central America, were subject to invasion by “foreign” plant species and resident animals and plants would constantly have had to evolve in response to this rain of immigrants.

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