

# Bipolar biogeography

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In PNAS, Popp et al. (1) present a convincing molecular phylogenetic analysis of a small group of ericaceous flowering plants, *Empetrum* (the crowberries), which includes species distributed at high northern latitudes and high southern latitudes but nowhere in between—a so-called bipolar (or anti-tropical or, broadly speaking, amphitropical) disjunction (Fig. 1). They contend that the best explanation for this distribution is that, sometime during the Mid-Pleistocene, a bird—perhaps a Whimbrel—ate the fruits of an *E. nigrum* plant, probably living in Alaska, and then flew to the southern tip of South America before depositing the seeds (1). At first blush, this sounds like the sort of trivia that you might find on a natural history blog. Why are we reading about this in PNAS? In what context could such a one-off historical accident possibly be of any general scientific interest? The answer, as I will develop, concerns the bipolar nature of biogeography itself.

Let us begin with Charles Darwin. Darwin devoted 2 of his 15 chapters in *The Origin of Species* (2) to biogeography, because he recognized the importance of explaining geographic distributions to his entire argument on evolution. It would seriously undermine the continuity of evolution if the same species could spring into existence in separate areas. Very wide geographic disjunctions seemed, to some at least, to negate the central idea that species stem from a common ancestor that originated at just one point in time and space. How, then, could the most challenging disjunctions—the bipolar ones—be explained in evolutionary terms?

In the sixth edition of *The Origin of Species*, published in 1872, Darwin included a section entitled “Alternate Glacial Periods in the North and South” in which he developed an explanation for bipolar distributions that relied on nothing more than the normal migration of species in response to climate change (2). His explanation took advantage of newly emerging ideas on glacial cycles, which suggested that a glacial period in the north would correspond to an interglacial period in the south. Darwin saw in this glacial seesaw a pumping mechanism. During cold periods in the north, cold-adapted species would move south, where they would come in contact with more tropical elements. When it warmed up, some of these plants would move up into any nearby mountains, say the Andes. Likewise, when

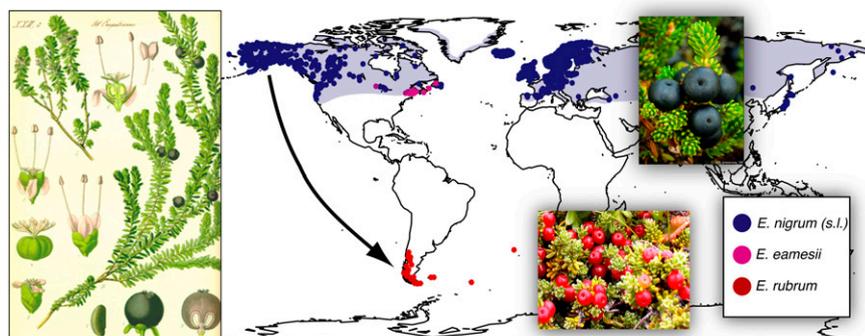


Fig. 1. (Left) *E. nigrum* (reprinted from ref. 21). (Right) Map showing the Popp et al. (1) finding that the red-fruited southern species, *E. rubrum* (image courtesy of Arthur Chapman), originated from *E. nigrum* (image courtesy of Atli Arnarson) in northwestern North America with black fruits, not from red-fruited *E. eamesii* in Eastern North America. Specific collection localities were obtained from the Global Biodiversity Information Facility (<http://www.gbif.org>). (Figure prepared by Jeremy Beaulieu.)

the south next cooled, southern organisms would move north and then south again as cold climates receded, but this time, “carrying southward with them some of the northern temperate forms which had descended from their mountain fastnesses” (2). Ingenious!

Alfred Russel Wallace, even more the biogeographer, developed his own take on bipolarity. In *Island Life*, published in 1880 (3), he agreed that plants had moved mainly from the north but not by Darwin’s pump. Instead, during glacial periods, when tree-lines were depressed, he envisioned plants mountain-hopping southward along the Andes (3). As for missing elements in the Andes today, Wallace reasoned that “we may connect their disappearance with the passing away of the last glacial period which, by raising the snow-line, reduced the area on which alone they could exist” (3). In a letter to Wallace, Darwin expressed his doubt: “This is rather too speculative for my old noodle. I must think that you overrate the importance of new surfaces on mountains and dispersal from mountain to mountain”.

The Darwin and Wallace hypotheses differed in detail, but both envisioned the migration of plants during recent glacial periods, mainly from the north to the south, and neither of them invoked long-distance dispersal from one area all the way to the other. However, fast-forward 80 years to Peter Raven’s classic paper on amphitropical plant distributions (4), and long-distance dispersal becomes the leading explanation. In part, Raven (4) based this argument on new lines of evidence,

such as the preponderance of self-compatibility in bipolar plants (“Baker’s law”) (5), their lack of specialized pollinators, and their occupation of open habitats, all popular themes in the analysis of island colonization (6).

Just then, however, the field of biogeography was on the verge of a revolution, brought on by the rise of phylogenetic systematics (7) and the emergence of so-called vicariance biogeography (8). This entailed the rejection of one-off biogeographic stories, and the search, instead, for general biogeographic patterns in cladograms that showed relationships among areas of endemism. General patterns implied the existence of general causal mechanisms, which were sought in earth history events, especially continental moments. Dispersal of any sort was viewed as an explanation of last resort, and long-distance dispersal was basically dismissed as unscientific (9). Therefore, bipolar disjunctions required another explanation and were soon interpreted as reflecting the breakup of the supercontinent Pangea (10). If this were the cause of bipolar disjunctions, then the relevant phylogenetic splits would date to the Mid-Jurassic or early Cretaceous, roughly 170–140 million years ago.

Put in these terms, the choice between the major hypotheses could be made just by dating the relevant phylogenetic splits.

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See companion article on page 6520.

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However, this was not so straightforward when vicariance was emerging, because the only molecular option was to assume clock-like evolution. Curiously, even as molecular dating approaches have improved dramatically (11), some still maintain that dating should not enter into biogeographic analyses: “Using the inferred absolute age of a taxon . . . constrains or restricts the variety of possible area relationships that might be revealed” (p. 148 in ref. 12). Fortunately for the growth of the discipline, this outlook is fading fast as molecular phylogeneticists, using so-called relaxed clock methods, are discovering that many plant and animal groups are simply too young for their disjunctions to have been caused by continental drift (13).

This brings us back to the Popp et al. analysis of *Empetrum*. Their dating analysis shows quite convincingly that the relevant phylogenetic splits do not date to the Jurassic—not even close (1). Instead, they probably happened in the Pleistocene less than 1 Mya. We can, therefore, immediately rule out ancient vicariance, but it is not quite as easy to choose between a Darwin or a Wallace migration scenario and the long-distance dispersal favored by Popp et al. (1). As Popp et al. point out, *Empetrum* is not currently known along the Andes, and its distinctive pollen grains have never been found there. However, as Wallace (3) argued, this does not entirely rule out that they passed through the Andes and then disappeared as suitable habitats shrank.

Where does this leave us? I think we need to reconnect with the main motivation behind vicariance biogeography, namely that there are real benefits in identifying general patterns. In my view, the pendulum is swinging too far in the direction of the one-off scenarios that so hampered the development of biogeography. In the case of bipolar disjunctions, comparisons across groups will

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teach us a lot (e.g., refs. 14 and 15). I am guessing that we will find a range of disjunction times in different groups, including much older times even in plants (much deeper in phylogeny) but perhaps especially in animals, where such patterns abound in marine organisms (16). However, even for the class of recent arrivals, we can, in the spirit of Peter Raven (4), ask how many have relatives in the Andes? How many are self-compatible? How many are dispersed by what mechanisms? Additionally, we should increasingly be able to provide the kind of precision that

Popp et al. (1) do with respect to the probable location and attributes of ancestral populations.

In the end, I am less surprised by the young age of *Empetrum* (there were preliminary indications) (17) than I am by the biological details. Today, *E. nigrum* in Alaska is dioecious (pollen and seeds produced on separate plants) and bears black-colored berries (18) (Fig. 1). It seems odd that the source plant would come from there, as Popp et al. (1) show. After all, the establishment of a dioecious species requires the success of at least two individual plants, and as its name implies, the southern species, *E. rubrum*, bears red fruits (18). It would have been much simpler if the southern species was derived from *E. eamsii* in northeastern North America, where the plants are hermaphroditic and red-fruited (Fig. 1). Perhaps the establishment of dioecious plants is more common than expected (6), and changes in fruit color, which are common (think blueberries vs. cranberries), require only small changes in the mix of anthocyanins (19).

The study by Popp et al. (1) suggests the possibility of integrating not just credible age estimates into likelihood-based biogeographic analyses (20) but a variety of other biologically relevant factors as well, and, eventually, the discovery of generalities that transcend individual case studies. We are on the verge of a truly integrative approach, and in this new context, bipolar disjunctions will surely yield fresh insights for years to come.

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