Point of View

Searching for Ancestral Areas and Artifactual Centers of Origin in Biogeography: With Comment on East–West Patterns Across Southern Australia

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Stemming from acceptance of continental drift theory and development of cladistic systematics in the 1960s, interest in historical biogeography was revived. The field and methodology have since been reviewed several times (e.g., Nelson and Platnick 1981; Myers and Giller 1988; Morrone and Carpenter 1994; Humphries and Parenti 1999; Crisci et al. 2003; Ebach and Tangney 2007; Santos 2007; Parenti and Ebach 2009). In essence, early methods focussed on discovering relationships of areas based on phylogenies of taxa endemic to those areas and biogeographic patterns presented as summary area cladograms. Comparisons across different groups (clades) of organisms revealing congruent patterns were interpreted as evidence of simple vicariance, which could be compared with other data, such as geological breakup of Gondwana, whereas incongruence of patterns was interpreted as requiring a complex explanation or stochastic long-distance dispersal (Nelson and Platnick 1981). A plethora of methods to determine area cladograms arose to deal with widespread taxa (representing range expansions or a failure to differentiate), missing areas (extinctions), and other complications. But by the 1990s, there was no unifying accepted biogeographic method (Nelson and Ladiges 2001), and different methods applied to the same data gave different results, indicating that at least some of the results are artifacts of the method.

What is the current trend in methodology? Most recent studies follow a similar procedure: reconstruct taxon relationships based on molecular data, estimate clade divergences using a molecular dating method (sometimes employing few or distant fossils or only secondary calibration points), and employ a method of ancestral area reconstruction to determine areas at the internal nodes of the phylogenetic tree. The Progression Rule (acknowledged or implied) is often invoked to explain the results with interpretation constrained by the estimated ages of divergences.

THE PROGRESSION RULE

The Progression Rule is based on the ideas of Hennig (1966) and Brundin (1966) and assumes that the most primitive or basal taxa are likely to occur at the center of origin, indicating the ancestral area of the group. Progression from the basal nodes to the most derived is interpreted as the direction of dispersal of the group. To illustrate the argumentation, Hennig (1966, figure 40, p. 136) presented a phylogeny of 5 subspecies of flies in Mimegralla albimana, which occur in areas 1–5 in Southeast Asia from west to east to Tonga, although the relationships of the subspecies he described do not match the exact pattern in his Figure 40, which showed the tree 1(2(3(4,5))). Other patterns interpreted using the progression rule (e.g., Ross 1974, p. 214–219) include situations where particular areas occur more than once, such as in the hypothetical area relationship D(D(C(B(B,A)))) where areas D and B are “repeated,” as discussed by Parenti (2007, p. 63–71).

GEOGRAPHIC PARALOGY AND CENTERS OF ORIGIN

We have argued previously that the Progression Rule is invoked where there is geographic paralogy, with artifactual results (Nelson and Ladiges 1996; Nelson and Ladiges 2001). In molecular systematics, “paralogy” refers to misleading comparison between duplicated genes that have independent histories (Fitch 1970). Geographic paralogy is analogous to this use and is evident where there are partly or wholly overlapping distributions for different taxa—duplicated geographies of taxa that have had independent histories (Nelson and Ladiges 1996; Parenti and Ebach 2009). For example, in redFigure 1, the only information of area relationships in the tree is A(B+C), geographically informative nodes being 6 and 7; nodes 1–5 we see as paralogous and thus uninformative. In this example, the area relationship A(B+C) can be interpreted as a result of a vicariance event that affected 2 clades (nodes 4 and 5) and which occurred after speciation events at older nodes 1–3. Crisci (2001) also provides an example (his figure 2, p. 161) illustrating paralogy and sympathy of taxa. Similarly, in the example D(D(C(B(B,A)))) above, nodes leading to the repeated areas D and B are paralogous.

Ancestral area analyses (e.g., Ronquist 1997; Ree et al. 2005) that attempt to push optimization down to the
Eucalyptus Subgenus Eucalyptus (Family Myrtaceae)

A significant component of the Australian flora with east–west connections is Eucalyptus subgenus Eucalyptus (commonly called the “monocalypts”), with 111 species. Ladiges et al. (2010) recently published a phylogeny based on morphological and molecular data (Fig. 2). Eucalyptus subgenus Eucalyptus shows early lineages in the southwest and an east–west divergence at a higher node. The pattern of early lineages diverging in the southwest is not interpreted as evidence of the region being a center of origin, first because the lower nodes are paralogous and second because the sister taxon E. loeziana (subgenus Idiogenes) occurs in the east, which for a center of origin model would require dispersal from east to west and back to the east.

Ladiges et al. (2010) argued that the group was present in the Early Eocene across western and eastern Australia when conditions were warm and wet (Fig. 3). This time frame is supported by macrofossils of the sister group Eucalyptus subgenus Symphyomyrtus dated at 52.2 Ma from Patagonia, South America (Gandolfo et al. 2011), Paleocene–Eocene Eucalyptus macrofossils from Queensland, Australia (Rozefelds 1996), as well as Late Paleocene fossil pollen from the Lake Eyre Basin in central Australia (Martin 1994). The supposition that the eucalypts date back to at least the early Paleogene is supported also by molecular dating of family Myrtaceae (Sytsma et al. 2004). Figure 2 shows the earliest lineages of Eucalyptus subgenus Eucalyptus to include tall wet forest species, such as E. marginata (Jarrah) and taxa that occur today on lower nutrient soils on weathered lateritic plateaux. Later lineages include mallee species associated with granitic and quartzite hills and sands. The divergence of the western taxa from the monophyletic eastern group may date back to the earliest phase of marine inundation during the Late Eocene and major climatic change at the Eocene/Oligocene boundary. This is consistent with a molecular dating analysis of the eucalypt group by Crisp et al. (2004); their chronogram suggests divergence times between southwest and southeast temperate clades of Eucalyptus subgenus Eucalyptus as approximately 30–40 Ma. The oldest of the eastern lineages survive today in Queensland in a climate as warm as that of the Eocene, whereas more derived clades occur in the cooler southeast.

Of the 111 species in Eucalyptus subgenus Eucalyptus, there is one that occurs both to the west and to the east

**EAST–WEST PATTERNS ACROSS SOUTHERN CONTINENTAL AUSTRALIA**

Diels (1906) considered the southwest of Western Australia to be a center of origin of the autochthonous element of the Australian flora, from which taxa dispersed to the east; some more recent authors have held similar views for particular plant taxa, for example, Thompson (1976) for Tremandraceae and Mast

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**Figure 1.** Hypothetical example of geographic paralogy: taxa I–VIII in areas A–C. Nodes 6 and 7 are informative of the area relations A(B,C); lower paralogous nodes are uninformative.
of the Nullarbor Plain. *Eucalyptus diversifolia* (Fig. 2) is a western species tolerant of coastal limestone soils that has evidently expanded its range eastwards, probably during periods of low sea level (Wright and Ladiges 1997).

**Phebalium Group (Rutaceae) and Tremandra Group (Former Tremandraceae)**

Family Rutaceae is a relatively old family, which has been estimated using molecular dating as Late Cretaceous (Muellner et al. 2007). The *Phebalium* group *sensu Wilson* (1998) in the family Rutaceae comprises 9 genera and approximately 97 species of woody shrubs, many of which are localized endemics found in temperate Australia. Molecular phylogenetic analysis by Mole et al. (2004) revealed 3 clades with southwest–southeast (W–E) connections: their clade E, including genera *Rhadinothamnus*, *Chorilaena*, and *Nematolepis*, shows the pattern of W(W,E); in clades D and F, *Asterolasia* and *Phebalium*, respectively, show simple W–E divergences.

*Tremandra*, *Platytheca*, and *Tetratheca* (previously family Tremandraceae) form a dry-adapted clade (ca. 49 species) that diverged from rainforest taxa within Elaeocarpaceae during the Paleocene, diversifying in the Oligocene and Miocene (Crayn et al. 2006). The clade is distributed in southern temperate Australia, with *Tremandra* and *Platytheca* endemic to the southwest.
and *Tetratheca*, the largest genus occurring in both the southwest and the east, with rainforest relatives in eastern Australia. Relationships of the dry-adapted taxa and clades show a pattern similar to that for the *Phebalium* group of *Eucalyptus* subgenus *Eucalyptus* in southwest, tall wet forest habitats, increasingly weathered soils and drying. Marine incursion splits west from east. (d) Eastern clades differentiate; range contraction toward the coast with increased aridity inland.

The area relationships for the *Phebalium* and *Tremandra* groups, which have earliest lineages in the southwest and later divergence between west and east, are congruent with those of *Eucalyptus*, providing support for the notion of a general shared history of widespread ancestral distribution and vicariance. The recognition of geographic paralogy in these examples and the congruence of the area relationships allows us to reject the hypothesis of Thompson (1976) that the southwest was the center of origin for the *Tremandra* group and the claim of Butcher et al. (2007) that “it is apparent that *Tetratheca* [the widespread genus in the group] underwent an early transcontinental radiation, and following the Eocene separation of the eastern and western populations, there was substantial diversification of lineages in the western region” (p. 135).

**Banksia (Proteaceae) Reinterpreted**

The tribe Banksieae (Proteaceae) provides an example of east–west connections that is open to reinterpretation. The group includes 2 subtribes: Musgraveinae, including 4 eastern species in 2 rainforest genera *Musgravea* and *Austromuellera* and Banksiinae, including sclerophyllous *Banksia* (91 taxa) and, nested within it, *Dryandra* (93 taxa). Mast and Givnish (2002) presented a molecular phylogeny of the tribe, aiming “to determine the area of origin” for the lineage *Banksia* + *Dryandra*. They used DIVA (Ronquist 1997) to determine ancestral distributions (Fig. 4a, based on their figure 5, p. 1318) and concluded that it “identifies the origin of subtribe Banksiinae as having occurred in southwestern Australia” (p. 1316). They also commented, however, that “The origin of subtribe Banksiinae is . . . incongruent with the distribution of the earliest fossils in New South Wales” (p. 1321). The earliest known fossils are southeast *Banksieaephyllum taylorii* of the Late Paleocene, whereas southwest fossils attributed to Banksiinae are Middle or Late Eocene; Musgraveinae from the southeast are dated Late Middle Eocene. Mast and Givnish (2002) concluded that “perhaps there is a problem with our choice of a vicariance framework” (p. 1321).

Their problem stems from optimization of ancestral nodes and application of the Progression Rule, which led to an artifactual result and explanation that the southwest is the center of origin for *Banksia*, which later dispersed (twice, clades C and P, Fig. 4a) to the east. A simpler explanation, not in conflict with the fossil record, is similar to that for *Eucalyptus* subgenus *Eucalyptus*. The 2 main lineages within *Banksia* (Fig. 4b) were ancestrally widespread and experienced a vicariant event.
Congruence of Patterns in Space and Time

Crisp and Cook (2007) considered competing explanations of multiple dispersal or vicariance and analyzed various plant groups across southern Australia. Their approach was to use molecular dating of phylogenies to compare various plant groups, arguing that any congruent temporal pattern among them would be evidence of vicariance—similar to the argument based on finding general area relationships. Crisp and Cook (2007) identified a congruent signal of divergence at a mean age of approximately 16–14 Ma (confidence limits ranging back to 30 Ma), indicative of vicariance driven by marine inundation, the uplift of the Nullarbor limestone plain, and periods of cooling. Their results also suggested earlier divergences for one of the major clades of Banksia (ca. 27.5 Ma) and Allocasuarina (21.7 Ma) (range to 40 Ma), corresponding with earlier marine transgressions and periods of cooling.

With regard to fauna, Morgan et al. (2007) also rejected dispersal (in this case from east to west) for anuran frogs and concluded from their molecular dating analyses that southwest endemics are ancient and east-west splits are contemporaneous with splits in elements of the flora (e.g., Banksia). In contrast, for Australian pygmy perches that have a disjunct distribution from the southwest to the east, Unmack et al. (2011) claim to have a clear example of multiple movements. Their dated phylogeography shows the area pattern W(E,W,E) and they state as “inescapable . . . that a minimum of two migrations/range expansions occurred . . . by two independent lineages.” An alternative interpretation is that their area tree shows geographic paralogy; the relictual and sympatric distributions of some of the taxa are suggestive of extinction, for example, in the earlier of the 2 eastern lineages (mean age 21.3 myr) that today includes only one narrow range species (Nannoperca variegata) sympatric with species from the other lineage.

The results of the dating studies of Crisp and Cook (2007) and Morgan et al. (2007) are in a broad agreement with conclusions based on patterns of area relationships described earlier, and the 2 approaches are similar in using congruence as the test of a vicariance history. Morgan et al. (2007) recommended that further studies of other taxa focus on divergence dates and that “exploring the pattern and timing of divergences will be an important step towards increasing our understanding of the biogeography of southern Australia. This would be an effective strategy even in the absence of accurate absolute calibration points . . .” (p. 383). However, seeking congruence among dates of taxon divergences and also with geological events poses a particular methodological challenge, which Crisp and Cook (2007) attempted to address by their statistical analysis. Over what period of time does a vicariant event occur? How variable are taxa in their evolutionary response to a vicariant event? How long do separated components of biota remain undifferentiated if the separated regions remain environmentally similar? How much variation in estimated divergence times is an accepted tolerance range?

Conclusions

In searching for ancestral areas, artificial results and the finding of centers of origin can stem from not recognizing geographic paralogy. Confidence in interpreting biogeography, based on spatial patterns and/or temporal patterns, relies on congruence among different clades.

Comparative studies support the conclusion that the southwest of Australia, with its high level of endemicity, is not a center of origin but a region that contains elements that represent old differentiation. Analysis of examples of extant flora and fauna that are distributed across the continent reveals lineages that first diverged in the southwest during the Paleogene, as Australia rifted from Antarctica and as environments differentiated earlier than in the more humid eastern part of Australia. The southwest later became isolated by marine inundations and periods of climatic cooling—vicariant processes that led to the isolation and differentiation of clades from west to east.

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