Southern Hemisphere Biogeography Inferred by Event-Based Models: Plant versus Animal Patterns

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Abstract.—The Southern Hemisphere has traditionally been considered as having a fundamentally vicariant history. The common trans-Pacific disjunctions are usually explained by the sequential breakup of the supercontinent Gondwana during the last 165 million years, causing successive division of an ancestral biota. However, recent biogeographic studies, based on molecular estimates and more accurate paleogeographic reconstructions, indicate that dispersal may have been more important than traditionally assumed. We examined the relative roles played by vicariance and dispersal in shaping Southern Hemisphere biotas by analyzing a large data set of 54 animal and 19 plant phylogenies, including marsupials, ratites, and southern beeches (1,393 terminals). Parsimony-based tree fitting in conjunction with permutation tests was used to examine to what extent Southern Hemisphere biogeographic patterns fit the breakup sequence of Gondwana and to identify concordant dispersal patterns. Consistent with other studies, the animal data are congruent with the geological sequence of Gondwana breakup: (Africa(New Zealand(southern South America, Australia))). Trans-Antarctic dispersal (Australia ↔ southern South America) is also significantly more frequent than any other dispersal event in animals, which may be explained by the long period of geological contact between Australia and South America via Antarctica. In contrast, the dominant pattern in plants, (southern South America(Australia, New Zealand)), is better explained by dispersal, particularly the prevalence of trans-Tasman dispersal between New Zealand and Australia. Our results also confirm the hybrid origin of the South American biota: there has been surprisingly little biotic exchange between the northern tropical and the southern temperate regions of South America, especially for animals. [Concordant dispersal; Gondwana; historical biogeography; parsimony-based tree fitting; Southern Hemisphere; vicariant history; West Wind Drift.]

Dispersal and vicariance are often considered competing hypotheses in historical biogeography. Disjunct distribution patterns can be explained either by fragmentation of widespread ancestors by vicariant (isolating) events or by dispersal across a preexisting barrier. Current methods of biogeographic analysis are based on the vicariance model because nearly any distribution pattern can be explained by dispersal, making dispersal hypotheses resilient to falsification (Morrone and Crisci, 1995). Vicariance hypotheses, however, can be tested by concordance between the phylogenetic and distribution patterns of different organisms. Taxa exhibiting the same phylogenetic and distribution pattern are assumed to share a common history of geological isolation events. The resulting pattern can be represented in the form of a hierarchical area cladogram, presumably reflecting the biotic relationships among the areas analyzed (Nelson and Platnick, 1981).

The biogeographic history of the Southern Hemisphere is considered a prime example of the vicariance scenario: disjunct trans-Pacific distributions resulted from the sequential breakup of the southern supercontinent Gondwana during the last 165 million years (MY) (Fig. 1), causing vicariant division of its ancestral biota (Brundin, 1966; Raven and Axelrod, 1972). Long-distance dispersal is usually discarded as the primary causal explanation of Southern Hemisphere patterns. Most Gondwanan groups (e.g., marsupials, ratites) are presumed to be poor dispersers, unable to move across oceanic barriers. Moreover, dispersal is thought to be a random process, and hence it could not have given rise to the type of congruent or concordant patterns found in so many different groups (Croizat et al., 1974; Craw, 1982).

Paleogeographic reconstructions, however, indicate that the biogeographic history of the Southern Hemisphere cannot be entirely reduced to a simple sequence of vicariance events. For instance, some of the southern landmasses (e.g., New Guinea) were formed by the accretion of multiple terranes (Pigram and Davies, 1987), whereas others (India) became isolated only to join new landmasses later on. Although recent molecular estimates indicate that the Cretaceous breakup of Gondwana was an important mechanism in the ordinal diversification of birds and mammals (Cracraft, 2001; Eizirik et al., 2001), molecular studies of other groups increasingly indicate that dispersal has played a more important role in the development of the Southern Hemisphere biota than traditionally assumed. Molecular clock estimates of divergence times show that many classic Gondwanan groups combine an ancient vicariance pattern with relatively recent dispersal events (Waters et al., 2000b; Cooper et al., 2001), whereas other groups originated after continental breakup, and their distribution can be explained only by long-distance dispersal across oceanic barriers (Baum et al., 1998; Waters et al., 2000a; Buckley et al., 2002). The notion that Gondwanan groups are poor dispersers has also been questioned by their occurrence on young volcanic islands (*Nothofagus*; Pole, 1994) or their presence in Gondwana landmasses that were isolated at the time of cladogenesis (e.g., ratite kiwis in New Zealand; Cooper et al., 2001). The flora of New Zealand and New Caledonia has traditionally been considered a relict of the late Cretaceous Gondwanan flora, isolated since the time of vicariance. However, according to Pole (1994), paleobotanical records indicate that most of New Zealand's present flora came by long-distance dispersal from Australia
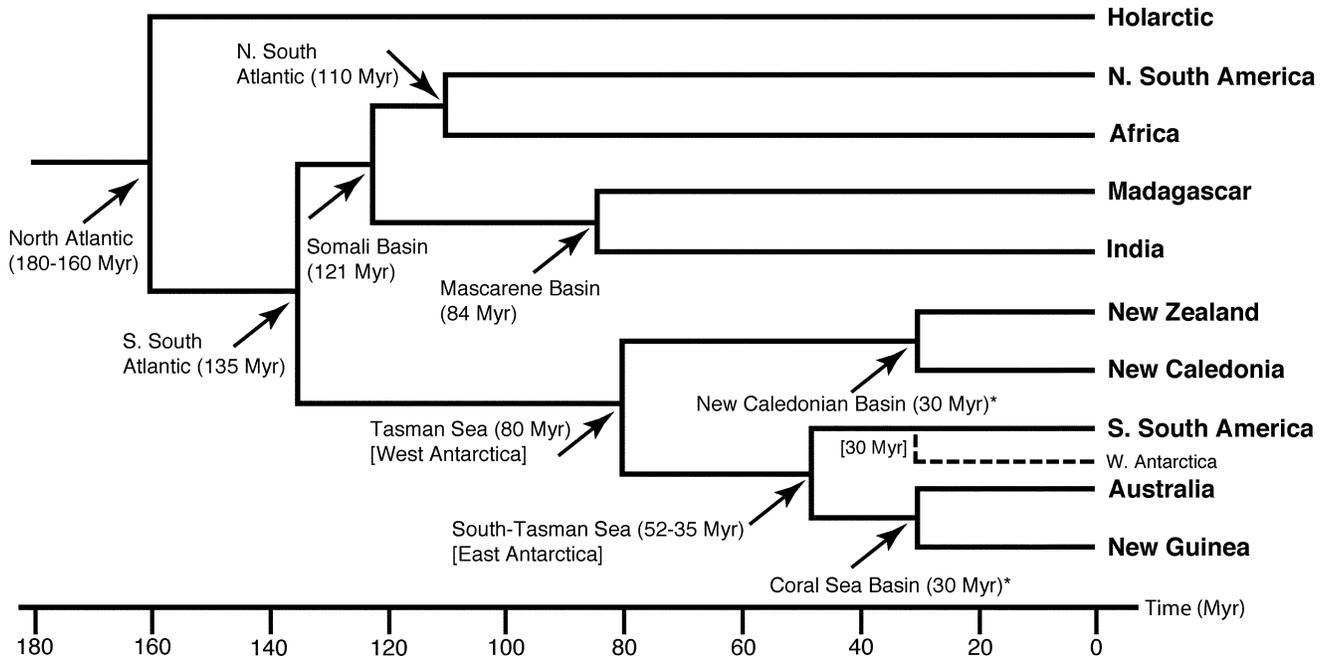
FIGURE 1.   Geological area cladogram representing the relationships among the Southern Hemisphere landmasses based on paleogeographic evidence (from several sources). The time of vicariance is the assumed primary fragmentation, (*) dated as 70–60 MYago (MYA) in alternative reconstructions.

during the late Tertiary after land connections with the rest of Gondwana were broken. Trans-Tasman dispersal via the West Wind Drift is often argued to explain the frequency of relationships ((Australia, New Zealand)South America) in austral plants, a pattern in conflict with the accepted sequence of Gondwana breakup (Linder and Crisp, 1995).

Despite numerous studies of single groups, a comprehensive analysis of Southern Hemisphere biogeographic patterns has not been attempted yet. The shortcomings of studies based on only a few groups and the necessity of large data sets in separating general biogeographic patterns from distributional noise are widely recognized (Crisci et al., 1991; Seberg, 1991; Linder and Crisp, 1995; Sanmartín et al., 2001). At the same time, recent methodological developments have made it possible to study complex biogeographic patterns in much more detail than previously. Thus, the time is ripe for a new look at Southern Hemisphere biogeography.

Traditional biogeographic methods are characterized by a relatively lose relation between pattern and process. This causes a number of problems, including difficulties in inferring and testing biogeographic hypotheses that include both dispersal and vicariance patterns. In contrast, recent event-based methods (Page, 1995; Ronquist, 1997, 1998) are derived from explicit (although not strict probabilistic) process models and reconstruct both ancestral distributions and biogeographic events. Each event (e.g., vicariance, duplication, dispersal, and extinction) is associated with a cost that should be inversely related to its likelihood: the more likely the event, the less costly

it should be (Ronquist and Nylin, 1990; Ronquist, 1998). The most-parsimonious solution is the one minimizing the total cost of the implied events (Ronquist, 1995, 1998, 2002a); it can be searched for using modifications of standard heuristic and exhaustive parsimony search algorithms (Ronquist, 1995, 1998, 2002a).

Dispersal–vicariance analysis (DIVA; Ronquist, 1997) is an event-based biogeographic inference method that does not force vicariance events to conform to a hierarchical pattern. DIVA is particularly appropriate when inferring biogeographic patterns in complex geological settings where areas have split and fused again (Sanmartín et al., 2001), but its generality causes unnecessary loss of statistical power when there is a strong underlying hierarchical pattern of vicariance events, as one might expect in the Southern Hemisphere. In this situation, it is more appropriate to use event-based tree fitting methods, which only allow vicariance events predicted by a hierarchical area cladogram (Page, 1995; Ronquist, 1998, 2002a). Tree-fitting methods have been used extensively for studying host–parasite systems but are still relatively unexplored in the biogeographic context. These methods are good for finding significantly supported area cladograms, and if these cladograms exist tree fitting will help to reduce the noise level in the data when looking at other patterns. For instance, tree fitting allows one to study dispersal patterns while accounting for the vicariance events predicted by a geologically based area cladogram. In the absence of geologically predicted vicariance events, parsimony-based tree fitting is essentially the same as DIVA with ancestral distributions restricted to two unit areas.

We analyzed Southern Hemisphere biogeography based on the published phylogenies of 19 plant and 54 nonmarine animal taxa. In total, the phylogenies included 1,393 terminals, which makes this the largest biogeographic analysis of the Southern Hemisphere attempted so far. We use parsimony-based tree fitting in conjunction with permutation tests to examine the relative role played by dispersal and vicariance in shaping the Southern Hemisphere biota. In particular, we wanted to test to what extent southern biogeographic patterns fit the breakup sequence of Gondwana and to search for the existence of concordant dispersal patterns in the southern flora and fauna.

Geological Scenario

There are several conflicting hypotheses on earth history that explain the evolution of continents by continental drift in the Mesozoic and Cenozoic. The sequential breakup of the supercontinent Pangaea (Scotese et al., 1988) is the most accepted and the one followed here, but the expanding earth theory (Shields, 1979) and the idea of the lost supercontinent of Pacifica (Kamp, 1980) have also been considered by biogeographers in explaining biogeographic patterns incongruent with the Pangaea model (Crisci et al., 1991; Seberg, 1991).

The following account is a synthesis of ideas presented by Scotese et al. (1988), Veevers (1991), Veevers et al. (1991), Lawver et al. (1992), and McLoughlin (2001) (see http://www.ebc.uu/systzoo/staff/sanmartin.html for a more complete account). They are summarized in terms of a geological area cladogram in Figure 1.

During the Triassic, Gondwana formed the southern portion of the Pangaea supercontinent. The climate of Gondwana was not uniform, and paleobotanists and biogeographers usually recognize two climatically different biotic provinces: a Northern Tropical Gondwana province, including northern South America, Africa, Madagascar, India, northern Australia, and New Guinea, with a tropical climate; and a Southern Temperate Gondwana province, including southern South America, Australia, Antarctica, New Zealand, and New Caledonia (Craw, 1982; Karol et al., 2000) and southern temperate Africa (Amorim and Tozoni, 1994).

Gondwana started to break up in the Jurassic (165–150 MY ago [MYA]), when rifting began between India and Australia–east Antarctica about 165 MYA. Shortly after, the continental block of Madagascar and India, which was then adjacent to Somalia, broke away from Africa and began moving southeast, attaining its present position in front of Mozambique in the early Cretaceous, 121 MYA (Rabinowitz et al., 1983). India separated from Madagascar in the late Cretaceous (88–84 MYA), with the opening of the Mascarene Basin (Storey et al., 1995), and began drifting northward, eventually to collide with Asia at about 50 MYA. South America began to separate from Africa in the Early Cretaceous (135 MYA) with the opening of the South Atlantic Ocean at the latitude of Argentina and Chile. Northern South America and Africa remained connected until the mid-late Cretaceous

(110–95 MYA), when a transform fault opened between Brazil and Guinea. As a result, Africa started drifting northeast and collided with Eurasia in the Paleocene (60 MYA), whereas southern South America drifted southwest into contact with Antarctica.

New Zealand, Australia, South America, and Antarctica remained connected until the late Cretaceous: east Antarctica was adjacent to southern Australia, and New Zealand and southern South America were in contact with west Antarctica (Fig. 2a). Antarctica had at that time a warm-temperate climate. New Zealand was the first to break away from Antarctica in the late Cretaceous. About 80 MYA the continental block of Tasmantis, including New Zealand and New Caledonia, broke away from west Antarctica and moved northwest, opening the Tasman Sea (Fig. 2b). During most of the Paleogene, New Zealand and New Caledonia were progressively submerged under a marine transgression, with probably >80% of New Zealand's present area beneath water by the mid-Oligocene (Brothers and Lillie, 1988; Cooper and Milliner, 1993). McLoughlin (2001), however, suggested that New Zealand was not completely submerged but was divided into smaller islands intermittently separated by shallow seas.

New Zealand and New Caledonia were finally separated in the mid-Tertiary (40–30 MYA), when the Norfolk Ridge foundered, opening the New Caledonian Basin (Walley and Ross, 1991). Australia and South America remained in contact across Antarctica until the Eocene. Australia began to separate from Antarctica in the late Cretaceous (90 MYA), but both continents remained in contact along Tasmania, and complete separation did not occur until the late Eocene (35 MYA) with the opening of the South Tasman Sea. Some authors, however, have proposed an earlier biotic separation (50 MYA), when a shallow marine seaway formed between Australia and Antarctica (Woodburne and Case, 1996). Southern South America and Antarctica remained in contact through the Antarctic Peninsula until the Oligocene (30–28 MYA), when the Drake Passage opened between these continents, allowing the establishment of the Antarctic Circumpolar Current and the onset of the first Antarctic glaciation. Following its separation from Antarctica, Australia began to drift rapidly toward Asia. New Guinea was then joined to the northern margin of the Australian Plate, although only the southern margin of New Guinea was emergent at that time. The collision of the Australian and Pacific plates in the Oligocene (30 MYA) initiated the tectonic uplift of New Guinea, but by the early Miocene, much of southern New Guinea was again submerged. Subsequent episodes of uplift began in the Miocene after the collision of the Australian and Asian plates and led to the accretion of numerous terranes to the northern margin of New Guinea (Pigram and Davies, 1987). A second phase of collision between Australia and the Asian Plate in the late Miocene–Pliocene (10 MYA) resulted in the rise of mountain chains in Southeast Asia, northern Australia, New Guinea, and New Zealand (e.g., the Southern Alps).

TABLE 1. The most commonly discussed area relationships in the Southern Hemisphere biogeographic literature. These biogeographic patterns are also represented as cladograms in Figure 3. For each pattern, some original references and suggested explanations are listed. Although many of these patterns have often been discussed, this is the first time they are named or studied in a comparative framework.

Biogeographic pattern[a]	Area cladogram[b]	References	Suggested explanations
SGP[c]	(AFR(NZ(SSA, AUS)))	Brundin, 1966; Edmunds, 1981; Patterson, 1981; Cranston and Edward, 1992	Vicariance: breakup sequence of Southern temperate Gondwana, extinction or primitive absence in some areas
PSP	(AFR(SSA(NZ, AUS)))	Seberg, 1988, 1991; Pole, 1994; Linder and Crisp, 1995	1. Alternative vicariance sequence 2. Dispersal: West Wind Drift
ISP	(AFR(AUS(SSA, NZ)))	Glasby and Alvarez, 1999; Swenson and Bremer, 1997; Renner et al., 2000	1. Alternative vicariance sequence 2. Dispersal: West Wind Drift
NGP	(AFR(MAD(IND(SEA (SWP(NG, AUS))))))	Croizat, 1958; Raven and Axelrod, 1972; Cranston and Hare, 1995; Macey et al., 2000	1. Post-Miocene dispersal 2. Late Cretaceous dispersal (Kerguelen Plateau) 3. Mesozoic–Cenozoic accretion of Gondwanan terranes
TGP	(MAD(AFR, NSA))	Goldblatt, 1993; Ortí and Meyer, 1997	Vicariance: breakup sequence of northwest Gondwana
AMP	(SSA(NSA, HOL))	Crisci et al., 1991; Lopretto and Morrone, 1998	1. Ecological barrier (Amazon Basin) 2. Uplift of Andes Mountains 3. Panama Isthmus

[a]SGP = southern Gondwana pattern; PSP = plant southern pattern; ISP = inverted southern pattern; NGP = northern Gondwana pattern; TGP = tropical Gondwana pattern; AMP = trans american pattern.

[b]AFR = Africa; AUS = Australia; HOL = Holarctic; IND = India; MAD = Madagascar; NC = New Caledonia; NG = New Guinea; NSA = northern South America; NZ = New Zealand; SEA = Southeast Asia; SSA = southern South America; SWP = Southwest Pacific.

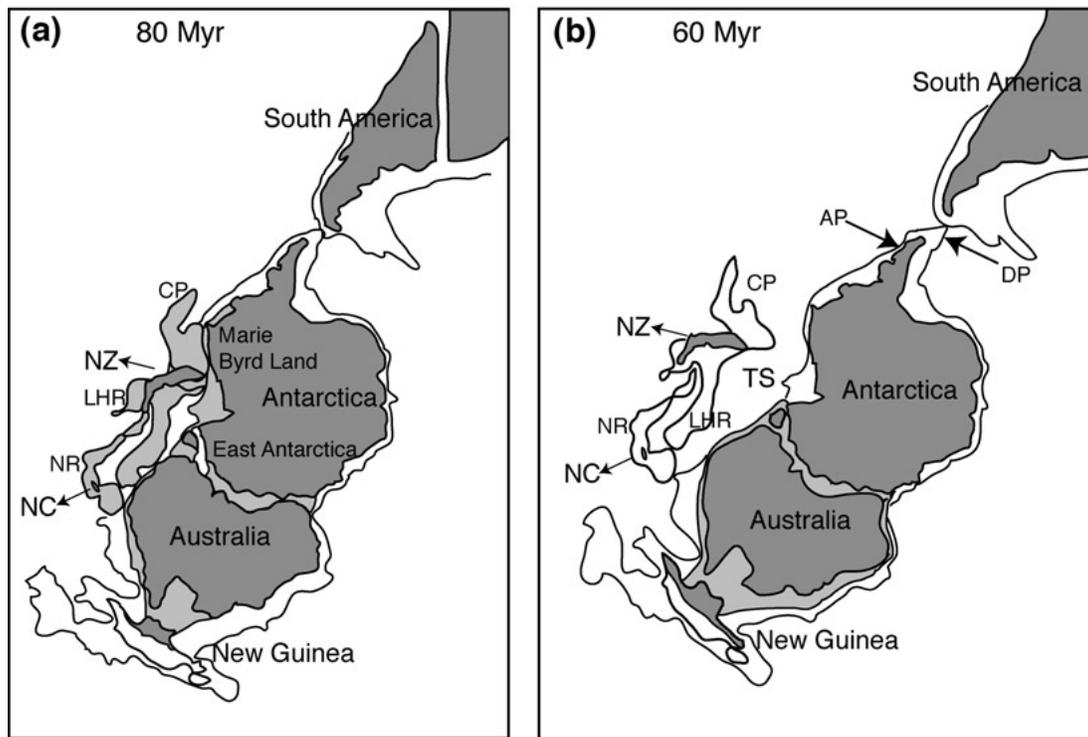[c]In some groups, this pattern includes New Guinea as the sister area to AUS.

FIGURE 2. Paleogeographic reconstruction of the Southern Hemisphere in (a) the late Cretaceous (80 MYA) and (b) the early Paleocene (60 MYA) modified from Barron et al. (1981). In this stereographic projection, emergent land is shaded light gray and the major southern landmasses are shaded dark gray. AP = Antarctic Peninsula; CP = Campbell Plateau; DP = Drake Passage; LHR = Lord Howe Rise; NC = New Caledonia; NR = Norfolk Ridge; NZ = New Zealand; TS = Tasman Sea.

(a) SGP

```
         ┌─── Africa
       ┌─┤
       │ └─── New Zealand
───────┤     ┌─── S. South America
       └─────┤
             └─── Australia
```

(b) PSP

```
         ┌─── Africa
       ┌─┤
       │ └─── S. South America
───────┤     ┌─── New Zealand
       └─────┤
             └─── Australia
```

(c) ISP

```
         ┌─── Africa
       ┌─┤
       │ └─── Australia
───────┤     ┌─── S. South America
       └─────┤
             └─── New Zealand
```

(d) NGP

```
         ┌─── Africa
       ┌─┤
       │ └─── Madagascar
       │     ┌─── India
───────┤   ┌─┤
       └───┤ └─── SE. Asia
           │     ┌─── SW. Pacific
           └─────┤     ┌─── New Guinea
                 └─────┤
                       └─── Australia
```

(e) TGP

```
         ┌─── Madagascar
       ┌─┤
───────┤ └─── Africa
       └──────── N. South America
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(f) AMP

```
         ┌─── S. South America
       ┌─┤
───────┤ └─── N. South America
       └──────── Holarctic
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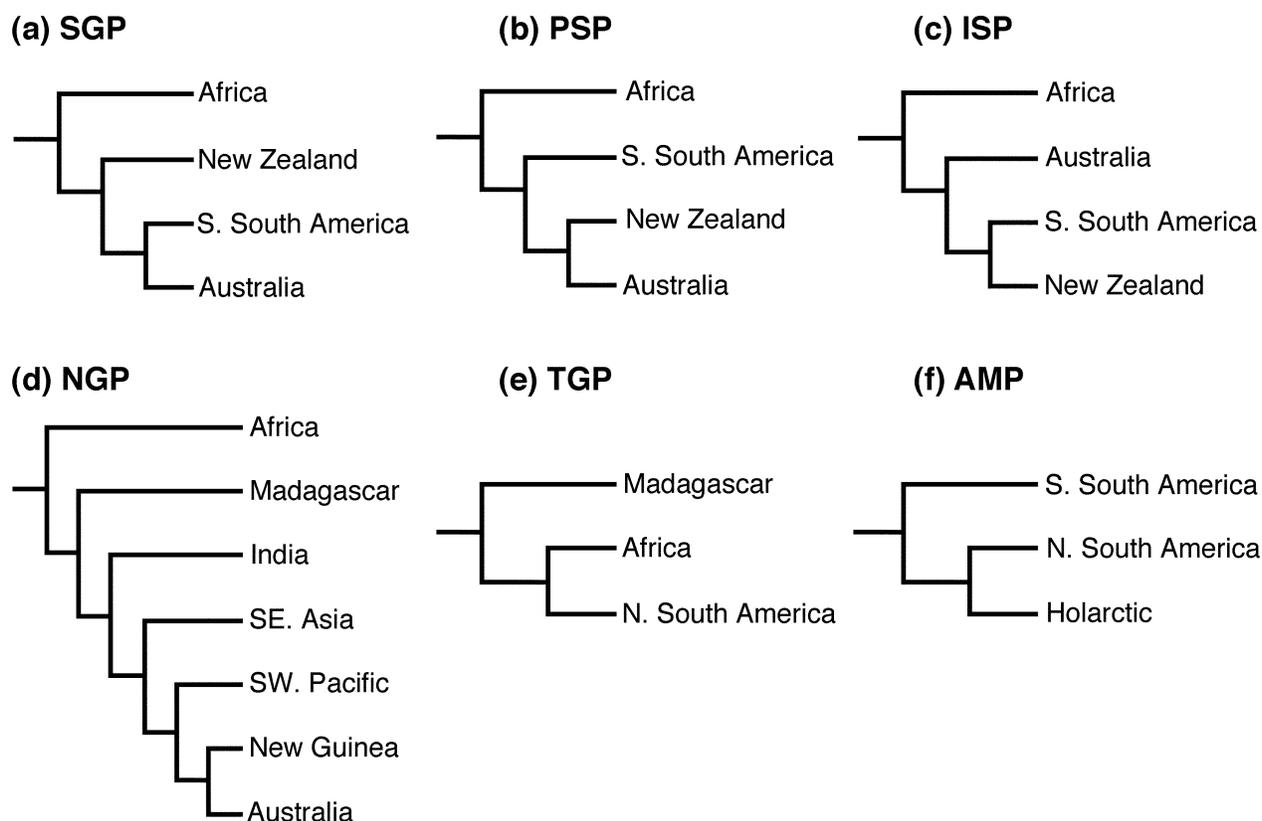
FIGURE 3. Area cladograms representing the hierarchical biogeographic patterns most frequently found in Southern Hemisphere organisms: (a) southern Gondwana pattern (SGP); (b) plant southern pattern (PSP); (c) inverted southern pattern (ISP); (d) northern gondwana pattern (NGP); (e) tropical gondwana pattern (TGP); (f) trans American pattern (AMP).

Biogeographic Patterns

As a background for the discussion of distribution patterns, we identified the most commonly discussed area relationships in the Southern Hemisphere biogeographic literature (Fig. 3, Table 1); several of these patterns previously had not been named or studied in a comparative framework. The most famous is the southern Gondwana pattern (SGP; Fig. 3a), which refers to Brundin's (1966) classic pattern based on his studies of chironomid midges (Diptera). This pattern, found in many other animal groups, shows African taxa diverging basally, followed by a New Zealand clade and then a southern South America–Australian clade. The relative position of these areas in the cladogram (Fig. 3a) is congruent with the sequential breakup of these continents from the Gondwanan landmass (Fig. 1): ((Africa...)(New Zealand(southern South America, Australia))). In some groups such as marsupials (Krajewski et al., 2000), New Guinea appears as sister area to Australia, a placement supported by geological evidence (Fig. 1).

The SGP is usually explained as the result of the sequential breakup of southern temperate Gondwana during the Mesozoic–Tertiary coupled with extinction or primitive absence in some areas (Brundin, 1966; Edmunds, 1981; Cranston and Edward, 1992). The tropical Gondwana pattern (TGP; Fig. 3e) is also explained by

vicariance: it follows the breakup sequence of the western part of the northern Gondwana province (Amorim and Tozoni, 1994). In contrast, the plant southern pattern (PSP; Fig. 3b) and the inverted southern pattern (ISP; Fig. 3c) are incongruent with the geological scenario (Fig. 1) and are typically explained by dispersal. The northern gondwana pattern (NGP; Fig. 3d) has been explained by either vicariance or dispersal. It shows a track between the landmasses that once formed northeast tropical Gondwana and is therefore complementary to the TGP. Some groups show a combination of the northern and tropical Gondwana patterns (e.g., Aplocheiloidei) or an NGP in which northern South America branches close to Africa (e.g., Eucnemidae). In most cases, however, groups support either one pattern or the other. The transamerican pattern (AMP; Fig. 3f) follows earlier biogeographic studies (Crisci et al., 1991; Lopretto and Morrone, 1998), which showed South America divided into two biotic provinces with different biogeographic affinities.

MATERIAL AND METHODS

Selection of Groups for Analysis

We searched the literature, mainly based on tips from colleagues, for data on groups meeting the following criteria: (1) monophyletic, distributed almost

exclusively in the Southern Hemisphere, and claimed to be of Gondwanan origin; (2) represented in at least two (preferably three or more) of the areas studied; (3) including four or more species; and (4) represented by a well-resolved phylogeny with no more than two trichotomies or one tetratomy (unless the extra polytomy occurred within a clade with the same distribution, in which case the clade was summarized in one taxon or one of the possible topologies was arbitrarily chosen for the analysis). In several cases, phylogenies were not resolved to the species level (genera or species groups as terminals) or did not include all the species in the group

(i.e., taxon sampling). The *Biological Abstracts* and *Zoological Record* databases were carefully searched to ensure that the included phylogenies were the most recent ones for the selected groups. Groups were separated into animal (54 phylogenies) and plant (19 phylogenies) data sets. Insects dominate the animal data set (Fig. 4a) and were also analyzed separately from the other animals. The most well-represented group in the animal data set is the beetle family Eucnemidae (Muona, 1991), with 22 of 54 phylogenies but only 17% of the total number of animal species. The large number of eucnemid groups potentially biased some analyses, which were therefore
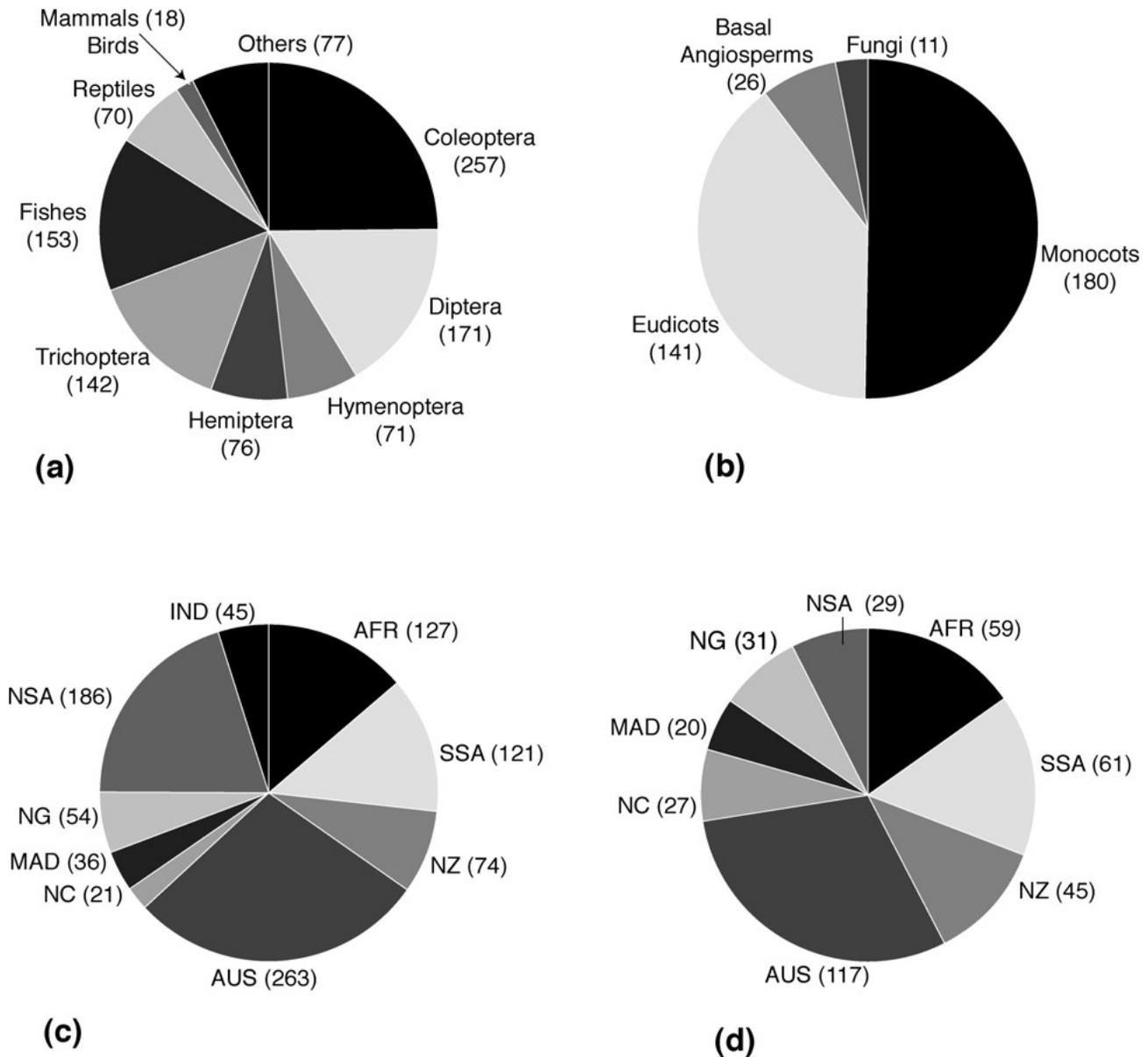

FIGURE 4. Pie charts summarizing various aspects of the plant and animal data sets analyzed in this study. (a, b) Taxonomic composition in terms of number of species in the animal (a) and plant (b) data sets. (c, d) Number of species distributed in each geographic area used in the analysis in the animal (c) and plant (d) data sets. AFR = Africa; AUS = Australia; IND = India; MAD = Madagascar; NC = New Caledonia; NG = New Guinea; NSA = northern South America; NZ = New Zealand; SSA = southern South America.

run both with and without eucnemids included. Vertebrates were represented by iguanid lizards and classic Gondwanan groups such as marsupials, ratites, and cichlid and galaxiid fishes. The plant data set (Fig. 4b) included all main groups in the angiosperm classification: monocots, eudicots, and basal angiosperms (APG, 2003). Following Linder and Crisp (1995), we also included *Cyttaria*, a fungus parasitic on *Nothofagus*, in the plant data set because despite being phylogenetically closer to animals, fungi and plants probably have similar means of dispersal (spores/seeds). Table 2 lists the selected groups and references and the oldest appearance of the group in the fossil record. The complete data sets (Appendix A) and supporting references for fossil occurrences and reference taxa (Appendix B) are available at the *Systematic Biology* website (http://systematicbiology.org/). Fossil evidence indicates that many of the selected groups are or could be old enough to display Gondwanan patterns (Table 2; Appendix B).

It has been customary in biogeographic studies to exclude groups occurring in less than three areas because they are not considered to provide evidence about area relationships. However, in event-based tree fitting, groups present in two areas do provide potential evidence concerning both dispersal patterns and vicariance events. Therefore, we included in the animal data set three groups that are present in only two areas: Arachnochampinae (NZ-AUS), *Botryocladius* (SSA-AUS), and characiform fishes (NSA-AFR) (Table 2). These groups have in common that they present a repeated pattern of sister-group relationships between the two areas they occupy. For these particular groups, a vicariance explanation is also supported in the original studies because either the fossil record or the sequence divergences between the taxa indicate that the group originated before the geological separation of the two landmasses (Ortí and Meyer, 1997; Cranston and Edward, 1999).

Not all potential groups are included in our sample. It was brought to our attention after the analyses were completed that the austral biota was undersampled and that there are data for several more Australian–New Zealand plant groups that we were not aware of. Had these groups been included, however, we predict that they would have strengthened the plant dispersal patterns found in the present study. An even more important sampling bias, which is very difficult to correct for, is that certain regions and certain organism groups have been extensively studied than others and therefore are significantly overrepresented in our data sets.

Delimitation of Areas

The areas used in the analysis correspond to historically persistent Gondwanan landmasses according to paleogeographic reconstructions. Composite areas, such as New Zealand (McLoughlin, 2001), were treated as single landmasses because, following accretion, they broke away from Gondwana as one unit. Small landmasses or oceanic archipelagos were included within a larger area when they shared a similar biota or recent land

connections during the Pleistocene. Nine areas were finally identified.

1. AFR: Africa, excluding the region north of the Saharan belt. We consider subsaharan Africa a single unit because the division between tropical and temperate regions was often not clear from the distribution of the terminal taxa in many of our study groups. In other groups (Karol et al., 2000), the fossil record indicates that the African taxa were part of the tropical African biota in the early Cretaceous but became restricted to South Africa in more recent times. We would have needed more African taxa to be able to differentiate between the histories of tropical Central Africa and temperate South Africa, if they are different.

2. MAD: Madagascar, including the Seychelles and the near Indian Ocean islands (Reunion, Mauritius, etc) with faunistically similar biotas (Johanson, 1998).

3. IND: India, including Nepal, Tibet, and Sri Lanka. Sri Lanka was connected to India during the Pleistocene glaciations (McLoughlin, 2001).

4. AUS: Australia and Tasmania. Tasmania was connected to Australia until 9,000–6,500 years ago (McLoughlin, 2001).

5. NZ: New Zealand, including the Kermadec and the subantarctic islands, which lie on the same continental block as New Zealand and probably have been colonized by New Zealand's biota via long-distance dispersal (Pole, 1994).

6. NC: New Caledonia.

7. NG: New Guinea, including the Solomon and New Hebrides islands, which show close biotic affinities (Raven and Axelrod, 1972; Muona, 1991).

   Following previous biogeographic studies (Crisci et al., 1991), we divided South America into two separate regions.

8. SSA: southern South America, defined as the southern temperate region (Argentina, Chile, Paraguay, Bolivia, and the Falkland and Antarctic islands), and north-central South America west of the Andes.

9. NSA: northern South America, defined as north-central South America east of the Andes (Brazil, Colombia, and Venezuela).

   Three other areas were recognized but considered as outside occurrences (not part of Gondwana).

10. SEA: Southeast Asia, including the Malaysian Peninsula, Philippines, Sumatra, Borneo, and the Inner Banda Arc. Southeast Asia was formed by the accretion of numerous small terranes that rifted away from Gondwana and accreted to Asia at different times during the Mesozoic–Cenozoic (Metcalfe, 1996). The region thus has a composite biogeographic history (Burret et al., 1991).

11. SWP: Southwest Pacific. In our analyses, this area includes the Melanesian archipelagos formed after the Oligocene collision of the Pacific and Australian plates (Fiji, Samoa, Tonga, and Vanuatu), and Hawaii but not New Zealand and New Caledonia,

TABLE 2. The 54 nonmarine animal groups and 19 plant groups with Southern Hemisphere distributions analyzed in this study. The number of terminals in each group is given in parentheses. For each group, the individual area cladogram(s) obtained with TreeFitter 1.2 and the biogeographic pattern(s) they support are detailed; the similarity score is given in parentheses (see Fig. 6). An approximate minimum age is given for each group based on the oldest appearance of the group in the fossil record.

Taxa (no. terminals)	Data partition[a]	References	Area cladogram	Biogeographic pattern	Age (MY)[b]
Animals (1,035)					
Podonominae: Insecta, Diptera, Chironomidae (53)	G_R/S	Brundin, 1966; Cranston and Edward, 1998; Cranston et al., 2002	(HOL(AFR(NZ(SSA, AUS))))	SGP (1.00)	121 (SG)
Aphroteniinae: Insecta, Diptera, Chironomidae (7)	S	Brundin, 1966; Cranston and Edward, 1992	(AFR(SSA, AUS))	SGP (0.50)	82 (SG)
Heptagyae + allied tribes: Insecta, Diptera, Chironomidae, Diamesinae (10)	G_R	Brundin, 1966	(AUS(HOL(AFR(SSA, NZ)))) (AUS((HOL, AFR)(SSA, NZ)))	ISP (0.33)	104 (RG)
Botryocladius: Insecta, Diptera, Chironomidae, Orthocladiinae (11)	S	Cranston and Edward, 1999	(SSA, AUS)	SGP (0.33)	82 (RG)[c]
Anisopodoidea: Insecta, Diptera, Anisopodomorpha (11)	G	Amorim and Tozoni, 1994	((SSA(NSA, HOL))(IND(SEA (((MAD, SWP)(NG, AFR) (NZ(NC, AUS))))))	AMP (1.0)	193 (SG)
Apioceridae: Insecta, Diptera (5)	S_T	Yeates and Irwin, 1996	(HOL(AFR(SSA, AUS)))	SGP (0.50)	29 (RG)[d]
Megascelinae: Insecta, Diptera, Mydidae (3)	G_R	Yeates and Irwin, 1996	(AFR(SSA, AUS))	SGP (0.50)	29 (RG)[d]
Arachnocampinae: Insecta, Diptera, Keroplatidae (4)	S	Matile, 1990	(NZ, AUS)	PSP (0.33)	100 (RG)
Cerotelion–Mallochinus: Insecta, Diptera, Keroplatidae (12)	S	Matile, 1990	(AUS((SSA, NZ)(SEA, HOL)))	ISP (0.50)	100 (RG)
Macrocerini: Insecta, Diptera, Keroplatidae (25)	S	Matile, 1990	((AFR(MAD, IND))(SSA(NZ (AUS(NG, SEA))))) ((AFR(MAD(IND(SEA, NG)))) (SSA(NZ, AUS)))	PSP (0.58)	100 (SG)
Australosymmerus: Insecta, Diptera, Mycetophilidae (30)	S	Munroe, 1974	(HOL(NSA(NZ(SSA, AUS))))	SGP (0.83)	175 (RG) 44 (SG)
Masarinae: Insecta, Hymenoptera, Vespidae (12)	G	Carpenter, 1993	((AFR; NSA)(AUS(SSA, HOL))) (NSA((AFR, AUS)(SSA, HOL))) (AFR(NSA(AUS(SSA, HOL)))) (NSA(AUS(AFR(SSA, HOL)))) (NSA(AFR(AUS(SSA, HOL))))		121 (RG₁), 82 (RG₂)
Groteini: Insecta, Hymenoptera, Ichneumonidae (15)	S_T	Gauld and Wahl, 2000	(NG(AUS(SSA(NSA, HOL))))	AMP (1.00)	151 (RG)
Labenini + Xenothyrini: Insecta, Hymenoptera, Ichneumonidae (36)	S_T	Gauld and Wahl, 2000	((NSA(SSA, AUS))(HOL(NZ, NG))) (HOL((NSA(SSA, AUS))(NG, NZ))) ((HOL(NSA(SSA, AUS)))(NG, NZ))	SGP (0.50)	151 (RG)
Megalyridae: Insecta, Hymenoptera (8)	G	Shaw, 1990	(NC, NG, SSA, AFR, MAD, SEA, NSA, AUS)		104 (SG)
Aquarius paludum group: Insecta, Hemiptera, Gerridae (8)	S	Damgaard and Zettel, 2003; Andersen, 1990	(IND(HOL(AUS(AFR, SEA))))		31 (RG)
Ceroplastinae: Insecta, Hemiptera, Coccidae, Coccoidea (68)	S_T	Qin et al., 1998 (based on Qin and Gullan, 1995)	((IND(NG, MAD))(AFR, NSA)) ((IND, NG)(MAD(AFR, NSA))) (IND((NG, MAD)(AFR, NSA))) (IND(NG(MAD(AFR, NSA)))) ((NG, MAD)(IND(AFR, NSA))) (NG(IND(MAD(AFR, NSA))))	TGP (1.00)	121 (RG)
Hydrobiosidae: Insecta, Trichoptera (48)	G_R	Henderson, 1991 (based on Schmidt, 1989)	(SWP, HOL, NSA, NG(NZ, NC) (SSA, AUS))	SGP (0.50)	82 (SG)
Helicopsychidae: Insecta, Trychoptera (94)	S_T	Johanson, 1998	(NC(NZ((AFR, MAD)((SEA, IND) (AUS(NSA(SSA, HOL))))))) (NC(NZ((AUS(SEA, IND)) ((AFR, MAD)(NSA(SSA, HOL))))))		121 (SG)
Metacorneolabium: Insecta, Coleoptera, Staphylinidae (22)	S	Thayer, 1985	(NZ(SSA, AUS))	SGP (0.83)	151 (RG)

(Continued on next page)

TABLE 2. Continued

Pilipalpinae: Insecta, Coleoptera, Pyrochroidae (11)	G_R	Pollock, 1995	((MAD, SSA)(NZ, AUS)) (AUS(SSA(MAD, NZ)))	PSP (0.17)	151 (RG)
Adeliini: Insecta, Coleoptera, Tenebrionidae (44)	G_R	Mathews, 1998	((NC, SSA)(NZ, AUS)) (SSA(NC(NZ, AUS))) (NC(SSA(NZ, AUS)))	PSP (0.61)	104 (RG)
Agalba group: Insecta, Coleoptera, Elateroidea, Eucnemidae (6)	G	Muona, 1991	((NZ, NG)(NSA(SWP, AUS))) (NG(NSA(SWP(AUS, NZ)))) (NZ(NG(NSA(SWP, AUS)))) (NG(NZ(NSA(SWP, AUS)))) (SWP(NSA(NG(NZ, AUS)))) ((SWP, NZ)(NSA(NG, AUS))) (SWP(NZ(NSA(NG, AUS)))) (NZ(SWP(NSA(NG, AUS))))		35 (SG)
Arrhipis: Insecta, Coleoptera, Eucnemidae (8)	G	Muona, 1991	((AFR, IND)(NSA((SEA, SWP), (NG, AUS)))) (SWP((AFR, IND)(NSA(SEA(NG, AUS)))))	NGP (0.13)	35 (SG)
Calyptocerus group: Insecta, Coleoptera, Eucnemidae (6)	G	Muona, 1991	(NG((HOL(SWP, IND))(NSA(SEA, AUS)))) (AUS((HOL (SWP, IND))(NSA(SEA, NG))))		35 (SG)
Cladidus group: Insecta, Coleoptera, Eucnemidae (9)	G_R	Muona, 1991	(MAD(AFR((SEA(IND, SWP)) (NG, AUS)))) (AFR(MAD((SEA (SWP, IND))(NG, AUS))))	NGP (0.33)	35 (SG)
Dromaeoloides: Insecta, Coleoptera, Eucnemidae (5)	S	Muona, 1991	(NC(SWP(NG, AUS)))	NGP (0.20)	35 (SG)
Dyscharachthis: Insecta, Coleoptera, Eucnemidae (9)	G_R	Muona, 1991	((NG, AUS)(SSA(NSA, HOL))) (NG(AUS(SSA(NSA, HOL))))	AMP (1.00)	35 (SG)
Entomosotapus: Insecta, Coleoptera, Eucnemidae (4)	G_R	Muona, 1991	(AFR(NSA, AUS))		35 (SG)
Epipleurus group: Insecta, Coleoptera, Eucnemidae (19)	G_R	Muona, 1991	(HOL((IND(MAD, AFR))(NSA ((SEA, SWP)(NG, AUS)))))	NGP (0.20)	35 (SG)
Eudorus group: Insecta, Coleoptera, Eucnemidae (4)	G	Muona, 1991	(SEA(MAD(AFR(NSA, AUS)))) (MAD(SEA(AFR(NSA, AUS)))) ((MAD, SEA)(AFR(NSA, AUS))) (MAD(AFR(NSA(AUS, SEA)))) (SEA(AFR(MAD(NSA, AUS)))) (AFR(SEA(MAD(NSA, AUS)))) ((AFR, SEA)(MAD(NSA, AUS))) (AFR(MAD(NSA(SEA, AUS))))		35 (SG)
Farsus group: Insecta, Coleoptera, Eucnemidae (6)	G_R	Muona, 1991	((AFR, MAD)(NSA(NG, AUS)))	NGP (0.13)	35 (SG)
Feaia group: Insecta, Coleoptera, Eucnemidae (8)	G_R	Muona, 1991	((MAD(NG, HOL))(NSA(AUS, SEA))) ((MAD(NG(SEA, HOL)))(AUS, NSA)) (NSA(MAD(AUS(NG(SEA, HOL))))) ((MAD(AUS(NG, HOL)))(SEA, NSA))		35 (SG)
Galbodema group: Insecta, Coleoptera, Eucnemidae (6)	G_R	Muona, 1991	(SEA(NSA(NG, AUS))) (NSA(SEA(NG, AUS)))	NGP (0.20)	35 (SG)
Heterotaxis group: Insecta, Coleoptera, Eucnemidae (8)	G	Muona, 1991	(NG, SWP((MAD, AFR)(NSA (AUS(SEA, HOL))))) (NG, SEA((MAD, AFR)(NSA (AUS(SWP, HOL))))) (AUS, SWP((MAD, AFR)(NSA (NG(SEA, HOL))))) (AUS, SEA((MAD, AFR)(NSA(NG (SWP, HOL)))))		35 (SG)
Macroscython: Insecta, Coleoptera, Eucnemidae (12)	G_R	Muona, 1991	((AFR, MAD)(SEA(NG, AUS)))	NGP (0.20)	35 (SG)
Mesogenus group: Insecta, Coleoptera, Eucnemidae (13)	G	Muona, 1991	(IND(AFR(MAD((NSA, HOL)((NG, NC) (SWP(SEA, AUS)))))))	AMP (0.67)	35 (SG)
Plesiofornax: Insecta, Coleoptera, Eucnemidae (7)	G_R	Muona, 1991	(MAD(AFR(NSA(SEA(NG, AUS))))) (AFR(MAD(NSA(SEA(NG, AUS)))))	NGP (0.27)	35 (SG)
Porraulacus group: Insecta, Coleoptera, Eucnemidae (13)	G_R	Muona, 1991	(IND((NSA, SEA)(SWP, NG))) (IND(NSA(SEA(SWP, NG)))) (IND(SEA(NSA(SWP, NG)))) ((IND(NSA, SEA))(SWP, NG))	NGP (0.13)	35 (SG)

TABLE 2. Continued

Prodirhagus: Insecta, Coleoptera, Eucnemidae (3)	G	Muona, 1991	(NG(AFR(NSA, AUS))) (AUS(AFR(NSA, NG)))		35 (SG)
Rhagomicrus: Insecta, Coleoptera, Eucnemidae (11)	G$_R$	Muona, 1991	((AFR, MAD)((NSA, HOL) ((SEA, SWP)(NG, AUS))))	AMP (0.67) NGP (0.13)	35 (SG)
Scython: Insecta, Coleoptera, Eucnemidae (6)	G$_R$	Muona, 1991	((AFR, MAD)(SEA, NG))		35 (SG)
Serrifornax: Insecta, Coleoptera, Eucnemidae (9)	G	Muona, 1991	(MAD(AFR(NSA(SEA(SWP, NG))))) (AFR(MAD(NSA(SEA(SWP, NG)))))	NGP (0.13)	35 (SG)
Spinifornax: Insecta, Coleoptera, Eucnemidae (8)	G	Muona, 1991	(IND(NSA(NG, SEA)))		35 (SG)
Aplocheiloidei: Teleostei, Osteichthyes, Cyprinodontiformes (23)	S$_T$	Murphy and Collier, 1997	((MAD(SEA, IND))(AFR, NSA))	TGP (1.00) NGP (0.13)	29 (RG)
Characiformes: Teleostei, Osteichthyes (38)	G$_R$	Ortí and Meyer, 1997	(AFR, NSA)	TGP (0.67)	82 (SG)
Cichlidae: Teleostei, Osteichthyes, Perciformes (64)	S$_T$	Farias et al., 1999	((MAD, IND)(AFR, NSA))	TGP (1.00)	48 (SG)
Galaxiidae: Teleostei, Osteichthyes, Osmeriformes (28)	S$_T$	Waters et al., 2000b	(AFR, AUS, SSA, NZ, NC)		60 (RG), 20 (SG)[e]
Chamaeleonidae + Agamidae: Reptilia, Squamata, Acrodonta (70)	S$_T$	Macey et al., 2000	((AFR, HOL)((SEA, IND)(AUS, NG))) (((AFR, HOL)(AUS, NG))(SEA,IND)) (((AFR, HOL)(SEA, IND))(AUS, NG))	NGP (0.12)	104 (SG)
Ratites + tinamous: Aves, Paleognathae (8)	G	Cooper et al., 2001; Haddrath and Baker, 2001	(NSA(SSA(AFR(NZ(AUS, NG))))) (NG(NSA(SSA(AFR(NZ, AUS)))))	PSP (0.33)	44 (SG)[f]
Marsupials: (Mammalia, Metatheria (10)	G	Springer et al., 1998; Palma and Spotorno, 1999 (Krajewski et al., 2000, for Dasyuromorphia)	(HOL(NSA(SSA(AUS, NG)))) (NSA(HOL(SSA(AUS, NG))))	SGP (0.17)	110 (SG)
Plectostylus group: Gastropoda, Stylommatophora, Bulimulidae (4)	G$_R$	Breure, 1979	(AUS(SSA, NSA)) (NSA(SSA, AUS))	SGP (0.17)	no fossils[g]
Peripatopsidae: Onicophora (67)	S	Reid et al., 1995 (for *Cephalofovea*); Reid, 1996	(NZ(AUS(AFR(SSA, NG)))) (AUS(NZ(AFR(SSA, NG)))) ((AUS, NZ)(AFR(SSA, NG)))		550 (RG)
Ballarrinae: Arachnida, Opiliones, Neopilionidae (6)	G$_R$	Hunt and Cokendolpher, 1991	(AFR(SSA, AUS))	SGP (0.50)	no fossils[h]
Plants (358)					
Nothofagus: eudicots, Fagales, Nothofagaceae (30)	S	Swenson et al. 2001 (based on Manos, 1997); Linder and Crisp, 1995 (for *Brassospora*)	((AUS, NZ)(SSA(NG, NC))) (SSA((AUS, NZ)(NG, NC))) ((SSA(AUS, NZ))(NG, NC))	PSP (0.61)	70 (SG)
Aristotelia: eudicots, Oxalidales, Elaeocarpaceae (5)	S	Coode, 1985	(AUS(SSA, NZ))	ISP (0.83)	82 (RG$_1$), 58 (RG$_2$)
Abrotanella: eudicots, Asterales, Asteraceae (19)	S	Swenson and Bremer, 1997	((AUS, NG)(SSA, NZ)) (AUS(NG(SSA, NZ))) (NG(AUS(SSA, NZ)))	ISP (0.61)	42 (SG)
Alseuosmiaceae–Argophyllaceae-Phellinaceae: eudicots, Asterales (7)	G	Kårehed et al., 1999	(AUS(NZ(NG, NC)))		82 (SG)
Cunoniaceae: eudicots, Oxalidales (29)	G/S	Bradford and Barnes, 2001	(AFR, NSA, MAD, NZ, SSA, AUS, NG, SWP, SEA, NC)		82 (SG)
Cunonieae: eudicots, Oxalidales, Cunoniaceae (27)	S$_T$	Bradford, 2002	(AUS((NC, AFR)((NZ(SEA(SWP, NG))) (SSA(NSA, MAD))))) (AUS((NC, AFR) (((NZ, SWP)(NG, SEA))(SSA (NSA, MAD))))) (AUS((NC, AFR) ((NSA, SSA)((NZ, MAD)(SEA (NG, SWP)))))) (AUS((NC, AFR) ((NSA, SSA)((MAD(NZ, SWP)) (SEA, NG)))))		82 (SG), 56 (RG), 31 (SG)

(Continued on next page)

Adansonia: eudicots, Malvales, Bombacaceae (8)	S	Baum et al., 1998	(AUS(AFR, MAD))		82 (RG), 38 (SG)
Embothrieae: eudicots, Proteales, Proteaceae (16)	S	Weston and Crisp, 1994	(NG(SSA, AUS))	SGP (0.33)	82 (RG), 65 (SG)
Iridaceae: monocots, Asparagales (57)	G	Reeves et al., 2001	(AUS((NSA, SSA)(HOL(AFR, MAD)))) (AUS((AFR, HOL)(MAD(NSA, SSA)))) (AUS(MAD((AFR, HOL)(SSA, NSA)))) (AUS((AFR(HOL, MAD))(NSA, SSA))) (AUS((MAD(AFR, HOL))(NSA, SSA)))		70 (SG)
Oreobolus: monocots, Poales, Cyperaceae (17)	S	Linder and Crisp 1995 (based on Seberg, 1988)	(SSA((AUS, NZ)(NG(SEA, SWP))))	PSP (0.50)	60 (RG)[c]
Restionaceae: monocots, Poales (53)	G	Linder, 2000	(SSA, NZ, NG, MAD(AUS, AFR))		70 (SG)
Danthonia clade: monocots, Poales, Poaceae, Danthonieae (10)	S_T	Linder and Barker, 2000	((HOL(NSA, SSA))(AUS, NZ)) (NSA((HOL, SSA)(AUS, NZ))) (HOL((NSA, SSA)(AUS, NZ)))	PSP (0.50)	70 (RG)[c]
Rytidosperma: monocots, Poales, Poaceae, Danthonieae (28)	S_T	Linder, 1999	(NG(SSA(AUS, NZ)))	PSP (0.83)	70 (RG)[c]
Haemodoraceae: monocots, Commelinales (12)	G_R	Hopper et al., 1999	(AUS(NSA(AFR(HOL, NG))))		82 (RG)
Strelitziaceae: monocots, Zingiberales (3)	G_R	Kress et al., 1994	(MAD(AFR, NSA))	TGP (1.00)	82 (RG)
Winteraceae: magnoliids, Canellales (12)	G/S	Karol et al., 2000	(MAD(AUS(SSA(NZ(NC, NG))))) (NG(MAD(AUS(SSA(NZ, NC)))))	ISP (0.17)	121 (SG)
Canellaceae: magnoliids, Canellales (6)	G_R	Karol et al., 2000	(NSA(MAD, AFR))		121 (RG)
Atherospermataceae: magnoliids, Laurales (8)	G_R	Renner et al., 2000	(AUS(NG(NC(SSA, NZ))))	ISP (0.50)	87 (SG)
Cyttaria: Fungi, Ascomycotina, Cyttariales (11)	S	Crisci et al., 1988	(SSA(NZ, AUS))	PSP (0.83)	no fossils

[a]S = phylogeny includes all (or at least 95%) of the species of the group; S_T = phylogeny includes only a small sample of the total number of species (i.e., taxon sampling); G_R = terminals in the phylogeny are mainly higher taxa (genera or species groups), usually restricted to one of the analyzed areas; G = terminals in the phylogeny are mainly higher taxa, usually widespread in two or more areas.

[b]Stratigraphic occurrences of fossil taxa (e.g., Cretaceous) were transformed into absolute ages (MY) by giving the midpoint of the geological interval according to the time scale of the Geological Society of America (Palmer and Geissman, 1999). When there was no fossil record for the studied group (SG), the oldest fossil record of a closely related group (RG) was used. For example, the fossil record of the plant family Winteraceae (early Cretaceous) was used to provide an age for Canellaceae, which is the sister family of Winteraceae (APG, 2003). In several cases, the fossil was only described as belonging to a higher taxon containing the studied taxon. For example, no fossil record is known for the subfamily Arachnocampinae but there are mid-Cretaceous fossils of the family it belongs to (Keroplatidae). These fossils have not been assigned to any known tribe, and their relationships to Arachnocampinae are unknown. Only fossils belonging to the nearest inclusive higher taxon were used for dating, and such cases are indicated as RG; in some cases several datings are provided (e.g., *Aristotelia*). See Appendix B (http://systematicbiology.org/) for information on supporting references for fossil occurrences and reference taxa.

[c] This age refers to the family, so the genus is probably younger.

[d] Many Diptera families can be traced back to the Jurassic, so these families are probably much older.

[e] There is a dubious galaxiid fossil from the late Cretaceous.

[f] Using these *Rhea* fossils, Cooper et al. (2001) estimated an age of 90 MY for the origin of ratites.

[g] Fossils of Stylomatophora are known from the late Jurassic, so Bulimulidae is probably of Cretaceous age.

[h] Fossils of Opiliones are described from the early Carboniferous, so Ballarrinae is probably at least of Jurassic age.

which have always been part of the Gondwanan continent.

12. HOL: The Holarctic region comprises the Palearctic (Europe, Asia, and North Africa) and Nearctic (North America and Mexico) infraregions. Central American distributions usually have been considered Nearctic except when the group is also present in northern South America, in which case they are coded as NSA.

Parsimony-Based Tree Fitting

For all analyses, we used parsimony-based tree fitting under the four-event model (Page, 1995) as implemented in the program TreeFitter 1.2 (Ronquist, 2002b). The general methodology, also known as tree reconcil-iation and implemented in TreeMap (Page, 1995; Page and Charleston, 1998), has been used widely in coevolutionary studies (e.g., Page, 2002, and references therein) but is relatively new to biogeographic analyses (but see Sanmartín et al., 2001). We used several important but not widely employed improvements of the original method (Ronquist, 1998; Sanmartín et al., 2001; Ronquist, 2002a; Sanmartín and Ronquist, 2002), described here (see Ronquist, 2002a, for more detailed coverage).

In the biogeographic context, the four events in the model are (1) vicariance: allopatric speciation caused by the origin of a dispersal barrier affecting many organisms simultaneously; (2) duplication (speciation within an area): usually allopatric and associated with a local or temporary dispersal barrier within an area;
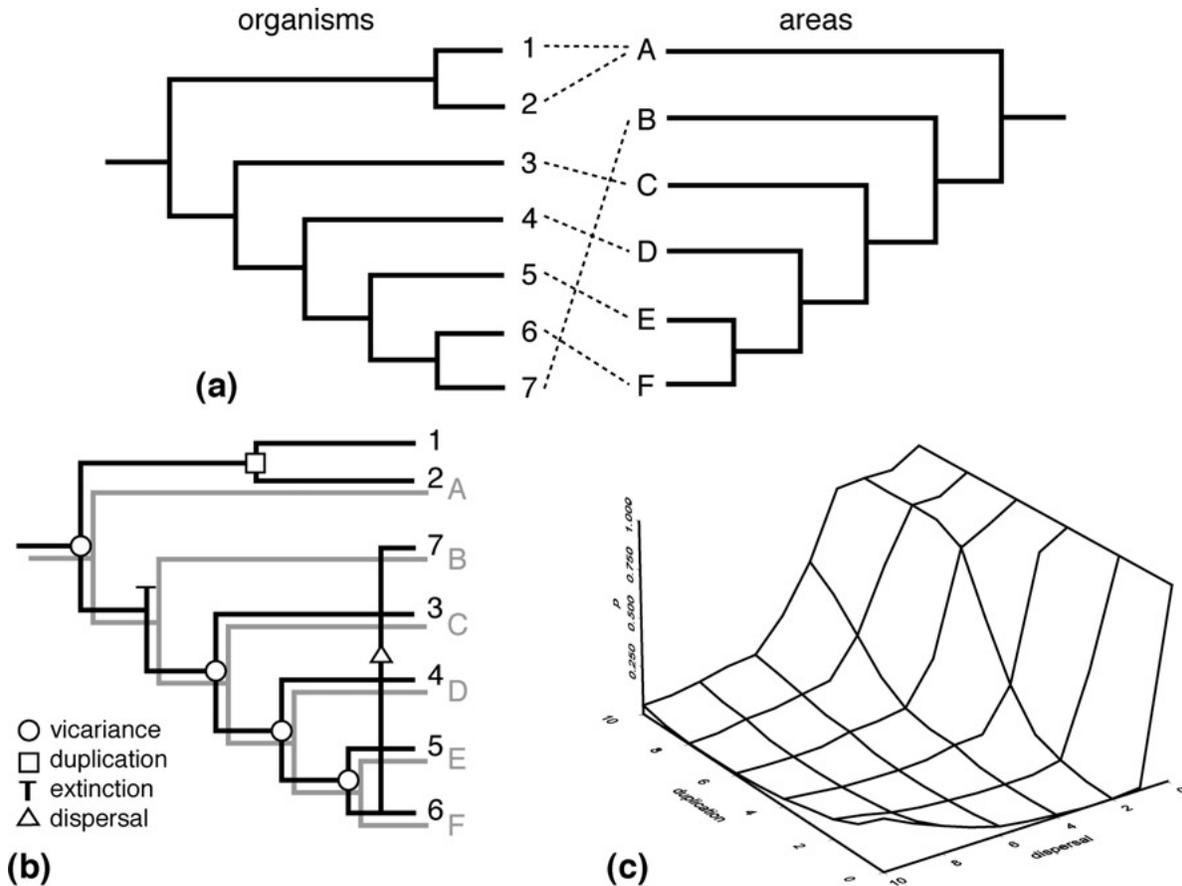
FIGURE 5. Parsimony-based tree fitting. (a) Tanglegram illustrating organism phylogeny (left), area cladogram (right), and the geographic distribution of the terminals in the organism phylogeny (lines connecting organisms and areas). (b) Trackogram illustrating one reconstruction of the distribution history of the organisms by showing the organism phylogeny (bold) on top of the area cladogram (shaded). The reconstruction specifies both the ancestral distributions and the biogeographic events that generated the observed data. Among other things, the reconstruction specifies the direction of the implied dispersal event and the geographical location and relative timing of the vicariance, duplication, and extinction events. (c) By varying the event costs and calculating the probability of obtaining the observed cost in randomly permuted data sets (the P value), we can find an optimal set of costs. In this case, the extinction (sorting) cost is arbitrarily set to 1.0 and the vicariance cost is set to 0.0, and the duplication and dispersal costs are varied between 0.0 and 10.0. The minimum P value is obtained with a low duplication and moderately high dispersal cost (2–3); in this region of cost space, the trackogram solution (b) is the optimal reconstruction.

(3) dispersal: occurring between isolated areas and associated with speciation; and (4) extinction: leading to the disappearance of a lineage from an area where it is predicted to occur. The intricacies of this model and its relation to alternative models are explained in detail elsewhere (Ronquist, 1998, 2002a).

Once each event in the model is associated with a cost, it is possible to fit an organism phylogeny and the associated geographic distributions of the terminals to any given area cladogram (Fig. 5a), producing a reconstruction of the biogeographic history of the organisms according to the area cladogram. Each reconstruction specifies a set of ancestral distributions and biogeographic events that could have produced the observed distribution patterns on the given area cladogram. The reconstruction can most easily be illustrated using a trackogram displaying the organism phylogeny on top of the area cladogram, with symbols denoting the four kinds of events (Fig. 5b). The cost of the reconstruction is simply the sum of the costs of the implied

events. Of particular interest in event-based tree fitting is the reconstruction with the minimum cost, the most-parsimonious reconstruction (MPR).

Searching for the optimal area cladogram.—The cost of the MPR fitting one (or more) group(s) of organisms to a given area cladogram represents a natural measure of the fit of that area cladogram to the organism data. The area cladogram with the lowest cost, i.e., the most-parsimonious area cladogram, best explains the taxon distributions in the phylogeny. This optimal area cladogram can be found, for instance, by explicit enumeration of all possible area cladograms or by heuristic search for the best area cladogram using algorithms similar to those used in ordinary parsimony analysis of phylogeny (e.g., stepwise addition followed by branch swapping). In our searches for optimal area cladograms, we used different hold settings in TreeFitter (determining how many trees are kept in each step of the stepwise addition algorithm) and different swapping neighborhoods (reconnection limits),

determining how exhaustive the branch swapping is (Ronquist, 2002b).

Randomization tests.—Any aspect of the MPR calculated from the observed data can be tested by comparing it to MPRs derived from random data sets. Depending on the property of interest, the random data sets can have the terminals in the organism phylogeny, the terminals in the area cladogram, or both randomly permuted (Siddall, 1996; Ronquist, 2002a). Alternatively, one can randomize the topology of the area cladogram or the organism phylogeny instead of permuting the terminals (Page, 1995). However, this approach can be slightly biased if the random trees are not generated in the appropriate way (Ronquist, 2002a). Therefore, we consistently used permutation of terminals.

To examine whether organism distributions are phylogenetically constrained in general according to a given area cladogram, we permuted both areas and organism terminals. The null hypothesis of no phylogenetic constraint was rejected when few of the permutations fell below the observed MPR cost. For instance, the result was considered significant at the 0.05 level when <5% of the permutations had a cost less than or equal to that for the observed data. Often, one is interested in a particular event or process, in which case other types of permutations are more appropriate. For instance, to examine whether an area cladogram is successful in predicting vicariance events, touching the organism phylogenies will only cause unnecessary noise. To obtain maximum sensitivity in these tests, we used permutations of the terminals in the area cladogram when focusing on vicariance and extinction events and permutation of the organism terminals when focusing on dispersal and duplication events.

When the area cladogram is inferred from the organism phylogenies, it is inappropriate to randomize the area cladogram because the error rate will be inflated (Siddall, 1996). Instead, the organism phylogenies must be randomized and the best area cladogram inferred for each random data set. This approach was taken here for the area cladograms based on organism data and not on geological evidence.

Event costs.—Setting the event costs is the central problem in parsimony-based tree fitting. Using the same cost for all events is not a viable approach because then we can guarantee that no events are fitted to internal nodes and internal branches in the area cladogram (Ronquist and Nylin, 1990). As a possible solution, Page (1995) suggested maximizing codivergence events (MC), which is equivalent to maximizing vicariance events in biogeographic problems. Although MC has been popular in coevolutionary studies, it has serious drawbacks. In particular, MC is sensitive to dispersal and duplication events (Ronquist, 2002a). Even a moderate number of such events can make it impossible to identify a strong underlying vicariance pattern. Therefore, it is not possible to use MC in inferring predominantly dispersal patterns or mixed vicariance–dispersal patterns (Ronquist, 2002a).

Assigning a positive cost to all events is more in line with the parsimony principle in general and produces a more powerful analytical tool. However, it does leave the difficulty of setting the exact costs to be used. Ronquist (2002a) proposed a procedure for selecting the optimal event costs based on maximizing the chances of finding significance in permutation tests focusing on total cost. The individual event costs are simply varied until a cost combination is found that minimizes the probability of permuted data sets having a total cost lower than that of the observed data (Fig. 5c). Using this approach in examining a variety of hypothetical data sets, Ronquist (2002a) found a set of event costs that performed well under a wide range of conditions. This solution has an arbitrarily low cost for vicariance and duplication events and a higher cost for dispersal than for extinction events. It performs well because both vicariance and duplication generate phylogenetically constrained distribution patterns, whereas dispersal and extinction do not. We used the default cost assignments of TreeFitter 1.2 (0.01 for vicariance and duplication, 1.0 for extinction, 2.0 for dispersal), which conform to this scheme. The primary results given here (fitting the entire animal or plant data set to the geological area cladogram) indicate that these event costs are in the optimal range for our data, given 1,000 permutations of organism area cladogram terminals.

An alternative to setting specific event costs is to enumerate all possible solutions under a range of event costs (the jungle approach; Charleston, 1998; see also Ronquist, 2002a). This approach is still too computationally complex to be employed in a large study such as the one attempted here.

Algorithms.—When the event costs are fixed, it is possible to use fast polynomial algorithms for finding the upper and lower bounds on the total cost of the true MPR (Ronquist, 1995, 1998, 2002a). In practice, lower-bound solutions are almost always identical to the true MPR (differences may arise because of incompatible dispersals; see Ronquist, 1995). Here, we consistently used the lower-bound algorithm implemented in TreeFitter 1.2.

Widespread terminals.—Widespread taxa (terminal taxa distributed in more than one area) pose a problem in biogeographic reconstruction because they introduce ambiguity in the data set (Morrone and Crisci, 1995). This problem has traditionally been dealt with using Assumptions 0, 1, and 2 of Nelson and Platnick (1981), but these assumptions are inapplicable to event-based methods for several reasons. Each of them specifies a set of possible solutions but not the relative cost of these solutions. This approach may result in nonoverlapping solution sets (Van Veller et al., 1999) and other problems, but more critically it is incompatible with the fact that all area cladograms must have a relative cost in an event-based method (Ronquist, 2002a). Therefore, Sanmartín and Ronquist (2002; see also Sanmartín et al., 2001; Ronquist, 2002a) introduced three novel event-based options to treat widespread taxa. Under the Recent option, the widespread distribution is assumed to be the result of recent dispersal. Thus, only one of the areas in the distribution is considered ancestral. The

Ancient option assumes that the widespread distribution is the result of a failure to vicariate and explains any mismatch between the distribution and the area cladogram by extinction. Under this option, all of the areas in the distribution are considered ancestral. The Free option treats the widespread terminal as an unresolved higher taxon consisting of one lineage occurring in each area and permits any combination of events and any resolution of the terminal polytomy in explaining the widespread distribution. Each of these options can be easily implemented in algorithmic form (Sanmartín and Ronquist, 2002) and are available in TreeFitter (Ronquist, 2002b).

Comparing the event-based options with the traditional assumptions is like comparing apples with oranges, but there are some similarities. The Ancient option is, in some sense, a combination of Assumption 0 and Assumption 1, and the Free option is reminiscent of Assumption 2. The Recent option, however, is a different concept altogether; it is similar to the way polymorphic taxa are usually treated in ordinary parsimony analysis of phylogeny. Using empirical data, Sanmartín et al. (2001) showed that the Recent option, unlike the Free and Ancient options, forces vicariance events onto the ancestral nodes in the phylogeny, and this option is therefore more powerful in separating phylogenetically constrained distribution patterns from random data in permutation tests. For this reason, we consistently used the Recent option in treating widespread terminals. When examining dispersal patterns, we excluded dispersals within widespread terminals and only looked at inferred ancestral dispersals, unless explicitly stated otherwise. By focusing exclusively on ancestral events, we reduced the inherent problem of comparing phylogenies that have widespread higher taxa as terminals with phylogenies that have endemic species as terminals.

Analyses

Best area cladogram.—We first searched for the best area cladogram fitting the animal and the plant phylogenies, respectively. We used the heuristic tree search of TreeFitter because the exhaustive search was too time consuming. An initial tree was constructed by stepwise addition, holding 100 trees in each step, followed by tree bisection-reconnection (TBR) branch swapping with a reconnection limit (neighborhood) of 20 nodes (essentially identical to a full standard TBR search). Using the same approach, we searched for the best area cladogram for each of three different subgroups of the animal data set (animals excluding insects, insects alone, and insects excluding eucnemids).

Randomization tests implemented in TreeFitter 1.2 were used to assess the statistical significance of the fit between the best area cladograms and the organism phylogenies (Ronquist, 2002a). We generated 1,000 random data sets for which the terminal distributions in the organism phylogenies had been permuted and inferred the best area cladogram for each (hold = 5, neighborhood = 20). We then compared the total cost and the number of vicariance events obtained when fitting each of the random data sets to its best area cladogram, with the corresponding values obtained when fitting the observed data to its best area cladogram obtained under the same search conditions. The significance value (P) was calculated as the percentage of random data sets with a lower cost or a higher number of vicariance events than the original data set.

Biogeographic patterns.—We also searched for the optimal area cladogram for each individual group in the data sets (Table 2) and then compared that area cladogram with each of the biogeographic patterns (Fig. 3). To calculate the degree of congruence (similarity) between the area cladogram and the biogeographic patterns, we used a modification of the method of Robinson and Foulds (1981) for calculating the metric distance between two phylogenetic trees (see Fig. 6).

The biogeographic pattern with the highest positive score for a particular organism group was assigned a support value of 1.0 for that group, except when the score was lower than 0.1, in which case the group was considered as not supporting any biogeographic pattern. When a group supported two compatible biogeographic patterns such as TGP and NGP (e.g., Aplocheiloidei, Table 2), the pattern with the highest score received a support value of 1.0 and the pattern with the lowest score received a value of 0.5. The total support for each biogeographic pattern was computed by summing across all individual groups in the animal and plant data sets separately.

Fit to the geological scenario.—To address whether the biogeographic history of the Southern Hemisphere reflects the geological breakup of Gondwana, we fitted the geological area cladogram (Fig. 1) to each of the organism phylogenies and used randomization tests in TreeFitter to assess the significance of the fit. When the group fitted the geological scenario significantly ($P < 0.05$), we calculated the frequency of each of the four different biogeographic events required to explain the fit (vicariance, duplication, dispersal, and extinction) and tested whether the observed frequency of the events departed from what would be expected by chance, as indicated by 1,000 randomly permuted data sets.

Dispersal analysis.—We also examined the role played by dispersal in shaping Southern Hemisphere biogeographic patterns by fitting the organism phylogenies to the geological area cladogram, i.e., we looked at the dispersals remaining after geologically predicted events, such as vicariance, had been removed.

First, we compared the overall frequency of dispersal events in animals and plants. For this analysis, we divided dispersal events into terminal dispersals, occurring within widespread terminal taxa, and ancestral dispersals, associated with interior nodes in the organism phylogenies. Ancestral and terminal dispersals were considered both separately and combined. To test whether the frequency of these dispersals differed significantly between the animal and plant data sets, we used a permutation test. The distribution of expected values
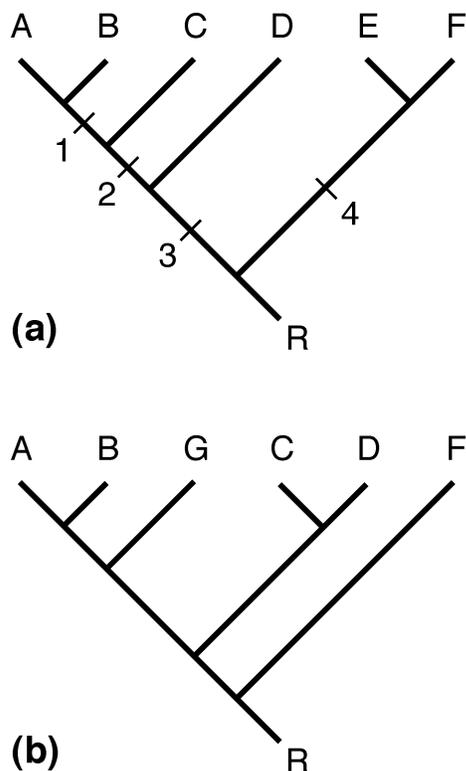
FIGURE 6. Modified partition metric used to compare the best area cladogram for a group of organisms with each of the discussed biogeographic patterns in Figure 3 (see Table 2). The biogeographic pattern (a) and organism area cladogram (b) are both rooted cladograms that can be thought of as including an additional terminal representing the root, (R). Both cladograms may have unique terminals that are not present in the other cladogram, as in this example. Each clade in the biogeographic pattern (a) belongs to one of five different types depending on how well it fits the organism area cladogram (b), and each type is associated with a score. A perfect match is a clade in the biogeographic pattern matching a clade in the organism area cladogram perfectly. The perfect match is informative (score 3) when there is at least one area in the biogeographic pattern outside the matching clade that is also represented in the organism area cladogram; otherwise the match is uninformative (score 2). A clade in the biogeographic pattern is consistent (score 1) when it is an informative perfect match after all unique areas are pruned away from the biogeographic pattern and area cladogram; when pruning results in an uninformative match then the clade is absent (score 0). A clade in the biogeographic pattern that conflicts with the organism area cladogram after pruning is contradictory (score −1). The scores for all partitions in the biogeographic pattern are summed, noting that each consistent match is counted only once (if there are many unique areas in the biogeographic pattern, there may be several clades in it resulting in the same consistent match with the organism area cladogram). The total score for the biogeographic pattern is divided by the maximum possible score to give an index between 1 and −1/3. Consider this example. The first clade (1: A, B) in the biogeographic pattern is an informative perfect match because the clade (A, B) is found in the organism area cladogram and there are three areas outside this clade shared between the two cladograms (C, D, F). The second clade (2: A, B, C) in the biogeographic pattern is contradicted by the organism area cladogram. The third clade (3: A, B, C, D) is consistent because after pruning it is present in both cladograms and there is one shared area outside it (F). The fourth clade (4: E, F) in the biogeographic pattern is absent in the organism area cladogram because it becomes uninformative after pruning of E, which is unique to the biogeographic pattern. The total score for the biogeographic pattern is $3 - 1 + 1 + 0 = 3$. The maximum possible score is $4 \times 3 = 12$ (four informative perfect matches), giving a relative score of $3/12 = 0.25$.

was obtained by generating 100 data sets in which each group was categorized as animal or plant at random while maintaining the original number of groups in each class (54 and 19), as in a partition homogeneity test. The null hypothesis, i.e., no association between the frequency of dispersals and the type of organism involved (plant or animal) would be rejected ($P < 0.05$) if the difference in dispersal frequency between the original animal and plant data sets were larger than the difference in $>95\%$ of the random data sets.

Second, we calculated the frequency of dispersal events between the major southern landmasses and tested the significance of the dispersal patterns using the randomization tests in TreeFitter. In these tests, the observed frequency of the predicted dispersal patterns was compared with that expected by chance by using a modified chi-square test in which the expected frequency and the reference distribution were both calculated from 100 randomly permuted data sets. Permuting the terminals of the area cladogram is not possible in these tests because such permutations would change the set of biogeographic events. Therefore, only the terminals in the organism phylogenies were permuted.

Before determining the direction of dispersal asymmetries, observed values were normalized against the number of expected events from the randomizations. This step is important because not all the southern landmasses are equally represented in our data sets (Figs. 4c, 4d), and this inequality would heavily bias the number of dispersal events (Wares et al., 2001). The corrected frequencies compared here represent the number of dispersal events in each direction that we would have seen if all areas had been equally well represented in the data set.

RESULTS

Area Cladograms

Figure 7 shows the optimal area cladograms for the animal and plant data sets found using the heuristic search in TreeFitter. All cladograms were significant in terms of overall cost ($P < 0.01$ in all cases) and had a higher number of vicariance events than expected by chance ($P = 0.01$ for the plant data set; $P < 0.01$ for all others). The animal cladogram (Fig. 7a) has a pattern in agreement with the SGP (Fig. 3a), except for the position of Africa, which appears closely related to other areas: (Africa, . . .)((New Zealand(S. South America, Australia))). The same area cladogram was obtained when insects were analyzed separately, but when the Eucnemidae were excluded from the insect data set the SGP became complete in that it now also included Africa (Fig. 7b). Separate analysis of the animal groups excluding insects (Fig. 7c) also reflected the SGP, in this case including New Guinea as sister group to Australia: (New Zealand (S. South America (Australia, New Guinea))). In contrast to all animal area cladograms, the plant area cladogram (Fig. 7d) supports the PSP (Fig. 3b): (S. South America(New Zealand, Australia)).

(a) Animals

(b) Insects (ex. Eucnemidae)*

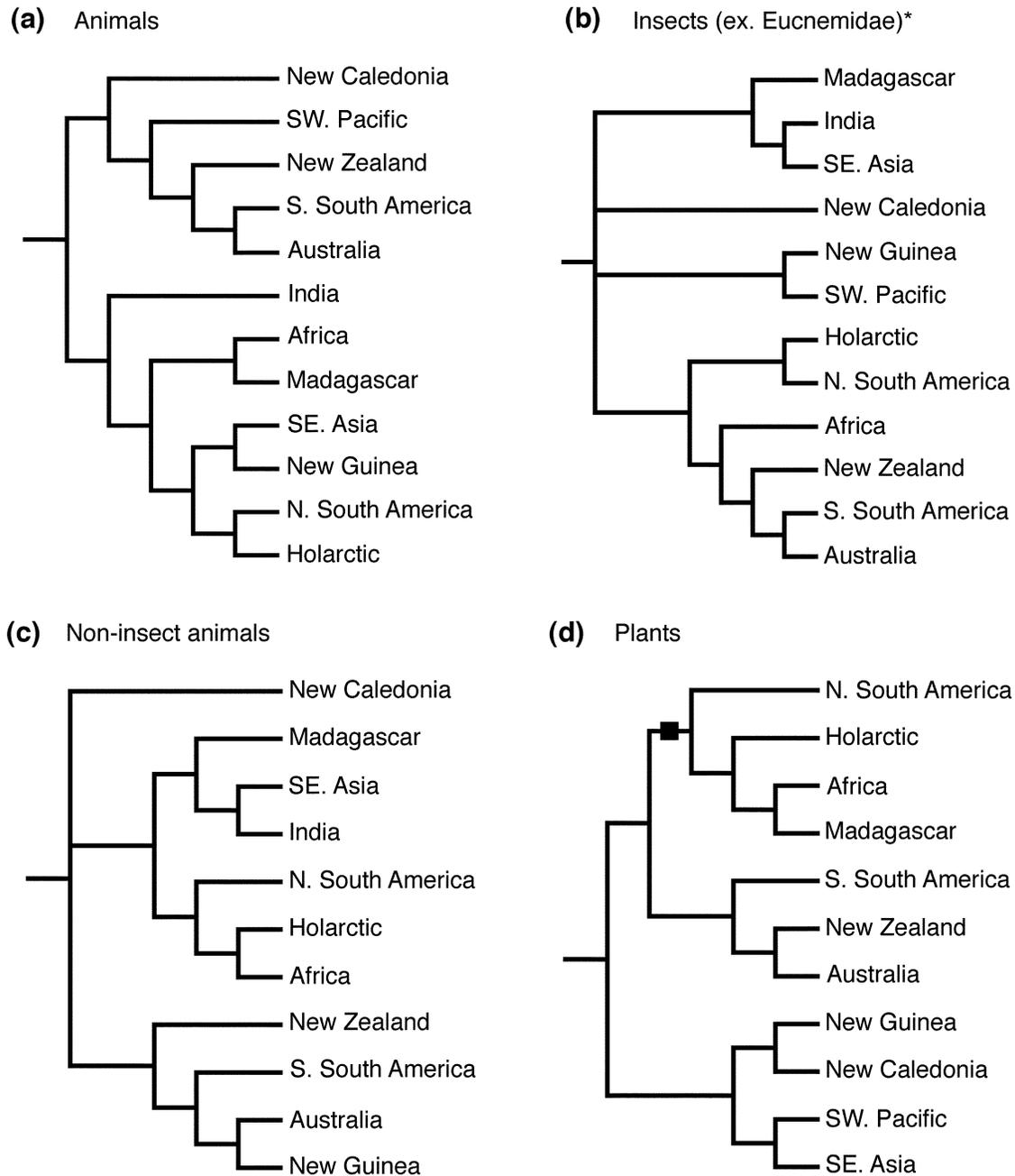**(c)** Non-insect animals

(d) Plants

FIGURE 7. Optimal area cladograms. (a) Whole animal data set, cost = 465.94. (b) Insect data set excluding Eucnemidae, cost = 241.79. (*) The complete insect data set gave a cladogram identical to that in (a), with cost = 381.28. (c) Animal data set excluding insects, cost = 67.96. (d) One of the two possible optimal area cladograms for the plant data set, cost = 133.63. The solid square indicates the alternative position occupied by Madagascar in the second area cladogram.

Both the animal and plant area cladograms support a hybrid origin for the South American biota (Crisci et al., 1991): northern South America is consistently grouped with the Holarctic region (mainly North American distributions), whereas southern South America appears more closely related to Australia or New Zealand (Fig. 7). None of the animal or plant area cladograms show the sister-group relationship between New Zealand and New Caledonia predicted by the geological scenario (Fig. 1);

instead, biotic relationships separate these areas in the area cladogram.

Biogeographic Patterns

Figure 8 shows a comparison between the animal and plant data sets in terms of the number of groups supporting each of the six major biogeographic patterns (cf. Fig. 3). The animal data set (Fig. 8a) is dominated by the SGP and by the NGP. Support for the NGP, however,
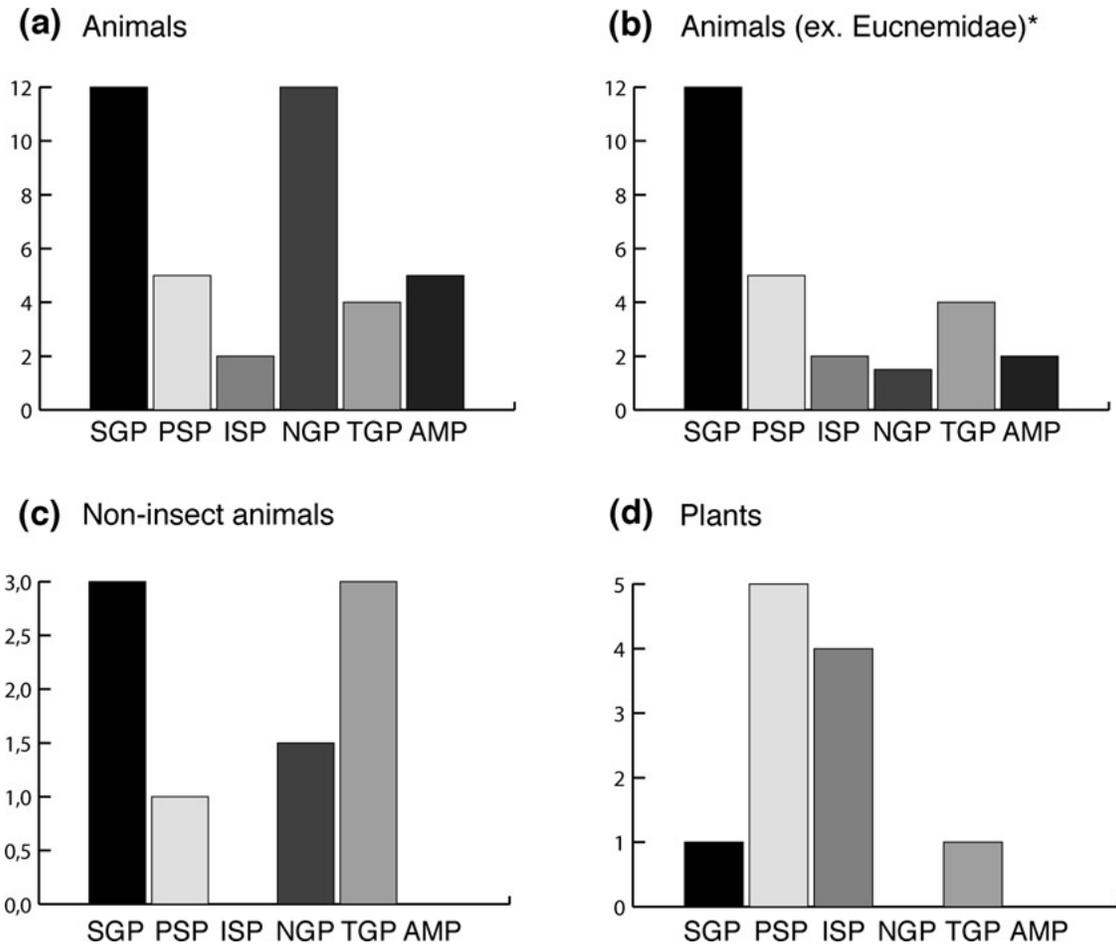
FIGURE 8. Histograms showing the number of groups supporting each of the biogeographic patterns in Figure 3. (a) Whole animal data set. (b) Animal data set excluding Eucnemidae (*the insect data set excluding Eucnemidae supports a histogram nearly identical to that for animals excluding Eucnemidae). (c) Animal data set excluding insects. (d) Plant data set.

is almost exclusively due to the eucnemid beetles. They constitute a small percentage of the animal data set in terms of number of species (17%), but they represent a significant proportion of the groups (22 of 54; 41%). When the Eucnemidae are removed from the analysis, the SGP becomes the overwhelmingly dominant pattern in animals and in insects (Fig. 8b). Similarly, most of the noninsect animal groups support the SGP or the TGP (Fig. 8c). In contrast, the majority of groups in the plant data set support either the PSP or the ISP, with almost no support for the SGP (Fig. 8d). Several groups did not support any clear pattern (multiple area cladograms) or supported a pattern different from those represented in Figure 3 (cf. Table 2).

Fit to the Geological Scenario

Both the animal and plant data sets display highly significant, phylogenetically conserved distribution patterns ($P < 0.001$) when fit to the geological scenario (Fig. 1). However, the processes responsible for the distribution patterns differ between plants and animals (Table 3). The animal data set as a whole shows a higher frequency of vicariance, extinction, and duplication events than expected by chance ($P < 0.05$), whereas dispersals are significantly rare. The plant data set also exhibits a higher frequency of duplication and a lower frequency of dispersal than expected, but the frequencies of vicariance and extinction events do not depart significantly from expected values. This difference can also be observed when individual groups are fitted to the geological area cladogram: with the exception of Strelitziaceae, none of the plant groups shows a significant frequency of vicariance or extinction, whereas many of the animal groups do (Table 3).

Dispersal Analysis

Comparison of the frequency of dispersal events between the animal and plant data sets shows that the frequency of terminal dispersals is significantly higher in

TABLE 3. Fit between the animal and plant data sets and the geological area cladogram in Figure 1. Only those groups with significant fit to the geological cladogram are included. Overall fit was tested by permutation of organism terminals and areas, vicariance and extinction events by permutation of areas, and duplication and dispersal events by permutation of organism terminals.

Taxon	Fit to geological cladogram[a]	Overall fit	Frequency of event[b]			
			Vicariance	Duplication	Extinction	Dispersal
Animals						
All groups	v + d + e + ci	<0.001	H (0.022)	H (<0.001)	H (<0.001)	L (<0.001)
Podonominae	d + e + ci	<0.001	ns (0.085)	H (<0.001)	H (0.025)	L (<0.001)
Apioceridae	v + e + ci	0.008	H (0.008)	ns	H (0.008)	L (0.008)
Macrocerini	v + d + ci	<0.001	H (0.036)	H (0.001)	ns	L (<0.001)
Australosymmerus	v + d + e + ci	<0.001	H (0.024)	H (<0.001)	H (0.014)	L (<0.001)
Labenini + Xenothyrini	v + d + e + ci	<0.001	H (0.047)	H (<0.001)	H (<0.001)	L (<0.001)
Hydrobiosidae	v + d + e + ci	<0.001	H (<0.001)	H (<0.001)	H (0.008)	L (<0.001)
Cichlidae	v + d + ci	<0.001	H (0.011)	H (<0.001)	ns	L (<0.001)
Acrodont lizards	v + d + e + ci	<0.001	H (0.030)	H (<0.001)	H (<0.001)	L (<0.001)
Marsupials	v + e + ci	0.002	H (0.016)	ns	H (0.017)	L (0.006)
Peripatopsidae	d + e + ci	<0.001	ns	H (<0.001)	H (0.043)	L (<0.001)
Groteini	d	0.015	ns	H (0.014)	ns	ns
Ceroplastinae	d	<0.001	ns	H (<0.001)	ns	ns
Characiformes	d	0.006	ns	H (0.018)	ns	ns
Aquarius paludum group	ci	0.041	ns	ns	ns	L (0.041)
Cerotelion + Mallochinus	d + ci	<0.001	ns	H (<0.001)	ns	L (0.012)
Helicopsychidae	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Metacorneolabium	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Adeliini	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Epipleurus	d + ci	0.001	ns	H (0.004)	ns	L (0.015)
Aplocheiloidei	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Galaxiidae	d + ci	0.003	ns	H (<0.001)	ns	L (0.013)
Cladidus		0.039	ns	ns	ns	ns
Farsus		0.044	ns	ns	ns	ns
Heterotaxis		0.024	ns	ns	ns	ns
Rhagomicrus		0.023	ns	ns	ns	ns
Masarinae		0.024	ns	ns	ns	ns
Plants						
All groups	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Nothofagus	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Cunonieae	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Iridaceae	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Restionaceae	d + ci	<0.001	ns	H (<0.001)	ns	L (<0.001)
Rytidosperma	d + ci	0.001	ns	H (0.002)	ns	L (0.044)
Cyttaria	d + ci	<0.001	ns	H (<0.001)	ns	L (0.032)
Abrotanella	d	0.001	ns	H (<0.001)	ns	ns
Embothrieae	d	0.005	ns	H (0.001)	ns	ns
Winteraceae	ci	<0.001	ns	ns	ns	L (<0.001)
Strelitziaceae	v + ci	0.019	H (=0.044)	ns	ns	L (0.044)
Oreobolus		<0.001	ns	ns	ns	ns
Danthonia		0.039	ns	ns	ns	ns

[a]v = vicariance; d = duplication; e = extinction; ci = conservative dispersal.

[b]H = the frequency of the event is significantly higher than expected ($P < 0.05$); L = the frequency of the event is significantly lower than expected ($P < 0.05$); ns = the difference is not significant. All p-values are based on 1,000 permutations.

plants than in animals ($P = 0.02$), but the frequencies of ancestral and total dispersals, although higher in plants, do not differ from expected values ($P = 0.42$ and 0.96, respectively). Thus, there is more dispersal in the plant data set, but it appears to be solely due to dispersal within widespread terminals.

Table 4 shows comparisons of the observed and expected frequencies of dispersal between the southern landmasses in the animal, insect, and plant data sets (the number of events in the noninsect animal data set was too small for statistical comparisons). Figures 9 and 10 represent the same comparisons for the animal and plant data sets, but the dispersal frequencies are reported as a ratio against the number of expected events from the randomizations to correct for the unequal representation of the areas in the data set. We found several significant concordant dispersal patterns in the data sets, but these patterns were different in animals and plants (the insect data set showed patterns identical to those observed for animals; see Table 4).

In animals, trans-Antarctic dispersal between Australia and southern South America (AUS ↔ SSA) is significantly more frequent than any of the other dispersal events involving the austral landmasses ($P = 0.01$, Table 4). In contrast, trans-Tasman dispersal (NZ ↔ AUS) is significantly more frequent than trans-Antarctic (AUS ↔ SSA) and trans-Pacific (NZ ↔ SSA) dispersals in plants ($P = 0.01$). New Zealand is more frequently the

TABLE 4. Comparisons of the frequency of different types of dispersals among the major southern landmasses in the animal and plant data sets. Frequencies are measured as the number of dispersal events inferred by TreeFitter. For each comparison, expected frequencies and significant deviations from these were calculated based on 100 randomly permuted data sets, in which organism terminals had been shuffled. The observed dispersal frequencies are heavily biased by the unequal representation of the areas in the data set (Figs. 4c, 4d). Therefore, in interpreting the direction of asymmetries relative to the frequencies, we have only considered the corrected dispersal frequencies, after normalizing the observed number of events against the expected values.

Dispersal events compared	Animals			Plants			Insects		
	Observed	Expected	P	Observed	Expected	P	Observed	Expected	P
Trans-Antarctic									
(AUS ↔ SSA)	20.58	17.52	0.01	7.22	7.92	0.50	18.08	14.99	0.01
(NZ ↔ AUS) + (SSA ↔ NZ)	24.64	27.70		17.41	16.71		19.89	22.98	
Trans-Tasman									
(AUS ↔ SSA) + (SSA ↔ NZ)	31.78	29.75	0.12	14.22	16.87	0.01	28.78	26.90	0.09
(NZ ↔ AUS)	13.44	15.47		10.41	7.77		9.19	11.07	
Trans-American									
(NSA ↔ SSA)	4.92	5.16	0.84	2.77	0.841	<0.01	4.42	5.33	0.10
(NSA ↔ AFR)	5.63	5.39		0.50	2.43		3.63	2.72	
North-American									
(NSA ↔ SSA)	4.92	9.66	<0.01	2.78	1.63	0.14	4.42	9.27	<0.01
(NSA ↔ HOL)	12.85	8.11		0.00	1.15		12.85	7.99	
West Gondwana									
(NSA ↔ AFR)	5.63	9.81	0.01	0.50	1.97	<0.01	3.63	7.12	0.02
(AFR ↔ MAD)	9.83	5.65		3.05	1.59		9.83	6.33	
Asymmetry trans-Antarctic									
(AUS → SSA)	11.80	12.30	0.71	2.89	4.40	0.03	9.80	9.72	0.97
(SSA → AUS)	8.78	8.28		4.33	2.82		8.28	8.36	
Asymmetry trans-Tasman									
(AUS → NZ)	8.96	9.85	0.27	7.11	5.78	0.27	5.63	6.20	0.41
(NZ → AUS)	4.48	3.59		3.30	4.63		3.56	2.99	
Asymmetry trans-Pacific									
(SSA → NZ)	5.83	7.92	0.01	6.00	3.70	<0.01	5.33	7.64	0.02
(NZ → SSA)	5.37	3.28		1.00	3.30		5.37	3.05	
Asymmetry trans-American									
(NSA → SSA)	1.69	2.74	0.04	2.19	1.85	0.56	1.69	2.45	0.08
(SSA → NSA)	3.23	2.18		0.58	0.92		2.73	1.97	
Asymmetry NSA-HOL									
(NSA → HOL)	8.54	6.05	0.11			No events	8.54	5.92	0.08
(HOL → NSA)	4.31	6.79					4.31	6.93	
Asymmetry AFR-NSA									
(NSA → AFR)	4.71	3.70	0.19	0.50	0.18	<0.01	2.71	1.75	0.05
(AFR → NSA)	0.92	1.92		0.00	0.32		0.92	1.87	
Asymmetry AFR-MAD									
(AFR → MAD)	6.83	7.22	0.75	1.36	1.42	0.90	6.83	6.86	0.99
(MAD → AFR)	3.00	2.61		1.69	1.63		3.00	2.97	

source area of trans-Tasman dispersal than is Australia in animals (Fig. 9), whereas the opposite pattern is found in plants (Fig. 10), but none of these differences are significant ($P = 0.27$, Table 4). There is, however, highly significant directional asymmetry in trans-Pacific biotic exchange (NZ ↔ SSA), but it follows opposite directions in animals and plants: New Zealand is the most frequent source area of dispersal in the animal data set ($P = 0.01$, Fig. 9), whereas southern South America is almost the only source of dispersal in the plant data set ($P < 0.01$, Fig. 10).

Trans-American exchange (SSA ↔ NSA) in animals is significantly lower than the biotic exchange between northern South America and North America (NSA ↔ HOL) ($P < 0.01$), and southern South America seems to be the main source area of these dispersals ($P = 0.04$). This comparison was not significant in plants.

Not surprisingly, dispersal between Madagascar and Africa (AFR ↔ MAD) is significantly more frequent than trans-Atlantic dispersal between northern South America and Africa (AFR ↔ NSA) in animals ($P = 0.01$) and plants ($P < 0.01$). Northern South America is more frequently the source area of trans-Atlantic dispersal than is Africa (AFR → NSA) in plants ($P < 0.01$), but the values are very small.

DISCUSSION

Hierarchical Vicariance Patterns

Sanmartín et al. (2001) found that a maximum-vicariance analysis of 57 Holarctic animal groups failed to support any hierarchical area cladogram, and they concluded that this occurs because the northern landmasses were joined to each other in various combinations over time, creating a reticulate biogeographic pattern. In contrast, if current distribution patterns in the Southern Hemisphere were shaped to a large extent by the sequential breakup of Gondwana and the associated
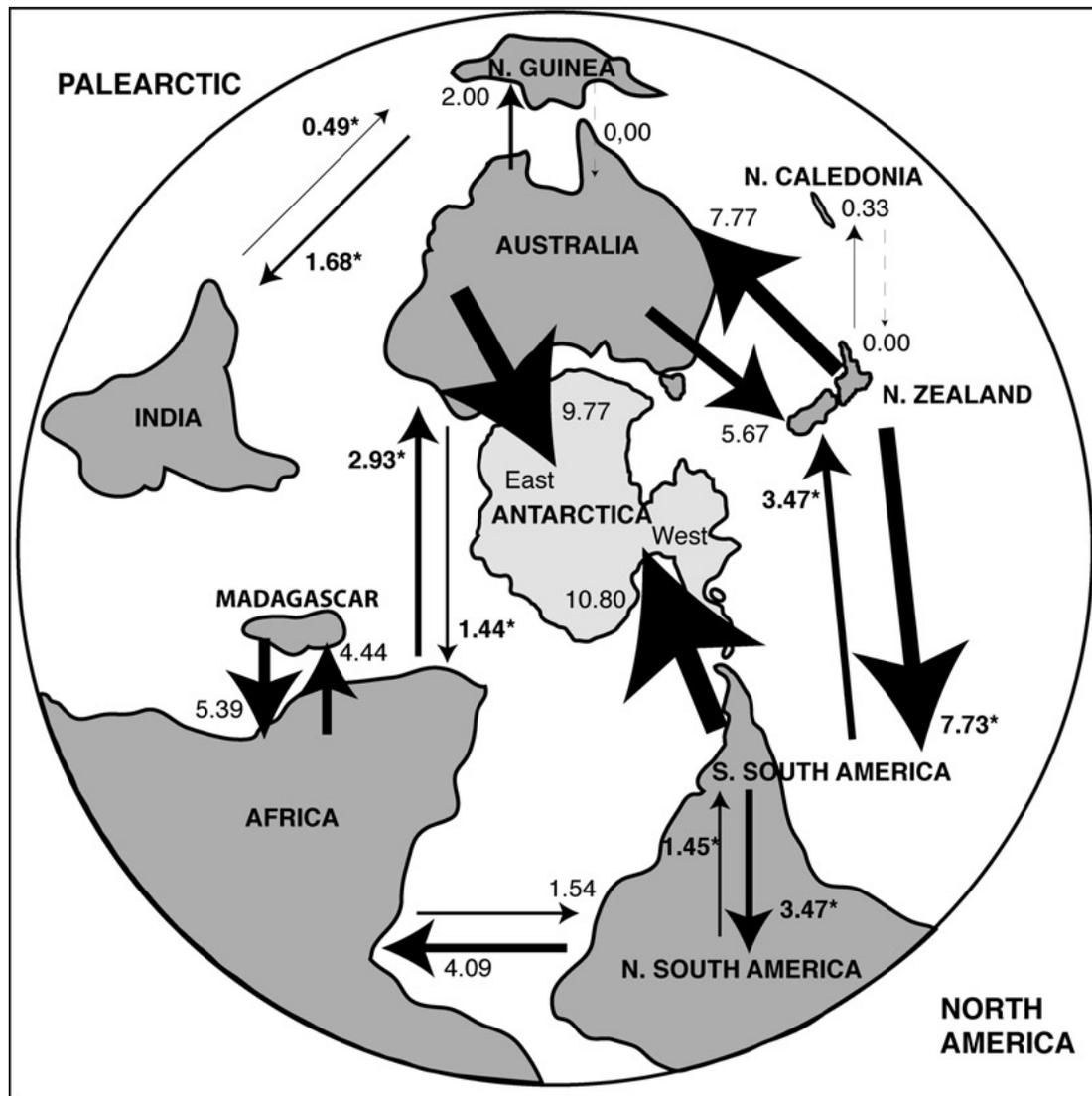
FIGURE 9. Polar view of the Southern Hemisphere in the late Cretaceous–early Tertiary, showing the frequency of dispersal (number of dispersal events inferred by TreeFitter) between the southern landmasses in the animal data set. The thickness of the arrows is proportional to the frequency of the dispersal event. To avoid the bias caused by the unequal representation of the areas in the data set, dispersal frequencies are given here as a ratio against the number of expected events from the randomizations. The corrected figures represent the number of dispersal events in each direction that we would have seen if all areas had been equally well represented in the data set. Antarctica is not shaded because although it was a major biotic route for dispersal between Australia and South America none of the studied groups are now present there so it was not considered in the analysis. Significant patterns are marked with an asterisk ($P < 0.05$).

vicariance events, we should be able to retrieve a strongly supported hierarchical pattern reflecting the geological area cladogram (Fig. 1).

Our results indicate that the breakup of Gondwana has indeed played an important role in molding the biogeography of our animal groups (presumably Mesozoic). The best area cladograms for the animal data set as a whole and for different animal subgroups (Figs. 7a–c) all contain important components of the geological area cladogram (Fig. 1). Geologically predicted vicariance events are significantly more common than expected by chance in animals (Table 3), and many of the species-rich animal groups support the SGP (Fig. 8b), which agrees well

with the hypothesized geological breakup of southern temperate Gondwana (Fig. 1).

The congruence between zoogeographic patterns and southern temperate Gondwana breakup implies that many of the animal groups studied here could be old. Although the precise timing of the loss of land connections among southern Gondwana landmasses is unclear, most authors agree on a date of 80 MYA for complete continental separation between New Zealand and Australia, and a date of 35 MYA is generally agreed for the final breakup of terrestrial connections between South America and Australia (Veevers et al., 1991), although some authors maintain that biotic exchange was terminated already
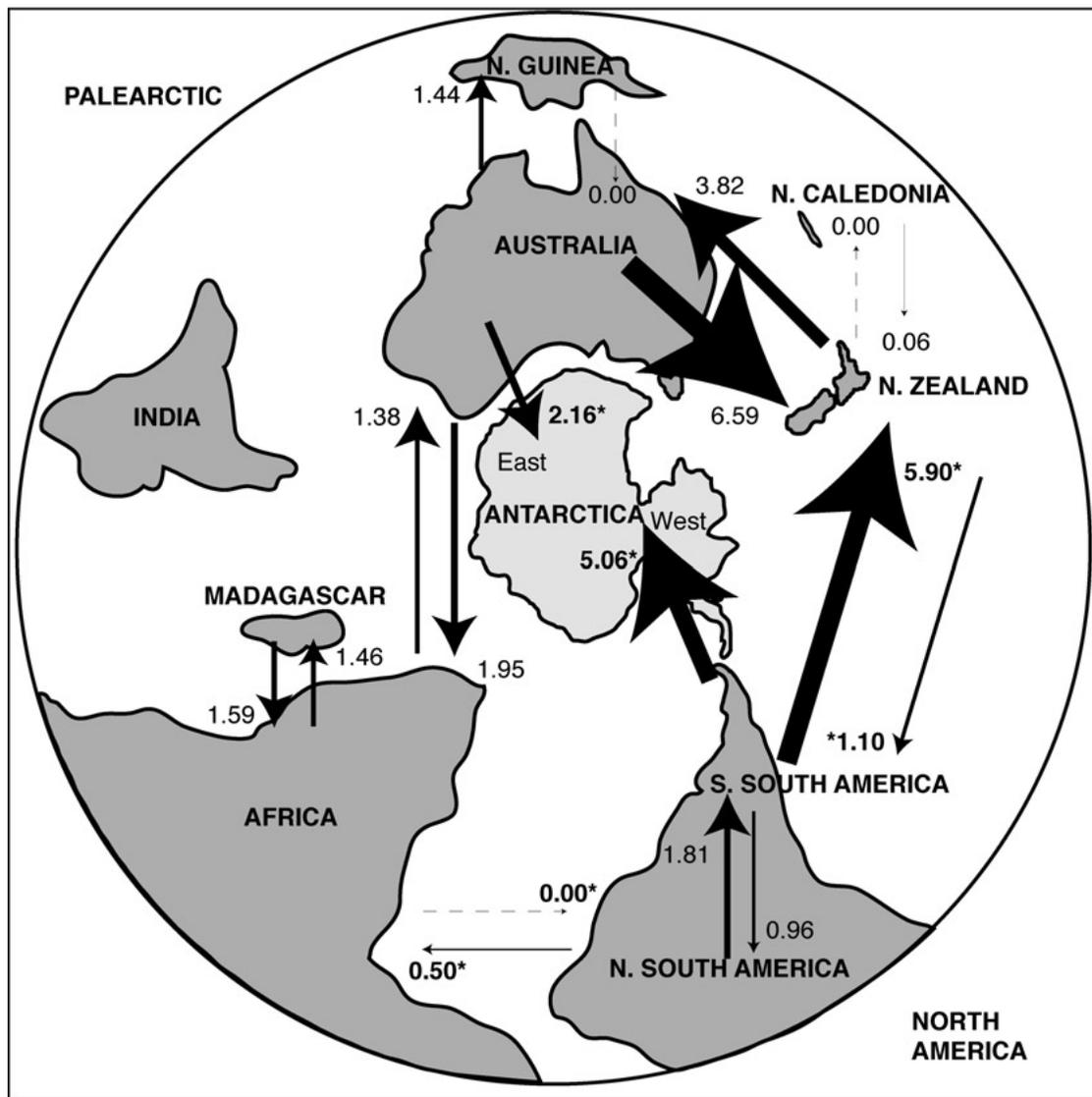
FIGURE 10.   Polar view of the Southern Hemisphere in the late Cretaceous–early Tertiary, showing the frequency (number) of dispersal events between the southern landmasses in the plant data set (see Fig. 9).

in the early Eocene, 50 MYA (Woodburne and Case, 1996).

Somewhat surprisingly, our results suggest that biogeographic patterns in our plants (of presumably Mesozoic or early Cenozoic age) have not been significantly influenced by the Gondwanan breakup. The best plant area cladogram supports the PSP (S. South America(New Zealand, Australia)), which has often been found in plant biogeographic studies (Seberg, 1991; Linder and Crisp, 1995) but is in conflict with continental fragmentation patterns (Fig. 1). The dominance among individual plant groups of the PSP and the ISP (Fig. 8d), two patterns typically explained by dispersal (Table 1), further corroborates the departure of plant phylogenies from geological vicariance. When the plant data set was fitted to the geological area cladogram, none of the plant groups (except Strelitziaceae) showed a higher frequency of vicariance

and extinction events than expected by chance. The same result was obtained for the entire plant data set. If plants had responded to the breakup of Gondwana with speciation (vicariance) followed by local extinction in some areas, both vicariance and extinction events should be more common than expected by chance.

Why do plant distributions show no traces of Gondwanan breakup? There seems to be two possibilities: either the studied plant groups are too young to have been affected or they once fragmented in response to Gondwanan splits but the original patterns were subsequently lost because of dispersal and extinction events. Several lines of evidence support the latter hypothesis for many of the plant groups studied here. First, fossil evidence (Table 2, Appendix B) indicates that many plant groups are old enough to have been influenced by at least the more recent Gondwanan

geological events (Fig. 1). Second, for at least one group, the southern beeches (*Nothofagus*), adding fossil distributions makes the biogeographic pattern congruent with the breakup sequence of Gondwana (Manos, 1997; Swenson et al., 2001). Thus, the distributions of southern beeches were initially shaped by geologically induced vicariance events, but subsequent extinctions have resulted in the extant species showing a pattern in conflict with geology, the PSP (Fig. 3b). Third, colonization of new areas might be expected to be successful more often in plants than in animals, given that plants have a resistant dispersal stage (seeds/spores), that should facilitate long-distance dispersal. Not surprisingly, there is also more specific evidence for some plant groups that suggests that recent dispersal has indeed been superimposed onto an ancient vicariance pattern, for example in Atherospermataceae (Renner et al., 2000). We found significantly more dispersal events among plant terminals than among animal terminals, consistent with the hypothesis that vicariance patterns in plants have been obscured by later dispersal. However, the number of terminal dispersals is also influenced by the proportion of terminals that are higher taxa, which tend to be more widespread and therefore imply more dispersal events. In our data set, there were more higher-taxon terminals in plants than in animals (12% vs. 5%), so it is possible that the difference in terminal dispersals was caused entirely due to this effect.

If plant biogeography has not been shaped by Gondwanan breakup, why do we find strongly supported hierarchical patterns, such as the PSP, among plants? It is difficult to exclude the possibility of other sets of geological events underlying these alternative hierarchical patterns, but a more likely explanation is probably that they are the result of recurring combinations of biotic events other than geologically induced vicariance. Consider, for instance, the close relationship between New Zealand and Australia in the PSP (Fig. 3b). This type of pattern could easily arise in old groups that were originally present on New Zealand, then went extinct there, and finally recolonized New Zealand from Australia. Unless the colonizing lineage was deeply nested within an Australian clade, it would be difficult or impossible to distinguish such a pattern from a true hierarchical vicariance pattern. The same pattern could have arisen in groups that were too young to be in New Zealand at the time of rifting (80 MYA) and instead dispersed there from Australia later. This appears to be the case in, e.g., ratite birds (Van Tuinen et al., 1998; Cooper et al., 2001). Thus, hierarchical biogeographic patterns could be created both by a classical vicariance scenario and by recurring combinations of dispersal and extinction events that generate hierarchical patterns.

Concordant Dispersal Patterns

To be able to infer with any confidence dispersal events from phylogenetic evidence, these events must be rare in comparison with the number of lineage-splitting events. That is, dispersal events must have occurred against a background of phylogenetically constrained events, such as vicariance or local speciation (duplication). This was indeed the case in both animals and plants: dispersals were significantly less common and vicariance or duplication events were significantly more common than expected by chance (Table 3). Once it has been determined that dispersals are phylogenetically constrained, so that the individual events can be inferred with reasonable confidence, it becomes possible to search for general dispersal patterns.

In biogeography, dispersals are often considered to be random, but our analyses reveal strong concordant dispersal patterns in the Southern Hemisphere, both in animals and in plants. In other words, dispersals tend to occur between certain areas and in certain directions.

Before discussing the individual patterns, it is useful to consider the way in which the four kinds of biogeographic events relate to each other when biogeographic patterns are looked upon from different perspectives. For example, consider local speciation (duplication) events. Even in groups with Gondwanan vicariance patterns, our results typically indicate that local speciation was significantly more common than expected (Table 3). However, if the same patterns had been analyzed in more geographic detail, with more groups represented, we might have discovered that some of the local speciation events correspond to vicariance or dispersal events within the broadly defined regions used in the present study. Thus, the high frequency of local speciation seen here undoubtedly reflects to some extent the lack of geographic detail.

A more subtle example of the effect of different perspectives concerns dispersal and vicariance events. A dispersal event is a range expansion across an existing dispersal barrier followed by allopatric speciation along the barrier. Thus, a dispersal event is just a vicariance event that is not predicted by the area cladogram. Under certain conditions, concordant dispersal events, possibly in combination with extinctions, may occur in a sequence that generates a hierarchical pattern, which is then indistinguishable from a sequential vicariance pattern. Fitting organism phylogenies to such a dispersal-generated area cladogram will result in the concordant dispersal events being identified as predicted vicariance events. It is only when the organism phylogenies are fitted to a geologically based area cladogram that these dispersal events can be identified as true dispersals. The situation is analogous to the mapping of ordinary characters onto phylogenetic trees. A feature that is indicated to be a homoplasy (dispersal) on one tree may appear as a synapomorphy (vicariance) on another tree. The best way to accurately separate homoplasies from homologies is to map characters onto the true phylogeny. However, most concordant dispersal patterns do not generate hierarchical distribution patterns (just like sets of convergences rarely conform to a hierarchical pattern), and the identification of them is hence more robust to the area cladogram used. The concordant dispersal patterns discussed here (Figs. 9, 10; Table 4) are all identified against

the background of the geological area cladogram (Fig. 1), and this approach should be borne in mind when interpreting them.

Trans-Antarctic exchange.—In animals, trans-Antarctic dispersal between Australia and southern South America was significantly more frequent than any of the dispersal events involving New Zealand and the other austral landmasses (Fig. 9; Table 4). This pattern is probably an effect of time and past continental connections. Given that the isolation of New Zealand (80 MYA) occurred before the vicariance between southern South America and Australia (35 MYA), we would expect extinction to have erased the traces of the old dispersal events involving New Zealand, making them rarer than Australian–South American dispersals among the events documented by extant organisms and their phylogenies. The dominance of trans-Antarctic dispersal also emphasizes the importance of the Antarctic route in southern faunal exchange. This route was established during the late Cretaceous–early Tertiary, when the Southern Andes became connected through the Scotia Arc to the Antarctic Peninsula, which in turn was connected to Australia through east Antarctica, and it was not broken until the late Eocene (35 MYA), when the South Tasman Sea opened between Australia and east Antarctica (Lawver et al., 1992). Throughout most of this time period, the connected landmasses had a temperate climate, and Antarctica was covered by an angiosperm-rich flora dominated by *Nothofagus*. The route thus allowed a long period of biotic exchange between Australia and southern South America. Paleogene fossils of marsupials (Woodburne and Case, 1996) and ratite birds (Van Tuinen et al., 1998) from Antarctica further document the importance of the trans-Antarctic dispersal route.

Trans-Tasman dispersal.—The dominance of trans-Tasman dispersal in plants (Fig. 10) is associated with the high frequency of sister-group relationships, (New Zealand, Australia)S. South America), in austral plant groups (Linder and Crisp, 1995). Although the PSP has been sometimes explained by an alternative sequence of breakup events involving the lost Pacifica continent (Crisci et al., 1991; Seberg, 1991), a more common hypothesis is that this pattern is the result of trans-Tasman dispersal between Australia and New Zealand after terrestrial connections were broken 80 MYA (Pole, 1994, 2001). The opening of the Drake Passage between South America and Antarctica in the Oligocene (30 MYA) led to the establishment in the region of the easterly directed West Wind Drift (Veevers, 1991). Historical records show that birds and insects are regularly blown across the Tasman Sea from Australia to New Zealand (Michaux, 1991). Marine dispersal in currents associated with the West Wind Drift is also invoked to explain sister-group relationships between New Zealand–Australian marine organisms (Fell, 1962; Waters et al., 2000a). Pole (1994, 2001) went even further in arguing that most of New Zealand's present flora came by long-distance dispersal from Australia during the late Tertiary because the old Gondwanan lineages, dating back to New Zealand's

isolation in the late Cretaceous, went extinct during New Zealand's submergence in the Paleogene (but see McLoughlin, 2001). The direction of the West Wind Drift, however, predicts that dispersal should be significantly more frequent from Australia to New Zealand than in the other direction. Although Australia was the main source of trans-Tasman dispersals in the plant data set (Fig. 10), this difference is not significant in permutation tests. In the animal data set, trans-Tasman dispersal seems to have been against the direction of the prevailing winds (Fig. 9), but the difference is again not significant. More data are needed to document whether the expected directional asymmetry due to the West Wind Drift exists. However, other studies on plants (Linder, 1999; Winkworth et al., 2002) have also documented trans-Tasman dispersal in both directions, contradicting the West Wind Drift hypothesis.

An alternative hypothesis is that much of the trans-Tasman dispersal has been over stepping-stone islands, making the predominant wind direction less important. This dispersal would have involved interconnecting islands and shallow water bridges across the Lord Howe Rise and Norfolk Ridge, which according to some reconstructions remained close to Australia until the Middle Tertiary (Walley and Ross, 1991). A new uplift in the late Tertiary would have permitted biotic dispersal as late as the Miocene (Herzer et al., 1997). However, the existence of these biotic routes is not clear because alternative paleogeographic reconstructions show the Lord Howe Rise and Norfolk Ridge covered by shallow seas since the end of the Cretaceous, 70 MYA (McLoughlin, 2001).

Trans-Pacific dispersal.—A sister-group relationship, (southern South America, New Zealand)Australia), in conflict with the geologically predicted vicariance pattern, is often found in the Southern Hemisphere flora and fauna (Swenson and Bremer, 1997; Renner et al., 2000; Winkworth et al., 2002). Although this disjunction has been explained sometimes by a different sequence of vicariance events (Glasby and Alvarez, 1999), a more convincing explanation is that it is the result of long-distance dispersal between New Zealand and South America after New Zealand drifted away from west Antarctica, 80 MYA. Wind dispersal in the South Pacific is presumed to be predominantly eastward, from New Zealand to southern South America, following the direction of the West Wind Drift (Winkworth et al., 2002). The dominance of eastward dispersals in the animal data set, with New Zealand acting as the main source area of trans-Pacific dispersal (Fig. 9), seems to provide evidence of the importance of the West Wind Drift in forming Southern Hemisphere biogeographic patterns. However, the highly directional dispersal asymmetry documented here in plants (Fig. 10) suggests exclusively westward long-distance dispersal (S. South America → New Zealand), against the prevailing direction of winds and ocean currents (see also Winkworth et al., 2002). A possible explanation is that dispersal from southern South America to New Zealand did not involve

direct jumps but rather stepping-stone dispersal along the coastline of Antarctica (Swenson and Bremer, 1997; Renner et al., 2000). This hypothesis is supported by the fact that temperate forests existed in the Antarctic coastal areas until at least the Pliocene (Swenson and Bremer, 1997). This dispersal could have been mediated by the west-flowing East Wind Drift, which runs close to the Antarctic coast, or could have followed the West Wind Drift around Antarctica, involving dispersal first to the subantarctic islands (and/or Australia) and from there to New Zealand (Swenson and Bremer, 1997).

South American Biotic Divide

North America and South America became connected during the middle Cretaceous (100 MYA) across the proto-Caribbean archipelago, located further to the west than it is today. This connection was broken in the early Eocene, about 49 MYA (Hay et al., 1999). Significant faunal exchange presumably took place across the Caribbean connection and involved a first invasion of placental and marsupial mammals (Springer et al., 1998). North and South America became connected again during the late Tertiary, first via the Panama Island Arc (15 MYA) and later across the Panama Isthmus in the late Pliocene (3.5 MYA). This connection established a second period of biotic exchange, the Great American Exchange, with the replacement of the southern marsupial fauna by a second invasion of placental mammals. The importance of this faunal exchange is supported by the sister-group relationship between northern South America and the Holarctic (North America) in the animal and insect area cladograms (Figs. 7a, 7b) and the close relationship in the noninsect cladogram (Fig. 7c) and the plant cladogram (Fig. 7d). In contrast, the biotas of northern South America and southern South America do not appear to be closely related. Southern South America appears more closely related to the austral landmasses (Australia, New Zealand) than to northern South America in the plant and all animal area cladograms. The frequency of trans-American dispersal between northern and southern South America is significantly lower than that between northern South America and the Holarctic in the animal and insect data sets (Table 4). This result confirms previous biogeographic results suggesting that the South American biota is formed by a northern tropical component and a southern temperate component, each with different biogeographic affinities (Crisci et al., 1991; Amorim and Tozoni, 1994; Lopretto and Morrone, 1998). It is difficult to explain this biotic divide on geological grounds. Northern and southern South America have always been connected, except during a brief period during the Cretaceous (100–80 MYA) when an epicontinental sea separated both halves. The most likely explanation is ecological: the tropical forests of the Amazonian Basin have probably constituted a long-lasting, powerful barrier to dispersal for temperate organisms. Dispersal of South American animals was significantly more frequent from the southern to the northern region than in the other direction, in contrast to the direction of the Great American Exchange, which is thought to have been predominantly southward. However, the presumed direction of the trans-American exchange is based on fossil evidence from mammals (Woodburne and Case, 1996), whereas most of the (few) South American dispersals are in the insect phylogenies (Table 4), the main component of our animal data set.

Northern Gondwana Pattern

Biogeographic relationships among the landmasses that form the southeastern tropics (Africa, Madagascar, India, Southeast Asia/Southwest Pacific, northern Australia, and New Guinea) are typically explained as the result of recent dispersal along the coasts of the Indian Ocean. These areas share a tropical biota, and exchange between the eastern landmasses has been frequent since the collision of the Australian and Asian plates in the Miocene (Raven and Axelrod, 1972). Long-distance dispersal over water barriers is probably the likeliest explanation for angiosperm groups such as the baobabs (Baum et al., 1998; see Table 2), which radiated long after the separation of Africa and Australia in the early Cretaceous, 135 MYA.

However, for other groups this pattern could be much older. The Kerguelen Plateau, a continental block situated off northeastern India that foundered at the end of the Cretaceous (McLoughlin, 2001), probably acted as a land bridge between Australia–Antarctica and India–Madagascar–Africa during the late Cretaceous, after the separation of Africa and Australia. The existence of this land link is supported by the pan-Gondwanan distribution of many late Cretaceous terrestrial floras (Karol et al., 2000; McLoughlin, 2001) and faunas (Cranston and Hare, 1995; Cracraft, 2001). Macey et al. (2000) propose an even older chain of dispersal events to explain the NGP observed in acrodont lizards (Table 2). Small continental fragments could have drifted off from Gondwana during the late Paleozoic–Mesozoic and accreted to the Eurasian Plate during the Mesozoic–Cenozoic, e.g., India or the small terranes forming Southeast Asia (Metcalfe, 1996). These fragments would have acted as vessels transporting taxa across the Tethys Sea long before the mid-Miocene collision between the Australian and Asian plates.

Tropical Gondwana Pattern

Madagascar diverged from Africa in the early Cretaceous (121 MYA) with the opening of the Somali Basin, whereas Africa and northern South America remained connected until the mid-Cretaceous, about 100 MYA (Fig. 1). However, Africa and Madagascar have always remained relatively close, whereas Africa and tropical South America quickly drifted away from each other once they started to separate. The narrow Mozambique Channel is probably less of a barrier to dispersal for plants and animals than the South Atlantic Ocean. This difference is obvious when comparing vicariance and dispersal patterns. Some of the plant and animal groups (e.g., Strelitziaceae, Aplocheiloid fishes)

support in their area cladogram the old vicariance pattern shown in Figure 3e: (Madagascar(Africa, N. South America)). However, the animal area cladogram (Fig. 7a) and one of the two plant area cladograms (Fig. 7d) show a sister-group relationship between Madagascar and Africa, with northern South America closer to the Holarctic. More significantly, the dispersal analysis shows that dispersal between Africa and Madagascar is significantly more frequent than that between Africa and northern South America (Table 4). It is therefore likely that the more recent dispersal pattern between Madagascar and Africa has obscured the basal vicariance pattern. Also, some of the studied groups are probably not old enough to have been present before the vicariance of Madagascar in the early Cretaceous (e.g., cichlid fishes, Table 2). When the direction of dispersals is compared, northern South America appears to have acted as the main source of dispersal in the trans-Atlantic exchange, but the difference is not significant in animals, although it is significant or close to significant in plants and insects, respectively (Table 4). If the asymmetry exists, it could be explained by differential extinction during the post-Miocene aridification, which was more severe in Africa than in northern South America (Farias et al., 1999).

New Zealand and New Caledonia

New Zealand and New Caledonia were linked by continental crust along the Norfolk Ridge from the Permian (McLoughlin, 2001) until the foundering of the Norfolk Ridge and the opening of the New Caledonia Basin in the early Oligocene (30 MYA). This long-lasting connection is presumably reflected in the presence of many common relict groups, which date back to the isolation of New Zealand and New Caledonia from Gondwana in the late Cretaceous (Raven and Axelrod, 1972). One would therefore expect to see the sister-group relationship in the geological area cladogram (Fig. 1) to be reflected in the biogeographic patterns of the southern flora and fauna. However, none of the animal or plant area cladograms in Figure 7 show New Zealand and New Caledonia as sister areas. On the contrary, New Zealand is grouped with other austral areas (Australia and South America), whereas New Caledonia usually appears more closely related to New Guinea or the Southwest Pacific. Our results, therefore, do not support the notion of a common relict late Cretaceous Gondwanan biota in the two landmasses (Raven and Axelrod, 1972). Pole (1994) argued that the old Gondwanan lineages went extinct during the Paleogene submergence of New Zealand and New Caledonia and that the biotic similarity between these areas is explained by post-Eocene long-distance dispersal. Another possibility is that this dispersal took place via stepping stones across the Norfolk Ridge (Cracraft, 2001). According to Herzer et al. (1997), a new uplift of the Norfolk Ridge and the Reinga Ridge during the Miocene could have permitted at least intermittent land connections between New Zealand and New Caledonia until the late Tertiary. Molecular stud-

ies seem to support this explanation for New Zealand cicadas (Arensburger et al., 2004).

CONCLUSIONS

Unlike in the Northern Hemisphere, biogeography in the Southern Hemisphere is characterized by significant hierarchical distribution patterns. However, these patterns are different in the animals and plants we studied. In the animal groups, the distribution patterns largely conform to the geological breakup of Gondwana, particularly the SGP, and appear to have been generated by geologically induced vicariance. In the plants we studied, however, the hierarchical patterns, e.g., the PSP and the ISP, are incongruent with the commonly accepted sequence of geological events and have apparently been shaped by concordant dispersal and extinction events. In many of the plant groups, it appears that old, geologically induced vicariance patterns have been obscured by more recent dispersal. The resistant dispersal stage of plants (the seed) may facilitate colonization events, making plants less constrained by geological history than are many groups of animals.

When organism distributions are fitted onto a geologically based area cladogram, several types of concordant dispersal patterns emerge. The animal data set is dominated by trans-Antarctic dispersals, i.e., faunal links between South America and Australia that cannot be explained by vicariance. This pattern is presumably due to the long period of geological contact between Australia and South America via Antarctica. In plants, however, there has been a lot of exchange between landmasses that were not connected at the time, for instance, trans-Tasman dispersal between Australia and New Zealand. Both animal and plant data sets point to the hybrid nature of the South American biota, with surprisingly few dispersals between tropical and temperate regions of the continent. New Caledonia and New Zealand appear to have retained few old Gondwanan lineages, particularly those of plants.

Although our results clarify some points concerning Southern Hemisphere biogeography, many questions remain to be answered. Further studies should provide additional resolution by further development of the analytical tools, by expanding the data sets to include more groups and more completely resolved phylogenies, by incorporating the fossil distributions into the phylogenies (Manos, 1997; Swenson et al., 2001), and by dating the pylogenetic events in order to discriminate between different biogeographic scenarios (Sanmartín et al., 2001).

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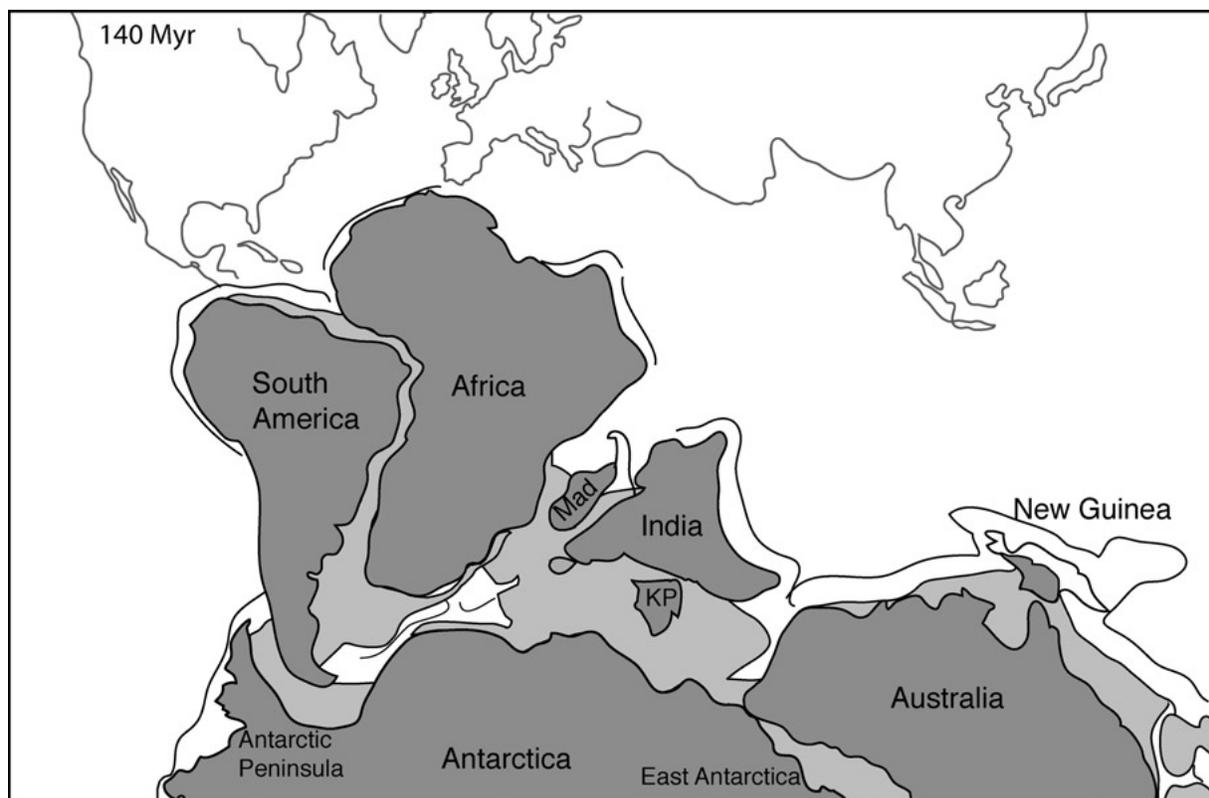
Late Jurassic reconstruction of the southern continent Gondwana in mercator projection (major source and symbols as in Fig. 2). KP-Kerguelen Plateau.