



Extent and timing of floristic exchange between Australian and Asian rain forests

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ABSTRACT

Aim We tested an entrenched concept – that the Australian rain forest flora is essentially a Gondwanan relict. We also assessed the role of regional-level source–sink dynamics in the assembly of this flora.

Location Eastern Australia.

Methods To avoid potential biases inherent in selective studies undertaken to date, we used an analytical, whole-of-flora approach integrated with the fossil record. We identified disjunctions between woody Australian rain forest plant taxa and relatives on other land masses. To test the strength of the fossil evidence for the regional antiquity of this flora, we evaluated the proportion of these disjunct clades represented in the Australian fossil record, and to minimize the effects of biases in this record, we compared late Quaternary (i.e. late Pleistocene and Holocene, 126–0 ka), Pliocene and late Oligocene–early Miocene Australian pollen records interpreted as tropical rain forest. Using within-species disjunctions as a proxy, we assessed the role of recent immigration from Asia into Australia. To assess the role of source–sink dynamics, we performed comparative analyses of disjunctions in major rain forest categories representing a north–south/climatic gradient.

Results Southern Australian, cool temperate (microthermal) rain forests contain many floristic disjunctions with Gondwanan fragments and most of these clades have Gondwanan fossils. Disjunct clades in Australian mesothermal rain forest mostly occur in Asia/Malesia and a low proportion of these clades show pre-Neogene records. Many clades in lowland tropical and ‘dry’ rain forest show disjunctions with Asia/Malesia and few have Australian fossil records. Rates of recent immigration from Asia/Malesia are high in these northern forests, and outweigh rates of recent emigration approximately nine-fold. The late Quaternary fossil record has many more rain forest angiosperms than Oligocene–Miocene and Pliocene floras, consistent with extensive late Cenozoic immigration.

Main conclusions The microthermal rain forests are largely Gondwanan relicts, but there is progressively greater, and more recent contribution from Asia/Malesia into more northern, and more lowland tropical rain forests. This variation reflects a strong gradient in geographic and ecological proximity between these forests and source floras in Asia/Malesia, and is consistent with a source–sink size model of immigration driven by late Cenozoic contractions and expansions of Australian rain forest.

Keywords

Australia, biome assembly, Cenozoic, disjunction, fossil record, macrofossils, molecular phylogeny, pollen, rain forest, tropical forest.

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INTRODUCTION

The origins of the Australian flora have been central to the development of ideas about historical biogeography and the assembly of biotas (Raven & Axelrod, 1974). This flora provides a natural experiment showing the interactions of ancient continental breakup, extended isolation, collision of continents and climatically driven extinction and speciation. Under current knowledge, the sources of this flora may include *in situ* origins from Gondwanan stock, immigration from Asia/Malesia since the Australian plate began to converge with the Sundaland Block approximately 25 million years ago (Ma), and immigration via transoceanic dispersal (Fig. 1). However, interpretations of the relative importance of these sources have varied over the past 150 years.

Prior to the era of plate tectonics, the views of Hooker (e.g. 1860) dominated ideas about the assembly of the Australian flora. Hooker interpreted the southern, cool temperate rain forests as 'Antarctic' in affinity and the northern, tropical rain forest as 'Indo-Malayan'. By comparison with the distinctive sclerophyllous flora, which was thought to be ancient in origin, rain forest groups were considered relatively recent migrants into Australia (Burbidge, 1960; reviewed by Barlow, 1981). However, plate tectonic reconstructions imply that Australia had maintained continuity with East Antarctica until the late Eocene, followed by a period of physical isolation as the continent drifted northwards, until making contact with Southeast Asian terranes no later than the early–middle Miocene (Hall, 2002). By the 1970s, this tectonic framework, combined with evidence that Late Cretaceous and Palaeogene fossil floras contained many taxa still present on temperate Southern Hemisphere land masses, fuelled the idea that Australia's cool temperate rain forests were living examples of the Gondwanan biota (Barlow, 1981), and that Australia's sclerophyllous flora was younger, having largely evolved from this ancient flora.

These ideas encouraged similar attempts to re-evaluate the origins of Australia's tropical rain forests in terms of Gondwanan inheritance (Barlow, 1981; Webb *et al.*, 1984,

1986). A high proportion of northern Australian rain forest taxa have genus- or species-level disjunctions with other tropical regions, which had long been interpreted as evidence for recent biotic exchange (Burbidge, 1960). However, Webb *et al.* (1984, 1986) argued that these disjunctions were products of ancient, Pangaeian vicariance. Truswell *et al.* (1987) used fossil pollen evidence to test the idea that Australia's tropical rain forest flora was assembled through late Miocene migration from Southeast Asia following contact of the Australian plate with the Sunda Arc. They argued that there was negligible evidence for palynological change between pre-contact and post-contact Australian fossil records of tropical/subtropical rain forest, and concluded that immigration from Southeast Asia had been minimal over the last 15 Ma. In combination with the work of Webb *et al.* (1984, 1986), this conclusion helped establish a view that both temperate and tropical rain forest types represent little-changed relicts of a formerly widespread Gondwanan biota (Barlow & Hyland, 1988).

Despite the persistence of the concept of *in situ* origins of Australian tropical rain forest (Stork *et al.*, 2008), dated molecular phylogenetic analyses provide evidence for some Neogene migration in both directions between Australian and Asian/Malesian rain forest. Thus, ancestral state analysis suggests an Australian origin, followed by Neogene migration into Asia for *Helicia* (Proteaceae) (Sauquet *et al.*, 2009) and Asian members of Loranthaceae (Vidal-Russell & Nickrent, 2008a,b). Evidence for Neogene movement into Australian rain forest was presented for *Aglaia* (Meliaceae; Muellner *et al.*, 2008), *Livistona* (Arecaceae; Crisp *et al.*, 2010), Aurantioideae (Rutaceae; Pfeil & Crisp, 2008), and *Pseuduvaria* (Annonaceae; Su & Saunders, 2009).

These studies of the assembly of the rain forest flora have, however, been restricted in scale; they have used exemplar approaches, investigating small subsets of the biota (often families or genera and occasionally multiple groups of organisms). Although useful in testing specific hypotheses, these studies may provide biased representations of the whole biota. For example, many studies of dispersal have focused on

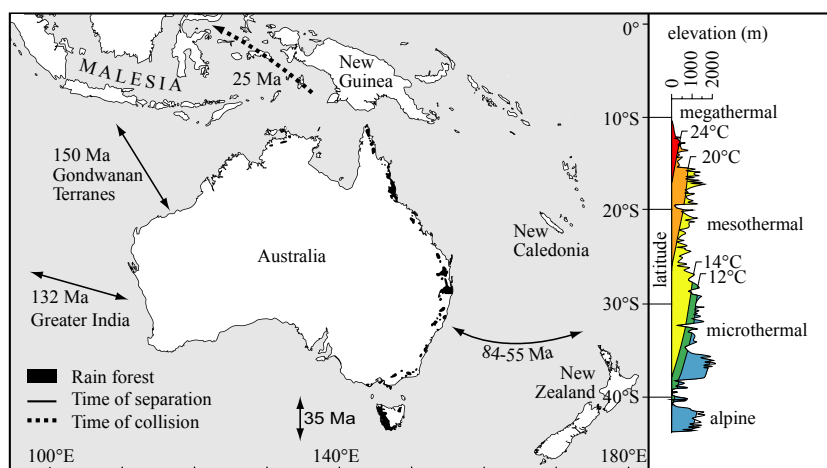


Figure 1 Left panel: The Australian region with areas of rain forest shaded. Arrows show times of divergence (solid arrows) and convergence (dashed arrows) between land masses (McLoughlin, 2001; Hall, 2002). Right panel: elevation profile along the eastern Australian margin and the distribution of bioclimatic classes defining major rain forest types (Nix, 1991).

groups that had been thought to have poor dispersal ability (e.g. *Nothofagus*; Cook & Crisp, 2005). In addition, molecular studies imply that many patterns of biogeographic disjunction are complex, leading to ambiguous inferences of polarity (e.g. Richardson *et al.*, 2004), which can be exacerbated by biases caused by extinction (Kodandaramaiah, 2010). However, improved information on the composition of floras, combined with the proliferation of molecular phylogenies and accumulated knowledge of the fossil record, make it possible to investigate whole biotas in contemporary analytical frameworks that have the potential to circumvent such biases.

Here, we re-assess the assembly of the Australian rain forest flora, using a whole-of-flora approach. We focus on rain forest biomes because they are relatively well studied taxonomically, and because they have been interpreted as evolutionary and ecological relicts with high conservation significance (Stork *et al.*, 2008). We compiled a comprehensive list of clades in the Australian woody rain forest flora that show biogeographic disjunctions with other land masses, and located the oldest Australian fossils that can be associated with these disjunct clades. To identify broad spatio-ecological patterns in the assembly of rain forest, we classified these disjunct clades according to major rain forest type. We tested explicit hypotheses that assess whether these rain forest disjunctions reflect migration in or out of Australia, and whether these migration events occurred relatively recently (i.e. following Miocene contact of Australia and Asia) or are likely to reflect Gondwanan inheritance. To test whether there has been extensive recent immigration from Asia/Malesia we used within-species disjunctions as a proxy for rates of recent migration (on the assumption that these disjunctions are relatively young), and polarized these disjunctions into inferred immigrations, emigrations and ambiguous movements. To test whether the fossil record supports the concept of antiquity of rain forest types, we analysed how many disjunct clades in different rain forest types are represented by fossils of different ages. Because strong taphonomic filters prevent the majority of taxa in any flora from being represented in the fossil record (Kidwell & Flessa, 1995), our compilation of fossil records of rain forest disjunct clades may in part represent a comparison of neocological apples with palaeoecological oranges. Therefore, in a reassessment of the comparison undertaken by Truswell *et al.* (1987), we compare a late Quaternary Australian tropical rain forest palynoflora with late Oligocene–early Miocene and Pliocene palynofloras representative of tropical rain forest.

MATERIALS AND METHODS

Identifying disjunctions

To identify biogeographic disjunctions we first compiled a list of trees, shrubs, vines and mistletoe species in Australian rain forest (see Appendix S1 in Supporting Information). We segregated this list into more than 1000 clades defined by disjunctions between Australian rain forest taxa and their non-

Australian closest relatives on any other land mass. Because the island of New Guinea is connected to Australia when sea levels are low and is partly a Gondwanan fragment (Hall, 2002), taxa shared between Australia and New Guinea were not counted as disjunct clades unless the taxon extended beyond those land masses. Wherever possible, molecular-based phylogenies were used to identify the disjunctions. There was some molecular phylogenetic evidence for approximately 60% of the disjunctions above the species level. Other disjunctions were identified on the basis of traditional taxonomy – a disjunction was assumed when the same taxon occurred in Australian rain forest and in any vegetation type outside Australia/New Guinea. Disjunctions were divided into two categories: those with Asia/Malesia; and those with southern continents, the Neotropics and/or Pacific islands. This distinction was unambiguous in all but two cases (*Quintinia* and *Pittosporum*). To give unbiased estimates of the number of disjunctions, one of these was allocated to Asia/Malesia and the other to the second category.

The disjunct clades were segregated into five categories representing the diverse array of Australian rain forest types (microthermal; mesothermal; lowland tropical; dry types; littoral and mangrove). The last four categories were forced to be mutually exclusive, but a small number of disjunct clades were attributed to both mesothermal and microthermal types, because their artificial exclusion from one rain forest type or the other would strongly bias our analysis of the relatively species-poor microthermal rain forest flora. In Australia, rain forest is considered to be fire sensitive, usually closed-canopy forests as distinct from the more widespread fire-dependent forests that are typically sclerophyllous and open canopied (Bowman, 2000). As such, rain forest in Australia encompasses not only closed, moist forests such as microthermal, mesothermal and lowland tropical types, but also drier types (Bowman, 2000). We tested the fossil histories of these bioclimatically and edaphically defined rain forest types separately because Webb *et al.* (1986) argued that they had distinctive floras as a result of long periods of ‘climatic and edaphic sifting’. Following the bioclimatic classification of Nix (1991), microthermal rain forest taxa are those that occur at mean annual temperatures (MAT) ≤ 12 °C. These represent cool temperate rain forests and occur in Tasmania and south-eastern and eastern Australia. These forests extend to sea level in the south but are restricted to high elevations (typically > 1000 m) in the northern parts of this range. Mesothermal rain forest taxa occur under MAT *c.* 14–20 °C. These include species occurring in well-developed rain forest (as defined by Hyland *et al.*, 2002) at elevations above 750 m in far north Queensland or at lower elevations further south. Although many clades within this group descend to lower elevations in far north Queensland, these clades were excluded from our lowland tropical rain forest category, which is a well-defined group of far north Queensland taxa confined to well-developed rain forest below 750 m in elevation, equivalent to the mesotherm–megatherm interzone (MAT 20–24 °C) and megatherm zone (MAT > 24 °C) of Nix (1991). Dry rain forest

types were defined as taxa that occur in monsoon forest, dry rain forest, thicket or other relatively open or dry habitats, but not in well-developed rain forest. Mangrove and littoral rain forest were defined as clades restricted to these habitats.

For microthermal rain forests, the disjunctions could be confidently identified because this vegetation type is species poor and well studied phylogenetically. However, more ambiguity occurs in our list of disjunctions for the other rain forest types, which are species rich (>2200 species), and phylogenetically less well studied. Multiple disjunctions may have been missed within some clades, and some disjunctions may have been falsely identified due to mistakenly assuming the monophyly of genera or species. However, progressive addition of phylogenetic evidence to the data during the development of this project showed a trend of slightly increasing the number of disjunctions. Considering the very large sample size (c. 1000 disjunctions), this means that the overall biases are likely to be relatively small and unlikely to alter the overall inferences.

Intraspecific disjunctions with Asia/Malesia were taken as evidence for recent migration either into or out of Australia. We estimated the polarity (direction of migration) of these disjunctions by assuming the monophyly of the disjunct species and of the genera, or higher taxa, to which they belong. Disjunct species with no congeners endemic to greater Australia (including New Guinea) but with non-Australian congeners in Asia/Malesia were considered to be immigrants into Australia. Conversely, disjunct species with endemic congeners in greater Australia but not in Asia/Malesia were considered migrants from Australia into Asia/Malesia. Other cases are treated as ambiguous, even in groups generally considered to be 'Australian' or 'Asian'. We excluded the possibility of ancient vicariance following parallel reasoning to that of Jordan (2001), who argued that intra-species vicariance would require that disjunct populations either remained very similar or evolved in parallel since the time of discontinuity. This appears extremely unlikely considering that the youngest Gondwanan terranes contributing to the Southeast Asian tectonic composite rifted from Gondwana by the Late Jurassic and India became disjunct from Gondwana by the Early Cretaceous (McLoughlin, 2001).

Linking disjunctions to the fossil record

We compiled a database of Australian plant fossils by surveying published Late Cretaceous and Cenozoic pollen and macrofossil records (Appendices S1 and S2), and evaluated the proportion of disjunct clades in each rain forest type that is represented by fossils. Presence of fossils of a clade in Australia provide evidence for antiquity of that clade in the region (though this evidence can be ambiguous because of regional extinction and subsequent recolonization; see Jordan *et al.*, 2010). Because of ambiguity in the identification of fossils, it was not possible to link all relevant fossils to specific disjunct clades. In these cases, a fossil type was used as supporting evidence for only one disjunction (Jordan *et al.*,

2010), selected to be the clade with the greatest number of species endemic to Australia/New Guinea. This rule assumes that clades with long histories in a region are likely to have more species in that region than recently arrived clades. Preferential extinction and recent radiation of clades would mean that this assumption may not be satisfied. However, the rule should not create a significant bias in the patterns of disjunctions versus fossil first appearances for the different vegetation types. There will be a small potential bias in the patterns of numbers of species versus fossils towards overestimation of the number of species associated with older fossil records. It is worth noting that Australian macrofossil floras include many unidentified leaves, and that future work may reveal the Palaeogene presence of additional extant Australian rain forest taxa. However, refinement of older palaeobotanical work has in some cases reduced the perceived phylogenetic extent of the Palaeogene flora rather than increased it. For example, Carpenter *et al.* (2006) showed that Eocene *Parafatsia*, which had previously been interpreted as an extinct genus of Araliaceae with affinities to Japanese *Fatsia*, was an unusual member of the Proteaceae.

In order to assess whether our estimates of migration direction applied in deeper time, we compared palynological diversity of Australian late Quaternary, Pliocene and late Oligocene–early Miocene pollen records considered to represent mesothermal (tropical) rain forest (Appendix S3). The late Quaternary records were derived from Lynch's Crater (Kershaw *et al.*, 2007) and other north-east Australian upland rain forest pollen assemblages (Kershaw, 1975; Haberle, 2005). The Pliocene record was from Butchers Creek, north-east Australia (Kershaw & Sluiter, 1982). The late Oligocene–early Miocene records were from sources given in Appendix S3. Our analysis differs from that of Truswell *et al.* (1987), in that those authors only considered a selective sample of the Latrobe Valley coal pollen flora in south-eastern Australia, whereas we expanded the scope to include all published Australian late Oligocene–early Miocene pollen records of rain forest taxa known to us. However, it is worth noting that all but 12 of these taxa were present in the brown coal record of Blackburn & Sluiter (1994). We also segregated the records into an 'ancient' group of pollen types, produced by taxa for which macrofossils provide independent evidence of a Palaeogene presence in Australia (conifers, cycads, *Nothofagus*, Myrtaceae, Cunoniaceae, Elaeocarpaceae, Casuarinaceae, *Diospyros* and Proteaceae); and another group representing all other angiosperms. Although fossil pollen records are biased in favour of wind-dispersed taxa, this bias should affect late Quaternary and late Oligocene–early Miocene fossil floras equally.

Statistical analyses

Logistic regression was used to test if the total number of disjunctions varied among rain forest types. Two-way contingency tests were used to determine whether the proportion of northern disjunctions and within species disjunctions varied among the five rain forest types. Tests of immigrant versus

emigrant lineages were restricted to within species disjunctions with Asia/Malesia and excluded microthermal rain forests, which showed no within-species disjunctions. Logistic regression was used to test whether the total number of immigrants exceeded the number of emigrants, and two-way contingency tests were used to assess whether the proportion of immigrants varied among rain forest types. A two-way contingency test was used to determine whether the groups with Palaeogene macrofossil records showed greater proportions of extant pollen types first appearing in the late Oligocene–early Miocene floras than groups without Palaeogene records. These tests were performed using JMP v. 7.0 (SAS Institute Inc. Cary, NC, USA). Differences among rain forest types in the median time of first appearances of fossils were assessed using the nonparametric test of medians implemented in the NPAR1WAY procedure of SAS v. 9.2 (SAS Institute Inc.). Where appropriate, pairwise tests between forest types were made, with probabilities adjusted for multiple comparisons using the Dunn–Sidak method (Sokal & Rohlf, 1995).

RESULTS

Disjunction patterns and the extent of their fossil representation clearly differ between microthermal and all other rain forest types (Fig. 2). The proportion of northern disjunctions in each rain forest type was highly significantly different ($\chi^2_1 > 13$; $P < 0.01$; adjusted for multiple comparisons) from that in each other rain forest type, with the exception that dry rain forest was not significantly different from lowland rain forest ($\chi^2_1 = 0.03$; $P > 0.05$). Microthermal and mesothermal rain forests showed highly significantly different proportions of within-species disjunctions ($\chi^2_1 > 15$; $P < 0.001$; adjusted for multiple comparisons) from all other vegetation types, but the proportions in lowland rain forest, dry rain forest and mangroves/littoral forests were not significantly different from each other ($\chi^2_1 < 1.9$; $P > 0.05$; adjusted for multiple comparisons; Fig. 2). In terms of within-species northern disjunctions, the numbers of immigrant lineages highly significantly outnumbered emigrants ($\chi^2_1 = 134$; $P \ll 0.001$), and the proportion of immigrants did not vary significantly among the four northern rain forest types ($\chi^2_1 < 3$; $P > 0.05$; adjusted for multiple comparisons; Fig. 3).

The median time of first appearances of clades in the fossil record varied highly significantly among all but three pairs of vegetation types ($\chi^2_1 > 5.6$; $P < 0.001$; adjusted for multiple comparisons). The three exceptions were that dry rain forests were marginally significantly different from mangrove/littoral forests ($\chi^2_1 = 2.9$; $P < 0.05$; adjusted for multiple comparisons); mangrove/littoral forests were not significantly different from lowland rain forests ($\chi^2_1 = 1.7$; $P > 0.05$); and lowland rain forests were not significantly different from dry rain forests ($\chi^2_1 = 1.1$; $P > 0.05$; Fig. 4).

Few disjunctions were inferred in microthermal rain forest clades. All of these disjunctions were above species level; most were with other Southern Hemisphere land masses, and most had ancient histories in Australia, with 27 out of 47 of the

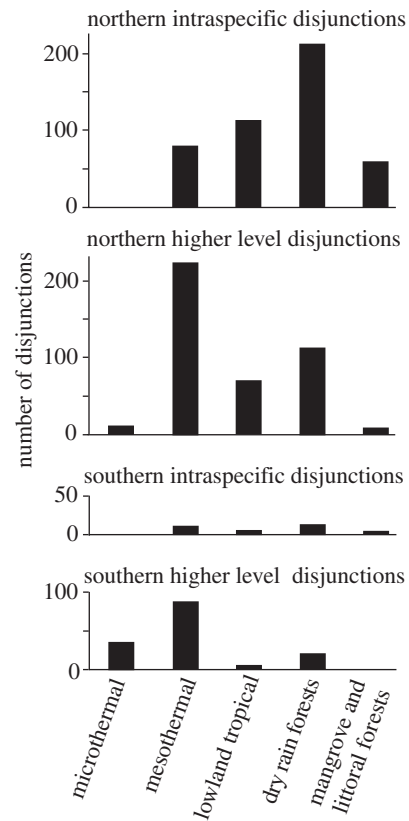


Figure 2 The number of disjunctions within microthermal, mesothermal, lowland tropical, dry and mangrove/littoral rain forest types in the Australian region. Each column is subdivided to show the proportion of the disjunctions that are with northern versus southern land masses, and the proportion that are within species or at higher taxonomic levels.

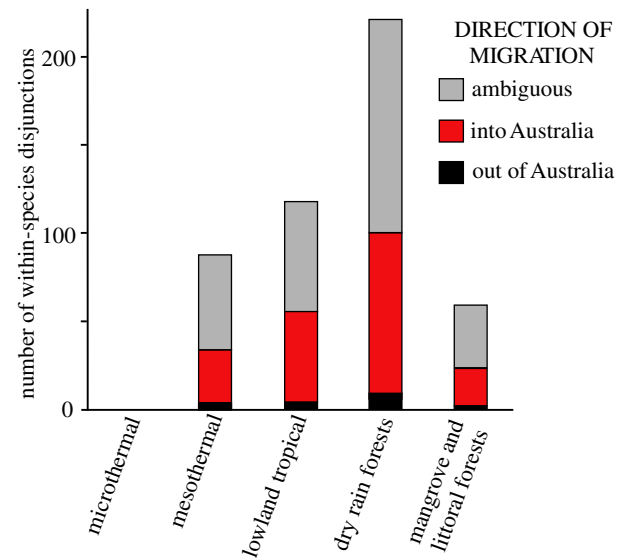


Figure 3 Within species disjunctions between Australian and Asia/Malesian rain forest types categorized according to direction of migration.

clades represented by Palaeogene fossils and 19 of them pre-dating the last possible connection with Gondwana at the end of the Eocene, approximately 34 Ma (Fig. 4). Microthermal rain forest taxa with good fossil evidence for antiquity include many 'classic' Southern Hemisphere groups, such as *Nothofagus* (Hill, 1991), southern conifers (Hill & Brodribb, 1999) and Cunoniaceae (Barnes *et al.*, 2001).

In contrast, the four 'tropical' and 'subtropical' rain forest types included 1019 disjunctions (Fig. 2), of which 85% were with Asia/Malesia, and 48% were within-species. Of 464 within-species disjunctions with Asia/Malesia, over one-third were inferred as being immigrants into Australia, but only 4% as migrations out of Australia (Fig. 3). Furthermore, fossils provide evidence for the pre-Pleistocene presence of only

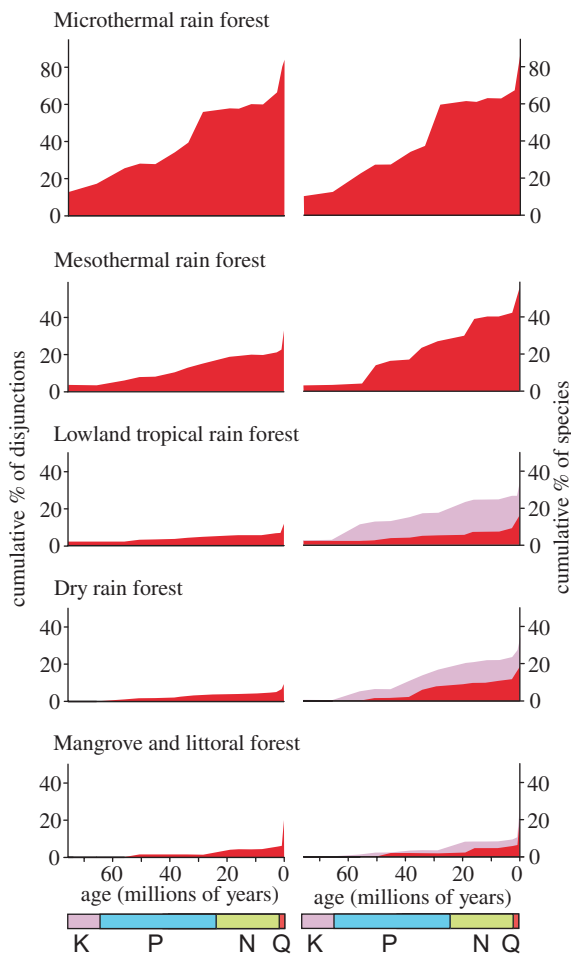


Figure 4 Percentage of disjunct clades (left) within each rain forest type that are represented in the Australian pollen and macrofossil record, in time bins defined by the Gippsland Basin pollen stratigraphy. Percentages of species represented in these clades are indicated on the right. The darker shaded area represents the numbers of species represented in those clades. For each forest type, the lighter shaded area represents additional species that are in disjunct clades assigned to different forest types. In the time scale; K, Cretaceous; P, Palaeogene; N, Neogene; Q, Quaternary.

about one clade in nine, and less than 7% have fossil evidence supporting an age in Australia of more than 34 Ma (Fig. 4). Among northern forest types, the mesothermal rain forests have the strongest fossil record (32% of the disjunct clades), the smallest proportion (23%) of within-species disjunctions and the highest representation of southern disjunctions (often with Gondwanan fragments). The other northern Australian rain forest types have very little fossil representation and high proportions of within-species disjunctions.

In terms of number of species, the proportion of the flora explained by fossils increased considerably for mesothermal, lowland tropical and dry rain forests, but was still less than one in three for mesothermal rain forest species, and considerably less for lowland tropical and dry rain forests (Fig. 4). More than half of the lowland tropical species were counted in mesothermal clades, increasing the proportion of this forest type explained by fossils. However, even including these, only 16% had Palaeogene records (lighter shaded areas in Fig. 4). The pattern in dry rain forest types showed even lower fossil representation than the lowland rain forest.

Comparison of late Quaternary, Pliocene, and late Oligocene–early Miocene rain forest palynofloras (Fig. 5 and Appendix S3) shows that 55.5% of the 166 pollen types have their first appearance in the late Quaternary or Pliocene palynoflora. Furthermore, there was a major difference between the group of taxa with independent evidence of antiquity and the group with no such record. Of the 38 pollen types in groups with Palaeogene macrofossil records, 19 (50%) were absent from the late Quaternary palynoflora, and 32 (84%) had been present since the late Oligocene. By contrast,

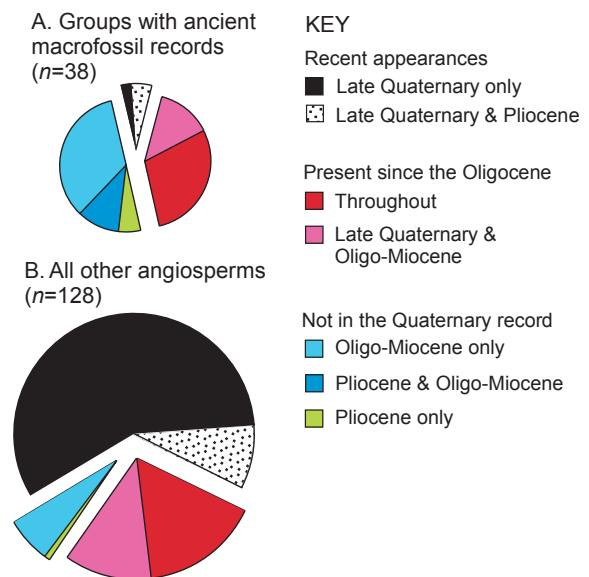


Figure 5 Comparison of late Quaternary, Pliocene and late Oligocene–early Miocene Australian rain forest palynofloras. Pie charts show the percentages of pollen types with Palaeogene macrofossil records, versus all other angiosperms. Numbers of pollen taxa (*n*) are noted.

the larger 'other angiosperms' group (128 types) was dominated by pollen taxa with first fossil appearances in either the Pliocene or the late Quaternary record (86 types, or 67%). Hence the majority of the late Quaternary palynoflora was not recorded in the late Oligocene–early Miocene palynoflora. The proportion of extant pollen types with recent (Pliocene or late Quaternary) first appearances was very highly significantly lower ($\chi^2_1 = 21.4$; $P \ll 0.001$) in the group of taxa with Palaeogene macrofossil records than in the taxa without such records. These comparisons suggest that late Quaternary tropical rain forest includes only a relatively small group of taxa which have been present in the region since at least the late Oligocene–early Miocene, and a much larger group that appear to have been present only since the Pliocene or Quaternary, implying that the floristic composition of extant northern Australian rain forest floras is partly a product of relatively recent additions through migration.

DISCUSSION

Our analyses provide evidence for a geographic/climatic trend in which rain forests in low elevation, low latitude regions show younger and less comprehensive fossil records, many more intraspecific disjunctions and more evidence for recent immigration than rain forests of colder and/or more southern regions.

Evidence for immigration from Asia

The presence of 462 intraspecific disjunctions is clear evidence for extensive recent interchange between Asia/Malesia and northern rain forest types (Fig. 2). This is 46% of the disjunctions inferred for these vegetation types, and represents approximately 21% of the species in these vegetation types. Most of this movement involved migration into Australia, inferred immigrations outnumbering emigrations more than nine-fold. The timing of these immigrations is difficult to quantify, but it is reasonable to assume that they are late Neogene or Quaternary. Although a small number may be anthropogenic, resulting from accidental or deliberate transport by indigenous peoples, we excluded such species where possible (e.g. Bean, 2007). Compared to lowland tropical, dry and mangrove/littoral forests, recent immigration appears to have made a smaller contribution to mesothermal rain forest, with only 9% of the species showing within species disjunctions. Consistent with expectations, there was no evidence for recent interchange of microthermal rain forest with any extra-Australian region.

The analyses of fossil evidence for disjunct clades are also consistent with significant immigration into northern Australian rain forest from Asia/Malesia, particularly in lowland tropical, dry rain forests and mangrove/littoral forests. Thus, of the small proportion (10%) of the disjunct clades in the four 'tropical/subtropical' Australian rain forest types identified as having Palaeogene fossil records, almost three-quarters were from mesothermal rain forest. In contrast, microthermal rain

forest disjunct clades are well represented by fossils, with many Palaeogene records, most of which pre-date the final rifting of Australia from Antarctica in the late Eocene. However, groups can be present within a region long before they are represented as fossils, and the flora present in the Palaeogene may have included clades represented by no, or only recent, fossils. Furthermore, the impact of this incompleteness of the fossil record may vary among rain forest types, with, for example, biases against preservation of fossils from dry environments reducing the representation of dry rain forest types. However, our comparison of late Quaternary, Pliocene and late Oligocene–early Miocene rain forest palynofloras reinforces the evidence for immigration. These results indicate a substantial increase in rain forest palynological richness between the relatively depauperate late Oligocene–early Miocene and Pliocene palynofloras, and the much richer late Quaternary record, which suggests that considerable enrichment of the mesotherm angiosperm rain forest flora has occurred subsequent to deposition of the Pliocene record. This conclusion differs from that of Truswell *et al.* (1987) because they compared only a subset of pollen types in these records.

In situ components of the rain forest flora

The fossil record suggests deep histories for many microthermal rain forest clades. Furthermore, approximately half of the remaining disjunct clades, with first appearances post-dating the break-up of Gondwana or with no record at all, almost certainly evolved *in situ* because they are embedded in Australia-centred groups with strong local fossil records (e.g. Cunoniaceae, Proteaceae and Elaeocarpaceae: Appendix S1). In summary, the microthermal rain forest flora can for the most part be referred to as 'Gondwanan' in origin. However, some records (e.g. late Eocene *Coprosma*, Rubiaceae) may represent Palaeogene long-distance dispersal events from elsewhere in the Southern Hemisphere, as they have no older Australian fossil record at higher taxonomic level and belong to lineages that radiated during the Palaeogene (Bremer & Eriksson, 2009). Additionally, it remains possible that some important clades only reached Australia late in the history of the supercontinent. For example, phylogenetic evidence indicates that the sister of the Australian-centred epacrid clade (Ericaceae subfamily Styphelioideae) is subfamily Vaccinioideae (Kron *et al.*, 1999), which is Northern Hemisphere-centred, apart from some highly derived taxa (Bush *et al.*, 2009). Macrofossil evidence shows the presence of at least two lineages of epacrids in Australia in the early Oligocene, well before contact between Australia and Southeast Asia (Jordan & Hill, 1996). Molecular estimates for the stem age of Styphelioideae are much too young to be explained by Pangaean vicariance (Wagstaff *et al.*, 2010). As such it is reasonable to hypothesize that Styphelioideae arrived in Australia by long-distance dispersal during the Cenozoic. An alternative of dispersal northwards is much more complex because the family is well represented in the Cretaceous and Cenozoic fossil record of the Northern Hemisphere. Fossil pollen of Ericaceae

does occur in Australia in the Late Cretaceous (Dettmann, 1994), but there is no reason to assign it to Stypelioideae in preference to other clades of that family (Jordan *et al.*, 2010).

The fossil representation of disjunct clades confirms that extant Australian mesotherm rain forest includes a significant number of lineages that were present on the continent during the Palaeogene. Furthermore, the incompleteness of the fossil record means that it is likely that some other modern Australian rain forest lineages were present in the Palaeogene but either left no fossils, or the fossils remain unidentified. However, the contrasts between late Palaeogene and Quaternary pollen floras (Fig. 5), argue in favour of the general pattern of late appearance of many rain forest groups. As noted for microthermal clades, some of the clades with only relatively young fossil records (e.g. *Acmena*, Myrtaceae) are likely to represent *in situ* radiations. For others (e.g. *Acronychia* and *Melicope*, Rutaceae) that are members of families with no Australian Palaeogene fossil record, it is unclear whether their appearance represents long-distance dispersal events or radiation within older, palynologically undetected lineages.

Some of the mesothermal rain forest clades represented in the fossil record (e.g. in Elaeocarpaceae, Myrtaceae, Proteaceae and Cunoniaceae) include relatively large numbers of Australian rain forest species (Fig. 4). As such, we estimate greater proportions of species in the rain forest represented by old fossils than the corresponding proportion of disjunctions. However, these species still represent only a minority of the species in modern northern Australian rain forest, particularly as the method used here tended to slightly overestimate this component. This may partly explain the difference between our conclusions and those of Truswell *et al.* (1987). Those authors emphasized the broadly similar pollen percentages of taxa shared by the late Oligocene–early Miocene and late Quaternary records, which reflects a consistent role of some angiosperm taxa such as Elaeocarpaceae and Cunoniaceae in mesotherm forests throughout most of the Cenozoic. However, Truswell *et al.* (1987) de-emphasized differences between the late Quaternary and older pollen records, though some pollen types achieve relatively high percentages in the late Quaternary records but are rare in (e.g. Arecaceae, *Rapanea*, Moraceae/Urticaceae), or absent from (e.g. *Trema*, *Argyrodendron*, *Ficus*, *Olea*, Hamamelidaceae, *Orianopsis*, *Myrsine*, *Hodgkinsonia*) the older records.

In contrast, our evidence strongly suggests that most of the clades restricted to the other three northern Australian forest types (lowland tropical rain forest, dry rain forest and mangrove/littoral forests) migrated recently from Asia/Malesia. However, these rain forests also contain many species from clades in which mesothermal disjunctions were inferred, and some of these clades have much longer histories in Australia (Fig. 4).

A model for patterns of immigration

We suggest that changes in Australia's climate and geography during the Neogene may explain the extensive recent migra-

tion from Asia/Malesia into Australia. The previously widespread Australian rain forest underwent extreme spatial reduction during the Neogene, and particularly the Quaternary (Kershaw *et al.*, 1994; Sniderman *et al.*, 2007) whereas the Malesian rain forest has remained extensive and diverse throughout that period (Morley, 2000). Hence, in the early–mid Neogene, Australia and Malesia may have contained similar area of rain forest, but given that Australia was *c.* 10° further south than today (Hall, 2002), invasions in either direction may have been infrequent and equally likely. As Australia approached Malesia in the late Neogene and its rain forests shrank (Kershaw *et al.*, 2005), source–sink dynamics would favour migration from the relatively stable, large area of Malesian rain forest, towards the increasingly unstable, relatively small area of Australian rain forest. In particular, rapidly expanding small populations may be particularly vulnerable to immigrants (Hubbell, 2001). Repeated phases of expansion and contraction in Australian lowland tropical rain forest (Hilbert *et al.*, 2007) would have provided opportunities for such invasion.

Furthermore, very little habitat for the clades currently restricted to lowland rain forest may have been available in Australia until approximately 1 Ma. Reconstructed sea-surface temperatures in the Coral Sea adjacent to north-east Queensland were *c.* 20 °C for much of the last 10 million years (Myr) and rose above *c.* 24 °C only in the middle Pleistocene, *c.* 0.7 Ma (Isern *et al.*, 1996). If regional air temperatures were correspondingly *c.* 3–4 °C lower than today during most of the past 10 Myr, the lower temperature limit of the meso–megatherm interzone (20 °C MAT) of Nix (1991) would have occurred close to sea level, making little area available for lowland tropical rain forest. As regional temperatures increased during the middle Pleistocene, climate became at least intermittently favourable for lowland Asian/Malesian taxa adapted to MAT > 20 °C. Our analyses of disjunctions suggest that newly available, warm climate habitats in north-eastern Queensland were colonized by taxa from the nearby, diverse equatorial Malesian flora as frequently as or more frequently than by taxa from the local mesotherm rain forest flora, consistent with widespread evidence for the importance of phylogenetic biome conservatism (Crisp *et al.*, 2009). These results therefore argue against previous assertions (Truswell *et al.*, 1987; Kershaw *et al.*, 2005) that there was no large scale late-Neogene enrichment of the Australian tropical rain forest flora.

We argue, therefore, that there has been extensive immigration into Australian rain forest, and propose that this process was controlled by proximity and sizes of sources, particularly Asia/Malesia, and driven by fluctuating size of the sink. The historical variation among rain forest types appears to be the consequence of differences in ecological and geographic isolation determining levels of biotic interchange. Potential sources for the microthermal clades in southern Australia and high elevation eastern Australia occur in distant and small places such as New Zealand and subalpine Malesia. Consistent with this, microthermal rain forest is dominated by

lineages that were *in situ* from at least the time of Gondwanan breakup. Mesothermal clades in high elevation northern Queensland and lower elevation eastern Australia are closer to larger areas of analogous climate in mid-elevation areas of Malesia, and our results imply that these rain forests represent a composite of *in situ* taxa and a significant immigrant component. Finally, the lowland tropical, dry rain forest and coastal/mangrove forests are much less isolated from regions of analogous climate, with extensive areas proximate in Malesia, and these floras appear to be dominated by geographic immigrants from Asia/Malesia and by 'ecological immigrants' from older mesotherm Australian rain forest, as represented in our mesothermal rain forest category. Thus, the assembly of northern Australian rain forest floras appears to reflect a Cenozoic history of episodic, small-scale enrichment that accelerated dramatically in the geologically recent past, perhaps as recently as the Pleistocene. Overall, these results suggest that the meeting of Australia and Asia resulted in considerable biotic exchange, and that in broad terms, the rates of exchange can be explained by simple processes, including source-sink dynamics, and proximity of suitable habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Estimated disjunctions between Australian rain forests and extra-Australian land masses.

Appendix S2 Age classes used for analyses of fossils.

Appendix S3 Pollen types found in the late Oligocene–early Miocene, Pliocene and late Pleistocene records.

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