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SPECIAL PAPER

Panbiogeography of New Caledonia, south-west Pacific: basal angiosperms on basement terranes, ultramafic endemics inherited from volcanic island arcs and old taxa endemic to young islands

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ABSTRACT

Aim To investigate areas of endemism in New Caledonia and their relationship with tectonic history.

Location New Caledonia, south-west Pacific.

Methods Panbiogeographical analysis.

Results Biogeographical patterns within New Caledonia are described and illustrated with reference to eight terranes and ten centres of endemism. The basement terranes make up a centre of endemism for taxa including *Amborella*, the basal angiosperm. Three of the terranes that accreted to the basement in the Eocene (high-pressure metamorphic terrane, ultramafic nappe and Loyalty Ridge) have their own endemics.

Main conclusions New Caledonia is not simply a fragment of Gondwana but, like New Zealand and New Guinea, is a complex mosaic of allochthonous terranes. The four New Caledonian basement terranes were all formed from island arc-derived and arc-associated material (including ophiolites) which accumulated in the pre-Pacific Ocean, not in Gondwana. They amalgamated and were accreted to Gondwana (eastern Australia) in the Late Jurassic/Early Cretaceous, but in the Late Cretaceous they separated from Australia with the opening of the Tasman Sea and break-up of Gondwana. An Eocene collision of the basement terranes with an island arc to the north-east – possibly the Loyalty Ridge – is of special biogeographical interest in connection with New Caledonia–central Pacific affinities. The Loyalty–Three Kings Ridge has had a separate history from that of the Norfolk Ridge/New Caledonia, although both now run in parallel between Vanuatu and New Zealand. The South Loyalty Basin opened between Grande Terre and the Loyalty Ridge in the Cretaceous and attained a width of 750 km. However, it was almost completely destroyed by subduction in the Eocene which brought the Loyalty Ridge and Grande Terre together again, after 30 Myr of separation. The tectonic history is reflected in the strong biogeographical differences between Grande Terre and the Loyalty Islands. Many Loyalty Islands taxa are widespread in the Pacific but do not occur on Grande Terre, and many Grande Terre/Australian groups are not on the Loyalty Islands. The Loyalty Islands are young (2 Myr old) but they are merely the currently emergent parts of the Loyalty Ridge whose ancestor arcs have a history of volcanism dating back to the Cretaceous. Old taxa endemic to the young Loyalty Ridge islands persist over geological time as a dynamic metapopulation surviving *in situ* on the individually ephemeral islands and atolls found around subduction zones. The current Loyalty Islands, like the Grande Terre terranes, have inherited their biota from previous islands. On Grande Terre, the ultramafic terrane was

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emplaced on Grande Terre in the Eocene (about the same time as the collision with the island arc). The very diverse endemic flora on the ultramafics may have been inherited by the obducting nappe from prior base-rich habitat in the region, including the mafic Poya terrane and the limestones typical of arc and intraplate volcanic islands.

Keywords

Dispersal, endemism, evolution, Gondwana, limestone, Melanesia, New Guinea, New Zealand, serpentine, vicariance.

INTRODUCTION

> 'New Caledonia has a complicated geological origin, which probably confounds a simple understanding of its biogeography' (Swenson *et al.*, 2001, p. 28)

New Caledonia is an archipelago in the south-west Pacific with a biota that is well known for its high diversity, endemism (including several endemic plant families and one bird family) and far-flung biogeographical affinities. There is a superb, ongoing flora of New Caledonia (Aubréville *et al.*, 1967–present) which includes hundreds of detailed distribution maps. Unfortunately, as Lowry (1998) observed, 'No comprehensive chorological analysis of the New Caledonian flora has yet been made to ascertain phytogeographical patterns within the territory, despite the availability of an exceptionally large and well documented specimen base…'. A comprehensive analysis is not attempted here, only a preliminary overview in which some of the more obvious main patterns are illustrated. There are also many localized centres of endemism which require much further study.

Perhaps the most obvious aspect of New Caledonia biogeography is the difference between the biota of the Loyalty Islands and that of the mainland, Grande Terre (Fig. 1). Many groups are in eastern Australia and Grande Terre, but not on the Loyalty Islands, for example the orchid *Acianthus amplexicaulis* (Grande Terre is also the eastern limit of the genus; Kores, 1995). Conversely, many taxa on the Loyalty Islands are shared with other parts of the Pacific, but are not on Grande Terre. However, New Caledonia as a whole (Grande Terre plus the Loyalty Islands) is itself an important centre of endemism; for example the parrot genus *Eunymphicus* comprises one species on Grande Terre and one on the Loyalty Islands.

Affinities with New Guinea and New Zealand are an important aspect of New Caledonian biogeography (Figs 1–3). *Eunymphicus* is sister to the New Zealand–central Pacific *Cyanoramphus* and connections between southern Grande Terre and islets off north-eastern New Zealand are illustrated by the monocot plant *Xeronema* (Fig. 3). Connections of New Caledonia with eastern Papua New Guinea (PNG) are exemplified by the tree genus *Hunga* (Fig. 1; Prance, 1979).

Analysis of smaller-scale patterns in New Caledonia requires data on distribution within Grande Terre. The taxa most likely to preserve terrestrial biogeographical patterns in areas where there is major disturbance, such as island arcs around subduction zones, are those with the highest 'coefficients of survival', such as lichens, grasses, small invertebrates and some lizards. Populations of these can survive even on fragments of land such as small rock stacks. For New Caledonian lizards, Bauer & Sadlier (2000) mapped 'chief areas of endemism' in north-western Grande Terre (Koumac Caves and Pindaï Peninsula), in the ultramafic massif of southern Grande Terre (especially Mounts Ouin, Mou, and Koghis), in north-eastern Grande Terre (Hienghène, Mount Mandjélia, Mount Ignambi, and Mount Panié), and in the Central Ranges (especially the Grottes d'Adio and Mount Aoupinié) (basement terrane). These four areas are also the main centres of endemism for plants, and, together with several common disjunct connections among the centres, are illustrated below.

METHODS

Vascular plants have been more intensively collected in New Caledonia than in any other tropical forested country (Jaffré *et al.*, 1998). The distribution patterns within the country described here are based largely on plant data (Aubréville *et al.*, 1967–present; Jaffré *et al.*, 2001, and an important website http://www.endemia.nc/). Aubréville *et al.*'s (1967–present) work is especially valuable as every species is mapped, an unusual feature of floras in the 1960s when the series commenced. Aubréville (1969) was an early advocate of Croizat's (1964) panbiogeography, a method of analysis that integrates biological distribution data with tectonics (Craw *et al.*, 1999; Heads, 2005a) and is employed here.

New Caledonia terrane tectonics

New Caledonia comprises the large island of Grande Terre and the three smaller Loyalty Islands 100 km to the east. Grande Terre and the Loyalty Islands represent emergent parts of two ridges, each more than 2000 km long (Figs 2 & 3). Grande Terre itself comprises seven distinct terranes. Those that are

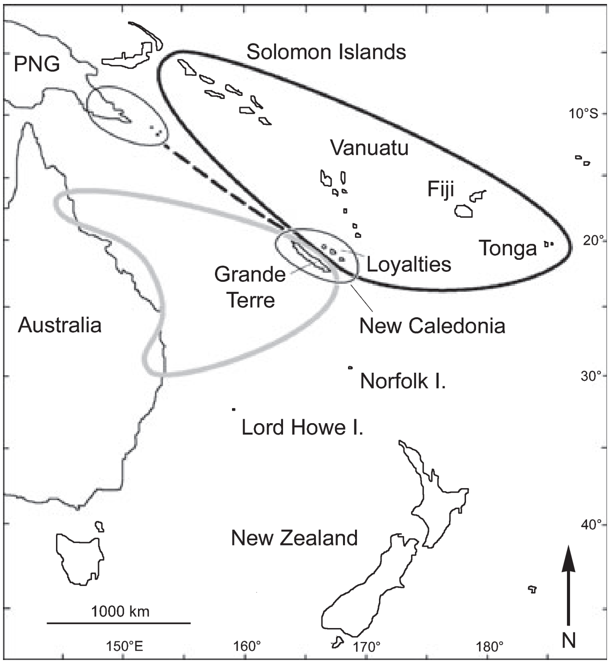

Figure 1 The south-west Pacific region, with distribution of the orchid *Acianthus amplexicaulis* (grey line), the tree *Hunga* (Chrysobalanaceae: areas with fine line connected by broken line) and the snake *Candoia bibroni* (heavy line).

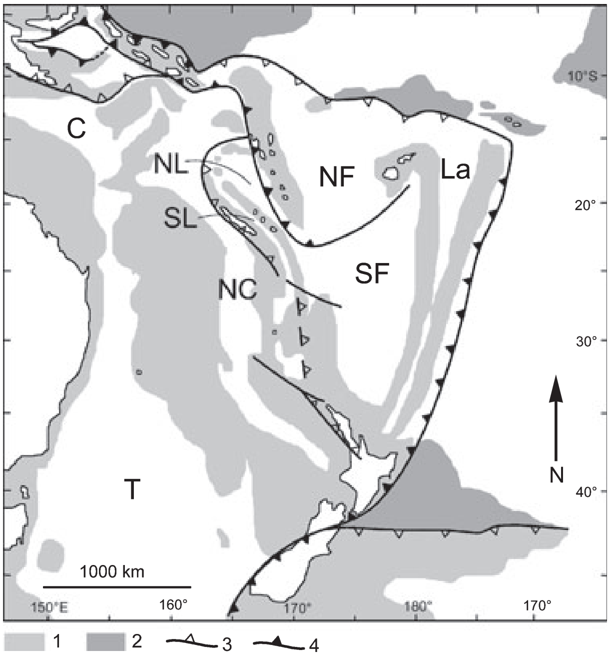

Figure 2 The south-west Pacific tectonic setting (based on Schellart *et al.*, 2006): 1, continental/arc crust; 2, oceanic plateau; 3, inactive or fossil subduction zone; 4, active subduction zone. Basins as follows: T, Tasman Sea; C, Coral Sea; NC, New Caledonia; NL, North Loyalty; SL, South Loyalty; SF, South Fiji; NF, North Fiji; La, Lau.

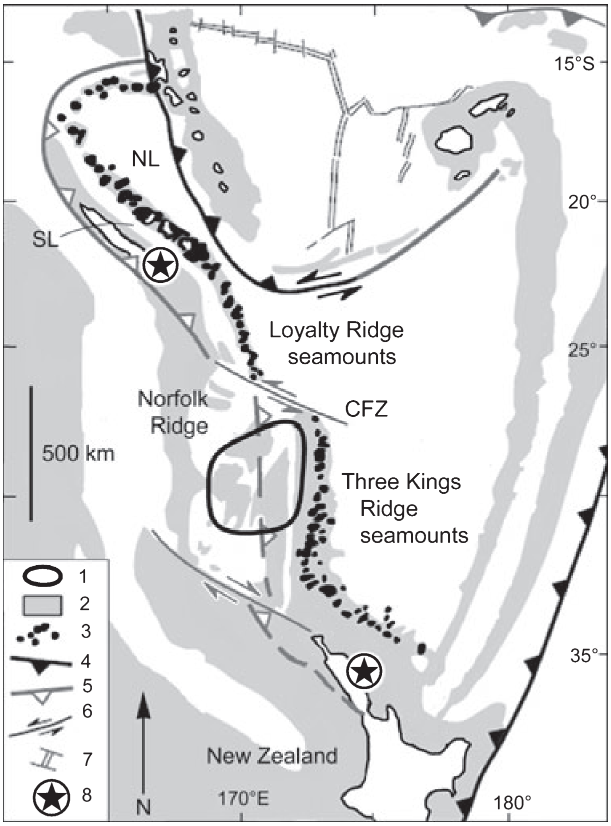

Figure 3 New Caledonia and northern New Zealand (based on Meffre *et al.*, 2006; Schellart, 2007): CFZ, Cook Fracture Zone; 1, area emergent 38–21 Ma (the whole area around this part of the Norfolk Ridge has undergone subsequent rifting); 2, continental/arc crust; 3, seamounts (subduction-induced arc volcanics); 4, subduction zone; 5, New Caledonia fossil subduction zone; 6, strike-slip fault; 7, spreading ridge; 8, the monocot *Xeronema* (Xeronemataceae).

old enough show evidence of two metamorphic–tectonic events. One, latest Jurassic–lower Cretaceous (150 Ma; Cluzel & Meffre, 2002), is associated with plate convergence in a subduction zone and amalgamation/accretion of the composite basement terrane. This was followed by a phase of rifting (opening of the Tasman, New Caledonia and South Loyalty Basins) associated with the break-up of Gondwana. The second phase of metamorphism occurred in the Eocene (44 Ma; Spandler *et al.*, 2005a) and represents collision of the basement (by then part of the Norfolk Ridge) with an island arc, probably the Loyalty Arc. Biogeographers are familiar with rifting in the Tasman Sea Basin causing disjunction between eastern Australia and New Caledonia (Ladiges & Cantrill, 2007). However, it is suggested here that the two phases of tectonism recorded in New Caledonia, with associated terrane accretion and orogeny, were also important for New Caledonian biogeography and would have involved deformation and accretion of biological distribution patterns in the region.

Terranes recognized here for New Caledonia (Fig. 4) include the following (Cluzel *et al.*, 1994, 2001, 2005; Aitchison *et al.*, 1995, 1998; Meffre *et al.*, 1996; Cluzel & Meffre, 2002).

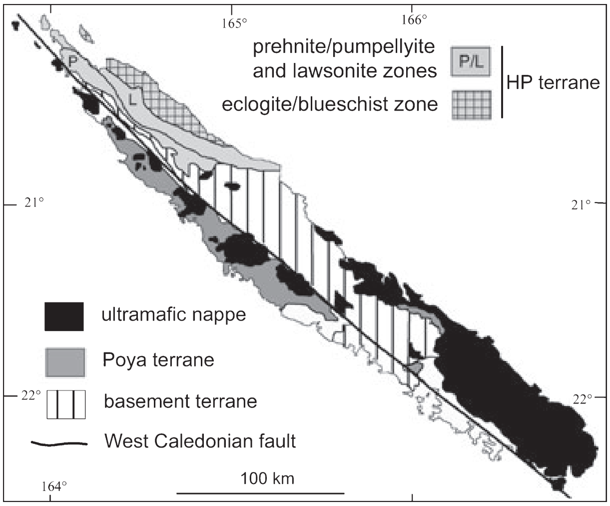

Figure 4 Grande Terre terranes (based on Baldwin *et al*., 2007).

(Further information is given in Appendix S1 in the Supporting Information).

1. Koh terrane, 2. Central Chain terrane, 3. Téremba terrane, 4. Boghen terrane

Together these make up the New Caledonia basement. All are pre-Cretaceous and were folded and metamorphosed in the Late Jurassic–Early Cretaceous orogeny, equivalent to the second phase of the New Zealand Rangitata Orogeny (Vaughan & Livermore, 2005). The terranes comprise arc sequences and ophiolites (sequences of ocean floor crust and mantle), with some terrigenous sediments, and are comparable with several New Zealand Eastern Province terranes. The New Caledonia basement terranes formed in the ocean an unknown distance off the eastern Gondwana coast from material derived from, or associated with, island arcs and dated as Carboniferous to Jurassic. These precursor arcs and their biota already existed in the pre-Pacific Ocean before it was invaded by the growing Pacific plate with its own arcs, from the Jurassic onwards. The ophiolite/arc terranes amalgamated to form the composite New Caledonia basement and were accreted to the Lord Howe Rise/East Australia in the Late Jurassic/Early Cretaceous. This was coeval with the second phase of the Rangitata Orogeny, the last major reorganization of New Zealand geography and biogeography (Heads, 1990). For most of their history the New Caledonian basement terranes were not part of Gondwana, and this relates to the many Pacific groups in the biota that are biogeographically quite distinct from Australian–Indian–African (Gondwanan) clades. The terranes were accreted to each other and Gondwana by the Early Cretaceous, but in the Late Cretaceous were separating again from Gondwana (as part of a large block of continental crust including Lord Howe Rise and New Zealand), with the opening of the Tasman Basin and break-up of Gondwana. Thus the history of the basement terranes has mainly been played out in the Pacific; they were only part of Gondwana for one phase of their evolution, although this was an important one.

Following the initiation of rifting in the Tasman Sea and New Caledonia basins, and deposition of deltaic sandstone, conglomerates (with blocks up to 40 cm in diameter) and coal shale (the *formation à charbon*), widespread subsidence continued. There was progressively less terrigenous sediment and deposition of deeper-water marine sediments began. Many biologists (e.g. Murienne *et al*., 2005) have accepted the idea, proposed by some geologists, that New Caledonia was totally submerged at some time in the Palaeogene. However, other biologists have preferred to stress biological evidence, and this does not support the theory. Morat *et al.* (1984) discussed the marine transgressions in New Caledonia and concluded that 'In spite of geological arguments, these submersions can never have been complete, since floral distributions indicate that considerable surface must have remained above water and served as refuges.' De Laubenfels (1996) drew the same conclusion based on study of the conifers. Lowry (1998) summarized the situation clearly: 'Geologists have contended that during at least some of [the Palaeogene] all of the land area comprising New Caledonia must have been submerged. Inference from the modern flora, however, strongly suggests that at least a portion of the land must have remained exposed throughout this process, serving as a refugium – although these sites may have been situated to the south and/or west of the present day Grande Terre in areas that are now submerged. Many attributes of New Caledonia's flora, such as its high generic and familial diversity, and the presence of numerous primitive groups, would be particularly difficult to explain by invoking long-distance dispersal…'. Recently Bauer *et al.* (2006) dated differentiation between New Zealand and New Caledonian gecko lineages back to the Late Cretaceous and ruled out the possibility that New Caledonia was completely submerged during the Palaeocene or later.

Spreading ended in the Tasman Basin at the start of the Eocene and a period of convergence began. An Eocene–Oligocene collision zone can be traced in New Zealand, New Caledonia, Rennell Island (south-west Solomon Islands), and south-eastern PNG (Aitchison *et al*., 1995). In New Caledonia a mid-Eocene collision of the basement with an intra-oceanic island-arc system to the north-east (probably the Loyalty Arc) disturbed the basement subsidence and resulted in the re-elevation of New Caledonia. The collision led to the following four terranes being accreted to the New Caledonia basement, all from the north-east.

5. Poya terrane

This basaltic mélange of oceanic crust formed as part of the South Loyalty Basin during its Late Cretaceous–Palaeocene opening. The terrane is allochthonous and was originally located perhaps 200–300 km north-east of its present location. It was obducted onto the basement and was then itself overthrust by the ophiolitic nappe. (In obduction, seafloor crust is ramped up onto land – not subducted – at a convergent margin.) Local alkali basalts accompanied by Palaeocene pelagic foraminifera in carbonate sediments may represent remnants of intraplate seamounts or islands.

6. The ultramafic nappe

This 3500 m-thick peridotite nappe, assumed to be the base of an obducted ophiolite, is the dominant geological feature of New Caledonia. The great massif in southern Grande Terre is the largest single unit and smaller massifs occur along the northern half of the west coast. The whole terrane is famous for its nickel deposits, serpentine soils and endemic plants. The nappe is not directly related to the Poya and Pouébo terranes but is north-east-dipping and more or less continuous with the oceanic crust of the South Loyalty Basin. Like the Poya terrane, it represents part of that basin that was obducted onto the Norfolk Ridge in the Eocene.

Many ophiolites are now interpreted as remnants of oceanic forearc basins stranded on continental margins in the course of arc–continent collisions (Milsom, 2003). This interpretation implies that an ophiolite was formerly associated with a volcanic arc 100–200 km away, and in New Caledonia there is good evidence for such a relationship. A hundred kilometres to the north-east of the ultramafic nappe are the coral islands of the Loyalty Islands, probably the remnants of an old island arc. The ophiolite may thus represent the forearc basin of the Loyalty Ridge. The tectonic relationship between ophiolites and arcs is reflected in the ecology of many Pacific plants endemic to limestone and ultramafic rock, as discussed below.

7. High-pressure (HP) metamorphic terrane

In north-eastern Grande Terre, allochthonous eclogite–blueschist facies rocks (Pouébo and Diahot terranes of Cluzel *et al.*, 2001) are exposed in a north-west–south-east-trending anticlinal range, *c.* 175 km long and 35 km wide, which includes the highest mountain in the country, Mount Panié (1650 m). The rocks, which represent part of a sediment-filled basin that was buried by subduction, have undergone high-pressure metamorphism at depths of up to 60 km. Baldwin *et al.* (2007) included the ecologite–blueschist zone along with bordering lawsonite and prehnite–pumpellyite zones in a single terrane. The three fault-bounded zones have resulted from metamorphism of Late Cretaceous to ?Eocene volcanics like those of the Poya terrane, and the Pouébo and Poya terranes may be related. Protoliths of the Pouébo terrane formed between Late Cretaceous and Eocene (85 and 55 Ma) in a back-arc basin (Spandler *et al.*, 2005a). The age matches that of the Poya terrane and is cited as evidence, with geochemistry, for a direct link between the two. However, the Pouébo terrane is not simply a metamorphosed equivalent of the Poya terrane and includes a diversity of rocks which indicate a mixed origin from both oceanic and continental terranes. As well as metamorphosed arc-related basalts there are associated metamorphosed terrigenous sediments, including remnants of cliff conglomerates, that are absent in the Poya terrane.

After metamorphism of the HP terrane associated with arc–continent collision there was a phase of extension and the terrane was rapidly exhumed. This resulted in a narrow orogen, < 100 km across. Peak metamorphism (44 Ma) predates by 10 Myr the obduction of both the Poya terrane and the ophiolite, which took place in a renewed phase of compression (Spandler *et al.*, 2005a). This model involves multiple episodes of compression and extension during the Eocene, in a belt of 'oscillating orogenesis' (Rawling & Lister, 1997, 1999; Rawling, 1998).

Terranes representing backarc basins were also obducted in Palaeogene New Zealand and New Guinea. In New Zealand, Late Cretaceous to Palaeocene ophiolites and sediments were obducted in the Northland–East Cape allochthon (Mortimer, 2004). North of New Caledonia, the Santa Cruz Basin (between the Solomon Islands and Vanuatu) and the Pocklington Basin (off south-east PNG) opened at the same time as the South Loyalty Basin, and ophiolites obducted in the Owen Stanley Mountains of PNG represent remnants of the Pocklington Basin. Rawling (1998) and Rawling & Lister (1997, 1999) related the exhumation and obduction to orogeny and inferred the existence of an Eocene mountain range stretching between New Caledonia and New Guinea. This idea has particular relevance for understanding endemism in north-eastern Grande Terre and biogeographical connections between New Caledonia and New Guinea.

The metamorphism and exhumation of the eclogite–blueschist terrane represent major tectonic events. Obviously the endemic biota of the modern Mount Panié, for example, did not always survive on the rock strata it currently grows on, as these have been buried tens of kilometres under the earth and then uplifted. But any land in the region, whether continental crust, volcanic island, or low atoll, would have had a biota and this would have been affected by the tectonism. Old orogenic belts in general, not just current mountain ranges, are usually associated with extant endemism. The highly-endemic HP terrane biota and its connections may reflect patterns established with the Eocene collision. For example, collision could have led to the biogeographical interdigitation of Loyalty Islands and Grande Terre biota evident in places like southern and north-eastern Grande Terre. The original Grande Terre/Loyalty Islands vicariance probably goes back to the earlier opening of the South Loyalty Basin in the Cretaceous. Belts of orogenesis, metamorphism, intrusion and obduction all represent phases of physiographic dynamism, and the multiple compression/extension events and oscillating orogenesis suggested for the HP terrane constitute an extreme form of this. These phases of tectonic dynamism were probably also periods of biogeographical dynamism, with populations changing their local and regional boundaries, undergoing changes in altitude, hybridizing and evolving. When the tectonism ended, the biogeographical dynamism also ceased, and the distribution patterns of the time, including endemism and disjunction, were left in 'frozen' form.

Emplacement of the HP terrane, ophiolite obduction and the West Caledonian fault: Complex field relationships have led to controversy over the structural evolution of the HP terrane (cf. Rawling & Lister, 2002). Baldwin *et al.* (2007) supported oblique collision between the Norfolk Ridge and the Loyalty Arc, with the two approaching each other from the earliest Eocene. Following peak metamorphism (44 Ma), the entire HP terrane was rapidly exhumed as a large, relatively coherent block during a phase of crustal extension (44–34 Ma). Baldwin *et al.* (2007) inferred that the HP terrane and the ultramafic rocks were spatially separated prior to exhumation of the HP terrane. Obduction of Poya terrane and the ultramafic nappe rocks and exhumation of the HP terrane coincide temporally but may have occurred in different along-strike regions of the plate boundary. Final juxtaposition of the HP terrane against the other New Caledonia basement terranes took place in the Oligocene (< 34 Ma), possibly as the result of movement on the West Caledonian fault.

The HP terrane, the Poya terrane, the ultramafic nappe and the South Loyalty Basin may all represent parts of a single sediment-covered backarc basin that opened to the north of the New Caledonia basement. The age range (85–55 Ma) is almost identical to the period of opening of the Tasman Basin. Synchronous formation of several independent ocean basins during the Late Cretaceous to the Eocene and many biogeographical disjunctions across the different basins could have formed at these times. However, the centres of endemism themselves (whether Loyalty Islands–Vanuatu in the east or New Caledonia–north-eastern New South Wales in the west) must have formed previously.

8. The Loyalty Ridge

The three Loyalty Islands east of Grande Terre are low and flat, and formed of recently uplifted coral reef. They form discrete bathymetric highs with distinctive volcanic morphology and represent the emergent part of the Loyalty Ridge, a mainly submarine feature that runs more or less continuously for more than 1500 km between Vanuatu and New Zealand, parallel to the Norfolk Ridge (Fig. 3; Cluzel *et al.*, 2001; Schellart *et al.*, 2006). The geology of the Loyalty Ridge is still poorly known due to the thick carbonate cover and lack of basement outcrops, but it is probably the remains of an ancient island arc. Eocene andesite has been recovered from the northernmost seamount on the ridge, Bougainville Guyot, west of Vanuatu (Collot *et al.*, 1992) and the arc may have been active back to the Cretaceous.

The Loyalty Islands: the Loyalty Arc, the Vitiaz Arc, and the Loyalty–Vitiaz precursor arc: The early Cenozoic location of the south-west Pacific plate boundary (and its associated island arcs) is of great biogeographical interest. The Vitiaz Arc was formerly continuous but was later rifted apart to form the separate archipelagos of the Solomon Islands, Vanuatu, Fiji and Tonga. From the Eocene onwards there is ample evidence in the volcanics of the Vitiaz Arc for south-west-dipping subduction, but the nature and location of the plate boundary east of the Norfolk Ridge from the Late Cretaceous to the Eocene is uncertain.

In Kroenke's (1996) model, the basement of the Vitiaz Arc formed as an intra-oceanic arc in the central Pacific over 1000 km from New Caledonia and converged on New Caledonia through the Cenozoic. (The 'Eua Ridge in Tonga was accepted as initially attached to the eastern end of the New Caledonia Arc until it was detached at 40 Ma.) However, other models propose that the entire Vitiaz Arc formed close to the eastern Gondwana margin. Hall (2002) suggested there was no good geological evidence to distinguish between the two alternatives.

In some recent reconstructions which follow the second model (Crawford *et al.*, 2003; Sdrolias *et al.*, 2003; Schellart *et al.*, 2006), the south-west Pacific subduction was adjacent to the eastern Norfolk Ridge. An arc formed along it and later this split into the Loyalty and Vitiaz arcs. The proposed Loyalty–Vitiaz precursor arc (unnamed in Schellart *et al.*, 2006; Fig. 3) stretched from New Zealand to New Guinea along the plate boundary. Crawford *et al.* (2003, Fig. 3) showed the belt as a subduction zone/island arc, but with question marks; Cluzel *et al.* (2006) portrayed it as a 'Late Cretaceous-Palaeocene extinct and/or subducted arc'. Sdrolias *et al.* (2003) concluded that the Loyalty–Three Kings Ridge was active back to at least the Cretaceous and Picard *et al.* (2002) inferred the presence of Late Cretaceous arc remnants in its basement.

Backarc basins form by extension in the over-riding plate above major subduction zones, on the side of the arc away from the trench. The south-west Pacific is the classic example of episodic backarc basin formation (for the Late Cretaceous–Cenozoic basins; see Schellart *et al.*, 2006). Generally, backarc basin opening and associated arc volcanism migrated to the east and north-east, along with the south-west Pacific subduction zone. The basins south and north of the Loyalty Islands opened sequentially.

South Loyalty Basin: In the Late Cretaceous, rifting was under way in the Tasman Basin. West of Grande Terre, rifting in the New Caledonian Basin was separating Grande Terre/Norfolk Ridge from the Lord Howe Rise. East of Grande Terre, formation of the South Loyalty Basin was separating Grande Terre/Norfolk Ridge from the Loyalty–Vitiaz precursor arc. The South Loyalty Basin reached a width of at least 750 km. Evolution during this period might explain the vicariance often seen between Norfolk Ridge/New Caledonia taxa and sister groups in the Loyalty Islands, Vanuatu and the Solomon Islands.

At 55 Ma (Palaeocene–Eocene boundary), 30 Myr after it began to open, the South Loyalty Basin began to close again. It was being consumed at an east-dipping New Caledonia subduction zone between the Norfolk Ridge and the Loyalty Arc. The Grande Terre/Norfolk Ridge and the Loyalty forearc started to converge and finally collided (35 Ma). The collision would have led to the secondary juxtaposition of biotas of the continental ridge and the arc. The location and identity of the island arc that collided with New Caledonia in the Eocene is not certain, but it was probably the Loyalty Arc. Following the collision, subduction began along the western side of the Norfolk Ridge (inactive by 25 Ma). Seismic tomography indicates an extinct subduction zone buried 80 km beneath the west coast of Grande Terre. In addition, Oligocene granitoid intrusions in the ultramafic nappe display features of volcanic arc magmas and may be due to post-Eocene, pre-Miocene subduction west of New Caledonia (Cluzel *et al.*, 2005).

North Loyalty Basin: When the South Loyalty Basin had reached its maximum width (earliest Eocene), the North Loyalty Basin began to open. This was at the expense of the South Loyalty Basin, which began to be subducted (Cluzel *et al.*, 2001; Schellart *et al.*, 2006). From the Eocene to the earliest Miocene, the Loyalty–Vitiaz precursor arc was split along its more or less north–south axis by formation of the North Loyalty Basin. This divided the arc into the Loyalty–Three Kings Arc in the west and the Vitiaz Arc in the the east and could account for vicariance between Loyalty Islands groups and related taxa in the Vitiaz Arc (Solomon Islands, Vanuatu, Fiji, Tonga). Currently, the North Loyalty Basin is being destroyed by subduction under Vanuatu at the New Hebrides trench.

Tectonic evolution and terrane dynamics

The south-west Pacific is one of the most tectonically complex regions on Earth. Geological evidence of its history is limited as most oceanic crust older than Cretaceous has been subducted and most on-land geology consists only of younger volcanics and limestone < 20 Myr old. It is not surprising that models of the region's evolution over the last 100 Myr vary significantly. There is even less geological information available for earlier periods, such as the Jurassic/Early Cretaceous, which were critical in the evolutionary and spatial development of modern biological groups.

New Caledonia evolved within the Australia–Pacific plate boundary zone and the rocks indicate a complex history of compressional and extensional tectonism, involving terrane accretion, orogeny and rifting. The following chronology, for the Cretaceous onwards, is summarized from recent papers (Crawford et al., 2003; Sdrolias *et al.*, 2003; Cluzel *et al.*, 2005, 2006; Spandler *et al.*, 2005a,b; Schellart *et al.*, 2006; Baldwin *et al.*, 2007):

120–100 Ma (Early Cretaceous). *Convergence* along the eastern side of the Norfolk Ridge (perhaps the Australia–Pacific plate boundary), with associated terrane accretion and orogenesis (Rangitata Orogeny).

100–90 Ma (Late Cretaceous). *Extensional regime* during the break-up of eastern Gondwana. Tasman Sea Basin opening from Late Cretaceous (83 Ma), New Caledonia Basin (west of Grande Terre) and South Loyalty Basin (east of Grande Terre) opening from Late Cretaceous (74 Ma), Coral Sea Basin opening from Palaeocene (61 Ma).

55 Ma (Palaeocene–Eocene boundary). Major change in plate boundary processes. *Cessation of spreading* in Tasman, Coral, New Caledonia and South Loyalty basins. Initiation of subduction in South Loyalty Basin.

44 Ma (Middle Eocene). Renewed *convergence* along the Vitiaz Arc. This arc was originally continuous and was active from the Eocene onwards.

44 Ma (or 53 Ma)–35 Ma. North Loyalty Basin opening. Convergence of Loyalty Arc with New Caledonia. The South Loyalty Basin, which formed as a backarc basin, was now in a forearc position and was largely subducted. Arrival of the Norfolk Ridge and its sedimentary pile at the subduction zone (44 Ma) jammed the subduction system.

44 Ma. Peak metamorphism in the HP terrane. Exhumation of the terrane from 40–34 Ma; juxtaposition of the terrane against the other basement terranes (34 Ma). Over the same period, the Poya terrane and the ultramafic nappe were also obducted (the ophiolite at 38–34 Ma).

Later back-arc basin formation in the region has been further east. The New Britain–New Hebrides trench began forming at 27 Ma, the North Fiji Basin at 10 Ma and the Lau Basin at 5 Ma, and these are all currently active.

Areas of endemism in New Caledonia

The following areas of endemism are especially conspicuous. Further information on their endemic taxa is given in Appendix S1.

Loyalty Islands

These islands are formed of raised coral reef and are much smaller, lower (138 m) and flatter than Grande Terre. In several places (especially on Lifou) a diverse rain forest still exists. Virot (1956) noted that while the biota of the Loyalty Islands is not as rich as that of Grande Terre it is distinguished by many taxonomic differences. He observed that the problem of the geological origin of the Loyalty Islands is reflected in a complex biogeographical problem: their biota is surprisingly rich for such low islands and it is not simply an attenuated subset of the Grande Terre biota. There are many Loyalty Islands endemics and also many taxa there that are more closely related to groups in southern Vanuatu and Fiji than to any in Grande Terre. This is correlated with the geological history of the Loyalty Ridge, which extends back to the Cretaceous and is distinct from that of the Grande Terre basement. On the other hand, Grande Terre plus the Loyalty Islands together form a centre with many endemics, such as the parrot genus *Eunymphicus*. These groups presumably evolved before the opening of the South Loyalty Basin. *Eunymphicus* (New Caledonia) and its sister *Cyanoramphus* (New Zealand, Lord Howe, Norfolk, New Caledonia and French Polynesia) currently show a great disparity in the size of their geographical ranges but this may not have always been the case.

The biogeographical 'enigma' of the Loyalty Islands lies in their unexpected differences from Grande Terre. Loyalty Islands endemics include palms, parrots and many others. Groups that are on the Loyalty Islands and elsewhere, but not on Grande Terre, are of special interest. For example, there are no indigenous snakes on Grande Terre but two families, Boidae and Typhlopidae, are represented on the Loyalty Islands.

In angiosperms, *Cyrtandra* (Gesner.) is diverse in New Guinea, the Solomon Islands, Vanuatu (11 species) and Fiji (37 species). There is a single species on the Loyalty Islands (Maré), which is unusual as *Cyrtandra* usually occurs in submontane rain forest, but the genus is totally absent from Grande Terre. Green (1979, p. 45) wrote that 'One speculates as to whether *C. mareënsis*…has arrived…by dispersal from the New Hebrides [= Vanuatu]…', but no real evidence was given for this idea. It seems unlikely that the genus would disperse to the Loyalty Islands but not to the nearby Grande Terre where there is much more suitable habitat. The genus is probably part of an old central Pacific biota (including snakes, mosses, etc.) which survives as a relic on the Loyalty Islands but has never invaded Grande Terre.

Alyxia stellata (Apocynaceae) is a widespread Pacific species, ranging in diverse habitats on many islands east from Palau and Queensland to Hawaii and south-east Polynesia (Middleton, 2002). The only substantial islands in this vast region that it does not occur on are New Guinea, the Bismarck Archipelago and Grande Terre. However, it is on the Loyalty Islands.

The *Lotus australis* complex (Leguminosae) is another widespread Australia–Pacific group. One member, *Lotus anfractuosus*, is endemic to the Loyalty Islands, Ile des Pins and Vanuatu, but not to Grande Terre. Kramina & Sokoloff (2004, p. 194) wrote that 'The disjunctive distribution of the *Lotus australis* complex around the Pacific Region should be explained by long distance dispersal rather than by vicariance. Indeed, *L. anfractuosus* [and one other species, *Lotus pacificus*] do occur on many islands of coral and volcanic origin. Interestingly, we are unable to indicate any peculiar adaptation to long distance seed dispersal in these plants (they have also no vegetative propagation). Seeds are of normal size for *Lotus*, not floating, smooth, and dry. It may be possible that long-distance dispersals are very rare events, which should explain absence of these species in many close islands…'.

However, the Australia/Pacific *L. australis* complex is vicariant with the rest of the genus (except for minor overlap on the Ryu Kyu Islands), and the Pacific species of the complex are vicariant with each other. There is no need for any dispersal, only vicariance, at both species and species-complex levels. The fact that the two *Lotus* species occur only on coral and volcanic islands was taken to mean that the species can be no older than these particular islands. But volcanic islands and associated coral atolls have been coming and going at the subduction zones, hotspots and other cracks active in the region since the Mesozoic – long before the formation of the currently emergent islands. Kramina & Sokoloff's (2004) observation that there are no adequate means of long distance dispersal in these species is 'interesting' (or, perhaps, inexplicable) in a dispersalist interpretation but has no special significance for a metapopulation model which does not involve long-distance dispersal. Finally, the idea that dispersal events might be very rare does not adequately explain the absence of *L. anfractuosus* and many other Loyalty Islands species from nearby Grande Terre, and the overall distribution of *L. anfractuosus* in the Loyalty Islands, Ile des Pins and Vanuatu is repeated in many other groups.

Tronchet *et al.* (2005) argued that the entire flora of the Loyalty Islands was 'almost certainly derived from elements that reached the archipelago by long distance dispersal, either from the New Caledonian mainland or other more distant islands such as Vanuatu'. This view was based on the idea that there have never been other islands on the Loyalty Ridge, but this is unlikely for both tectonic and biogeographical reasons. For example, in the New Caledonian cockroach genus *Angustonicus*, Pellens (2004) stressed the 'extreme endemism' in the genus and the tribe, and emphasized the 'nearly complete lack of sympatric distributions' among the species. Nevertheless, Murienne *et al.* (2005) adopted a similar approach to that of Tronchet *et al.* (2005) and equated the age of *Angustonicus* species endemic to the Loyalty Islands with the age of the carbonate rocks composing the current surface of the islands (2 Ma). However, as indicated, the Loyalty Ridge represents part of an island arc that was probably active back to the Cretaceous. Its current high points, the Loyalty Islands, are made up of recently uplifted coral reef limestone built on volcanic basement. The presence of thick reefs indicates prior subsidence and it is unnecessary to assume that the current islands are the only ones to have ever existed on the Loyalty Ridge, especially given the endemism and biogeography of the biota.

Murienne *et al.* (2005) noted that the recent dates derived for *Angustonicus* species using the age of the Loyalty Islands limestone match those calculated using a 'classical' nucleotide substitution rate derived in other studies of insects, but the calibration on which this last rate was based was not mentioned. It is likely to involve simplistic correlations with palaeogeography or the age of oldest fossils. Using the age of an oldest fossil to calibrate evolutionary clocks will usually give more or less drastic underestimates of clade age. Using the age of strata that taxa are endemic to will also generally result in severe underestimates of age and so any corroboration between the two methods is meaningless.

Murienne *et al.* (2005) concluded that the diversification of *Angustonicus* in New Caledonia 'cannot be dated to earlier than the emergence of the Loyalty Islands', that the palaeogeographical date is 'convincing…clear and unambiguous', and that *Angustonicus* 'first colonised the Loyalty Islands a maximum of 2 Myr ago from the New Caledonian mainland'. However, the proposed dispersal does not account for the Loyalty Islands/southern Vanuatu area of endemism or the biogeographical enigma of the Loyalty Islands – its profound difference from Grande Terre. There may be no direct geological evidence for prior islands on the Loyalty Ridge, but the absence of geological evidence for small areas of low-lying emergent land is hardly significant for such a poorly known structure in such an active region. It is certainly not enough to base biogeographical and evolutionary analyses on. In any case, much biogeographical evidence indicates a close bond of Loyalty Ridge biota with islands to the north-east rather than with the currently much closer Norfolk Ridge/Grande Terre, and this needs to be explained. Recently, the remains of an island emergent from 38–21 Ma were discovered near the Three Kings Ridge (Fig. 3; Meffre *et al.*, 2006) at the southern end of the Loyalty Ridge, and further similar finds can be anticipated.

The cricket genus *Agnotecous* is endemic to Grande Terre and has 14 species there (Desutter-Grandcolas & Robillard, 2005). Its sister is *Lebinthus*, not known on Grande Terre but on the Loyalty Islands, Vanuatu, the Solomon Islands and through to Southeast Asia. The sister of these two genera is *Cardiodactylus*, again, not on Grande Terre but on the Loyalty Islands and with a similar overall range to that of *Lebinthus* (T. Robillard, personal communication 18 October 2007). Desutter-Grandcolas & Robillard (2005) suggested that the distributions of these groups represent different episodes of colonization, with *Agnotecous* representing the oldest and the two other genera subsequently colonizing the Loyalty Islands after their recent emergence. This interpretation follows Murienne *et al.*'s (2005) model, but simple vicariance of *Agnotecous* and *Lebinthus* caused, for example, by the formation of the South Loyalty Basin and later convergence of Grande Terre and Loyalty Islands, explains the Grande Terre vs. Loyalty Islands–Melanesia difference (a standard pattern) more simply and there is no need for chance colonization, only *in situ* differentiation.

2. Loyalty Islands, Ile des Pins and southernmost Grande Terre

The biogeographical relationship of the Loyalty Islands with Grande Terre is complex. In addition to widespread New Caledonian groups on Grande Terre and the Loyalty Islands, and the pattern of simple vicariance between the two (the pattern discussed in the Loyalty Islands section above), a common area of endemism linking the two comprises the Loyalty Islands, Ile des Pins and southernmost New Caledonia (Fig. 5). Taxa defining this sector grow on ultramafic and limestone substrate sites – both base-rich habitats – in a generalized basicole ecology which also occurs in many other plants.

3. Loyalty Islands–(southernmost Grande Terre)–north-eastern Grande Terre

This resembles the last pattern with the addition of records from north-eastern Grande Terre. A variation of this pattern

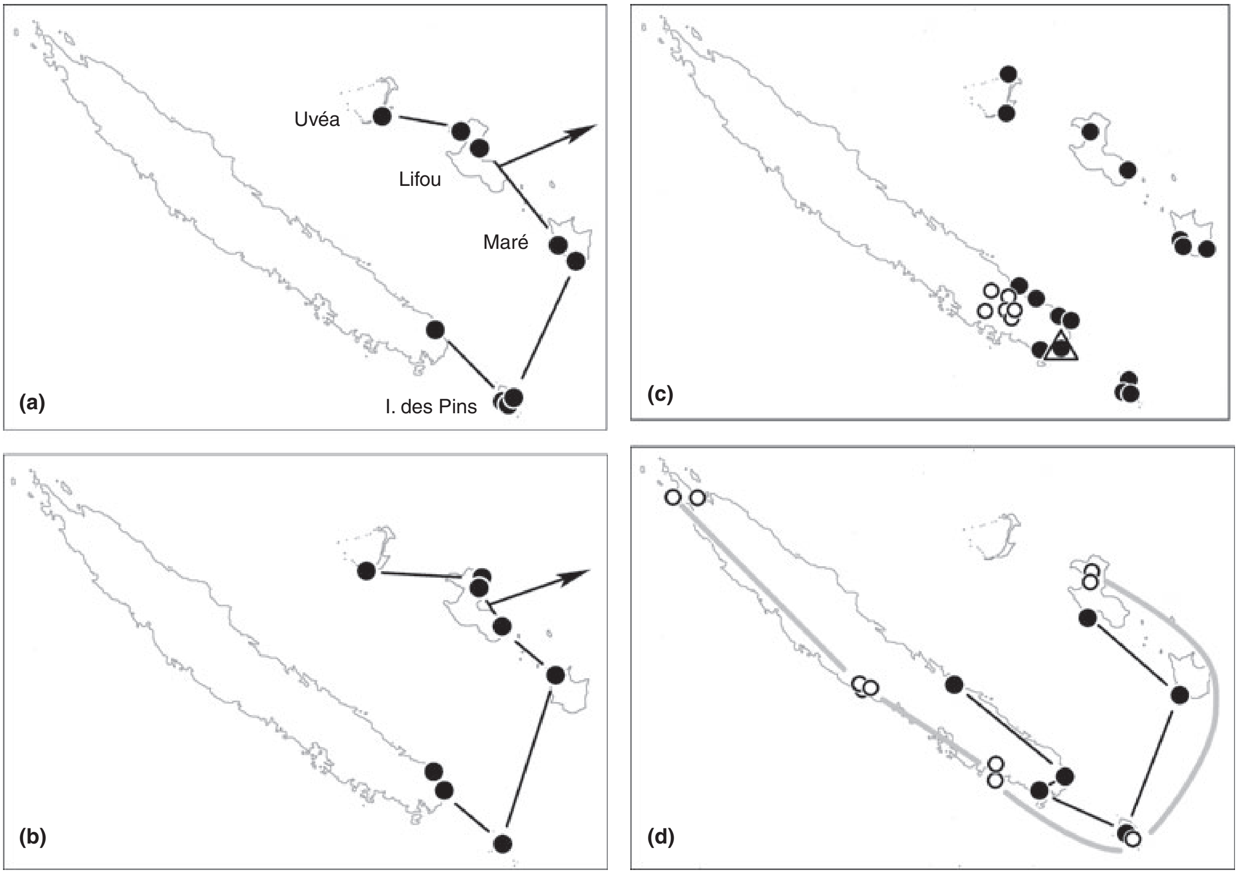

Figure 5 Loyalty Islands, Ile des Pins, south-eastern Grande Terre distribution. (a) *Nicotiana fragrans* (Solanaceae). Lines indicate the main trends in distribution and an additional population in Tonga. (b) *Xylosma orbiculatum* (Flacourtiaceae, also in Fiji, Tonga and Niue). (c) *Araucaria columnaris* (dots), *Araucaria nemorosa* (triangle) and *Araucaria humboldtensis* (circles) (Araucariaceae). (d) *Manilkara* (dots) and *Mimusops* (circles) (Sapotaceae) in New Caledonia.

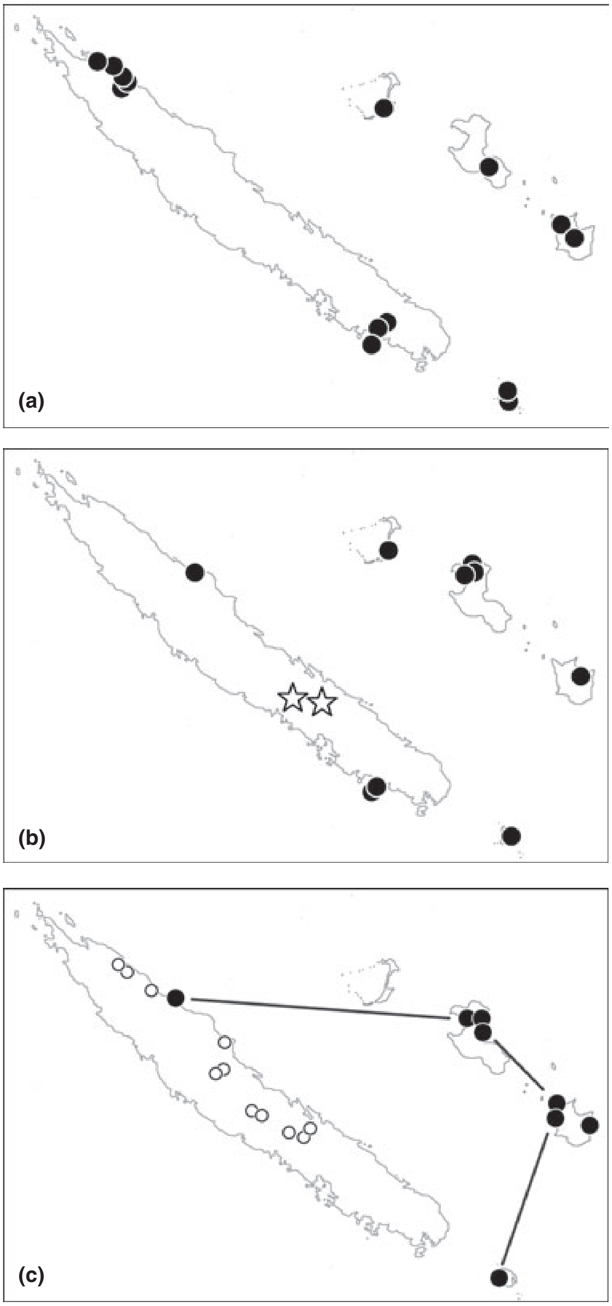

Figure 6 Loyalty Islands, south-eastern Grande Terre, north-eastern Grande Terre distribution. (a) *Spathoglottis unguiculata* (Orchidaceae), also in Vanuatu and Fiji. The gap in central Grande Terre is filled by *Spathoglottis vieillardii*. (b) *Cleidion verticillatum* (dots) and the related *Cleidion marginatum* (stars) (Euphorbiaceae). (c) The lizards *Bavayia crassicollis* (dots) and *Bavayia montana* (circles) (Diplodactylidae).

occurs in the lizard *Bavayia crassicollis* (Fig. 6c), known from the Loyalty Islands, Ile des Pins and north-eastern Grand Terre, but unlike the other taxa cited not present in southernmost Grand Terre (Bauer & Sadlier, 2000). Records from there would not be surprising. However, the palm *Cyphophoenix* has a similar range, with one species in the Loyalty Islands and one in north-eastern Grande Terre (Jaffré & Veillon, 1989). The closest relatives of *Cyphophoenix* are *Veillonia*, also endemic in the north-east, and *Campecarpus*, endemic to southern Grande Terre (cf. the *PRK* analysis in Norup *et al.*, 2006). The Loyalty Islands–northeastern Grande Terre (Hienghène) pattern is also seen in the beetle *Arrhenotoides* (Cerambycidae) (Gressitt, 1984).

The patterns in Fig. 6 might be the result of the HP, Poya and ultramafic terranes and the South Loyalty Basin all representing different parts of a single basin, as suggested above.

4. North-western Grande Terre (the 'West Coast Peridotite Belt')

The north-western region includes some of the country's most distinctive endemics (Fig. 7). The area is dominated by several ultramafic massifs which show considerable floristic differentiation. The four largest each have endemic plants (Jaffré, 1980). Many taxa endemic to the north-western region are widespread there, e.g. the monotypic genus *Myricanthe* (Euphorbiaceae *sensu lato*) (Fig. 7a). However, there are many disjunctions within the region, e.g. *Alstonia deplanchei* var. *ndokoaensis* (Apocynaceae) is disjunct between northern and southern parts of the region and surrounds *A. deplanchei* var. *deplanchei* (Fig. 7c,d). There are many local endemics at the southern node in this disjunction, around Pindaï and the Boulinda Massif, such as *Phyllanthus pindaiensis*, *Phyllanthus nothisii*, *Phyllanthus avanguiensis* (Euphorbiaceae *sensu lato*; Fig. 7e) and *Pittosporum aliferum* (Pittosporaceae). The only Pacific island species of *Oryza* (Gramineae/Poaceae) is *Oryza neocaledonica*, locally endemic at Pouembout in north-western Grande Terre (Fig. 7e). The species seems closest to *Oryza meyeriana* of Malesia (Morat *et al.*, 1994). Other species (e.g. *Solanum hugonis*) are endemic here and the spectacular, red-flowered pachycaul *Captaincookia* (Rubiaceae) is only known from Pouembout and Pindaï. Based around the same locations, *Callistemon* (now *Melaleuca*) *gnidioides* var. *gnidioides* (Myrtaceae) surrounds *Callistemon g.* var. *microphyllus* and *Callistemon brevisepalus* (Fig. 7f), as in *Alstonia deplancheii* cited above. *Melodinus guillauminii* (Apocynaceae) has a similar disjunction, with the gap filled by *Melodinus scandens*.

5. North-western Grande Terre–southern Grande Terre: dextral disjunction along the West Caledonian fault

Many taxa are widespread on the Grande Terre ultramafics, but other ultramafic taxa are more restricted. There is a major biogeographical division between the north-western belt and the southern massif, marked by the controversial West Caledonian fault. Some taxa show a clear boundary at the fault and others show a remarkable disjunction along it, with populations in the north-west separated by more than 100 km from those in the south. The pattern could be explained by lateral displacement along the fault (Heads, in press). Two

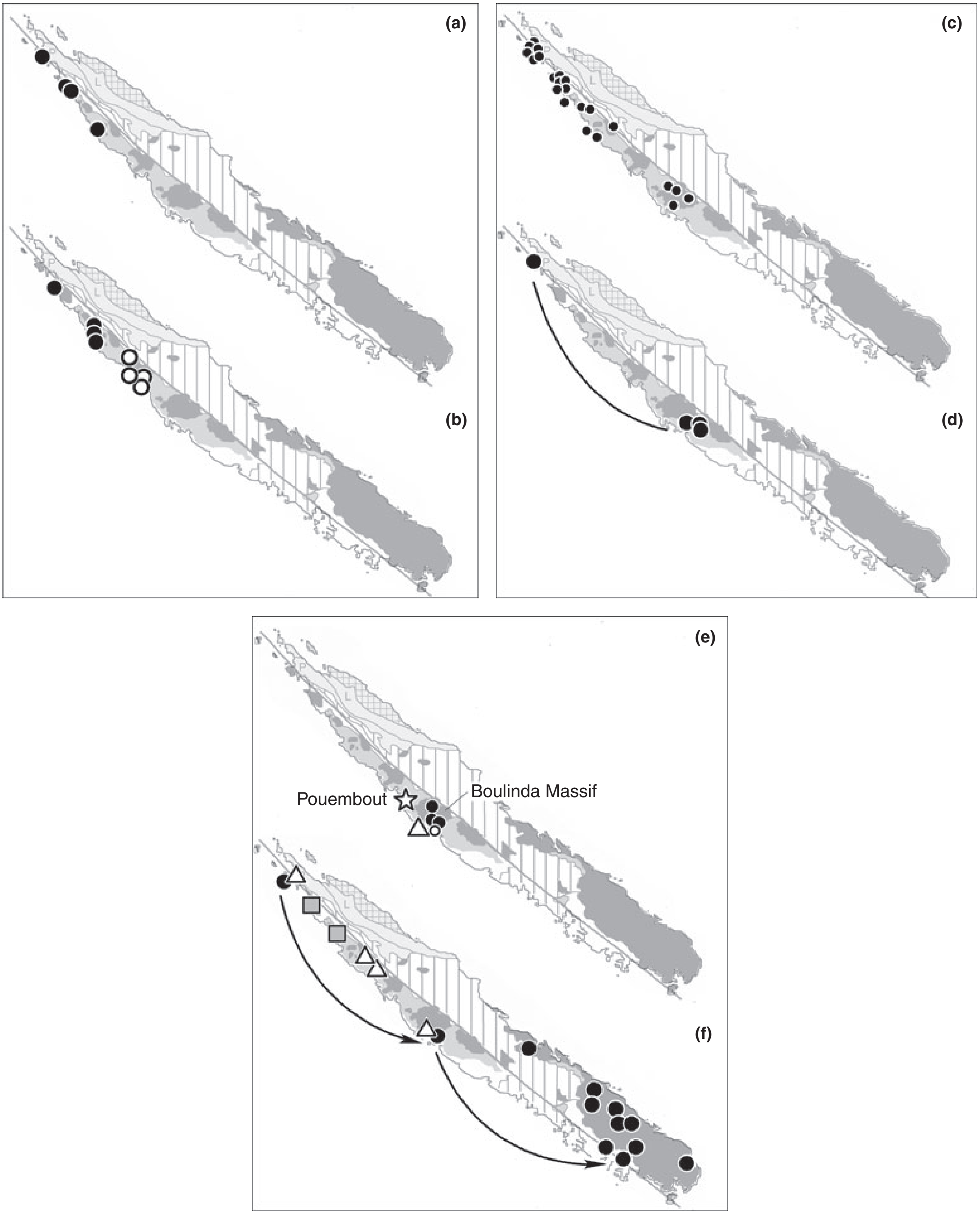

Figure 7 North-western Grande Terre distribution. (a) *Myricanthe* (Euphorbiaceae). (b) The two varieties of *Corchorus neocaledonicus* (Tiliaceae; formerly treated as *Oceanopapaver*): var. *neocaledonicus* (circles) and var. *estellatus* (dots). (c) *Alstonia deplanchei* var. *deplanchei* (Apocynaceae). (d) *Alstonia deplanchei* var. *ndokoaensis*. (e) *Phyllanthus nothisii* (dots), *Phyllanthus avanguiensis* (circle) and *Phyllanthus pindaiensis* (triangle) (Euphorbiaceae). *Oryza neocaledonica* (Gramineae; star). (f) '*Callistemon*' (now *Melaleuca*) *gnidioides* var. *gnidioides* (dots), *Callistemon gnidioides* var. *microphyllus* (triangles) and *Callistemon brevisepalus* (squares) (Myrtaceae).

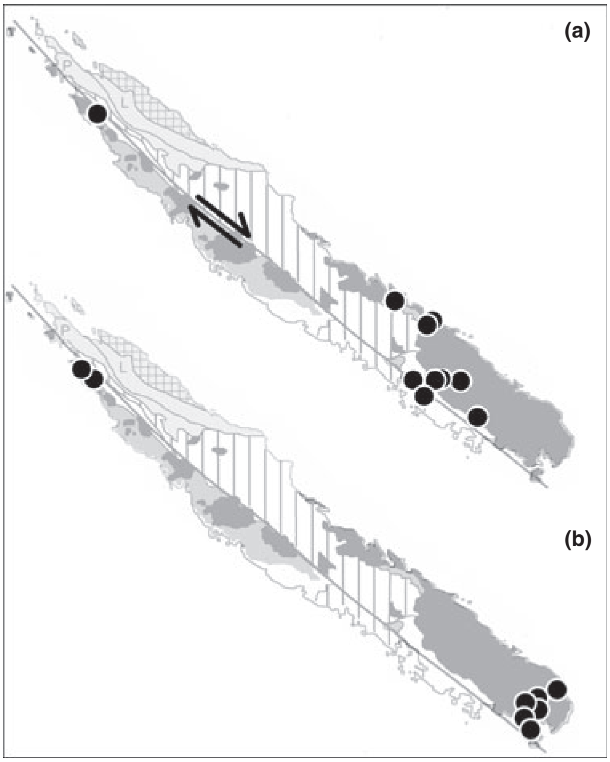

Figure 8 Southern Grande Terre–north-western Grande Terre disjunction. (a) *Xylosma nervosum* (Flacourtiaceae). (b) *Phyllanthus guillauminii* (north) and its putative sister species *Phyllanthus pronyensis* (south) (Euphorbiaceae).

examples are mapped here (Fig. 8a,b). *Acianthus amplexicaulis* (Orchidaceae) is disjunct along the West Caledonian fault and also occurs across the Tasman Sea in north-eastern Australia (Fig. 1).

6. Southern Grande Terre (the southern ultramafic massif)

Taxa endemic here include all three New Caledonian genera of Cupressaceae (Fig. 9a–c). The massif is not biogeographically homogeneous. For example, the three species of the New Caledonian endemic *Cerberiopsis* (Apocynaceae) (Fig. 9d) form parallel strips which divide the island into three and the southern massif into two. Distribution patterns within the area are complex and warrant detailed study.

7. Disjunction between southern Grande Terre and north-eastern Grande Terre

These taxa do not occur on the basement terranes in the central third of the island (Fig. 10). The pattern is related to pattern 3 described above, but without Loyalty Islands populations. The substrates involved are quite different: ultramafics in the south and schists in the north-east. A mechanism for the disjunction is not as obvious as in the southern Grande Terre–north-western Grande Terre disjunction (pattern 5). However, there are several possibilities as the complex tectonic history of the north-eastern and southern sectors includes Eocene collision with at least one island arc to the north-east, translation and accretion of the HP terrane, and obduction of the Poya terrane and the ultramafic nappe. Major strike-slip movements in addition to those suggested on the West Caledonian fault are possible.

8. North-eastern Grande Terre

This area of endemism is equivalent to the HP terrane and most of the endemism is in the eastern, eclogite–blueschist belt (Fig. 11). Mounts Panié and Ignambi are especially well known centres of endemism. The ultramafic rocks of New Caledonia are more well known for their endemism, but as many as 500 vascular plants are known only from forests on schistose, acidic substrate in central and north-eastern Grande Terre (Jaffré *et al.*, 1997).

Biogeographical nodes are characterized by absences as well as presences (Heads, 2004), and Jaffré (1995, p. 171) wrote that it is 'perhaps surprising that there are relatively few conifers in the North-East region, which is so rich in palms… and other primitive groups'. This phenomenon may be related to the geological derivation of the north-eastern terranes from the direction of the central Pacific, where palms have high diversity and endemism but conifers are totally absent.

9. North-eastern Grande Terre–central Grande Terre–south-western Grande Terre

The distributions of taxa such as the podocarp trees *Falcatifolium* and *Acmopyle* follow the high mountains of Grande Terre. A second, linear track (Fig. 12) runs along the island centrally and is seen in many groups, but does not correlate simply with topography, climate or geology. Distributions conforming to this pattern sometimes run between the ultramafic massifs but often these are occupied (e.g. in *Sleumerodendron* – Proteaceae). The track's linear nature gives the appearance of following an axial range, but centrally the highest mountains (Mount Boulinda and Mount Mé Maoya) are located west of the track, while in the south, the high points (Mount Sindoa and Mount Humboldt) are further east.

10. Central Grande Terre (basement terranes)

Many biologists have emphasized the presence of ultramafic rocks in New Caledonia and have explained the high floristic diversity and endemism in New Caledonia as the result of adaptation to these (e.g. Pole, 1994). Holloway (1993, p. 92) wrote that 'New Caledonia is renowned for its ancient, diverse and highly endemic seed plant flora that exhibits numerous Gondwanan relationships, and for the relationships of this to the extensive areas of ultramafic rocks'. Mueller-Dombois & Fosberg (1998) suggested that 'the ancient [plant] taxa are now predominantly found on the ultramafic material'.

However, while most genera in the New Caledonian flora are present on the ultramafic massifs, many of the most distinctive endemics are not. As Jaffré *et al.* (1987, p. 365)

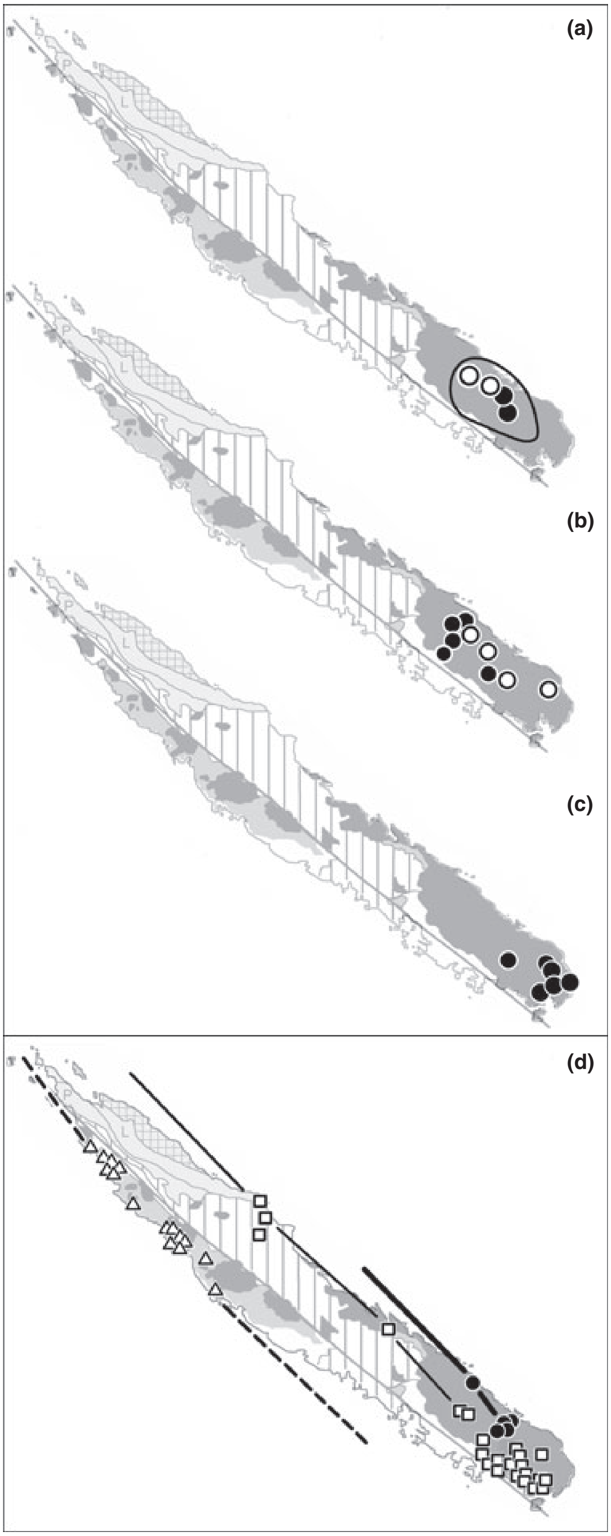

Figure 9 Southern Grande Terre. The five members of family Cupressaceae in New Caledonia. (a) *Libocedrus austrocaledonica* (line), *Libocedrus yateensis* (dots) and *Libocedrus chevalieri* (circles). (b) *Callitris sulcata* (dots) and *Callitris neocaledonica* (circles). (c) *Neocallitropsis pancheri*. (d) The three species of the New Caledonian endemic genus *Cerberiopsis* (Apocynaceae): *Cerberiopsis obtusifolia* (triangles), *Cerberiopsis neriifolia* (dots) and *Cerberiopsis candelabra* (squares).

noted, 'If it is true that most of the genera absent [from the ultramafics] are panpacific, pantropical or cosmopolitan, one must also not forget the significant absence of paucispecific genera such as *Fontainea* (Euphorbiaceae), *Trimenia* (Trimeniaceae), *Moerenhoutia* (Orchidaceae) or even genera endemic to New Caledonia such as *Amborella* (Amborellaceae), *Kibaropsis* (Monimiaceae), *Pichonia* (Sapotaceae), *Captaincookia* (Rubiaceae) and seven genera of palms (of the 17 in the territory)'.

In fact the basement terranes (not just the non-ultramafic terranes) are an important centre of endemism, for example in *Pittosporum* (Pittosporaceae; Fig. 13a,b). *Amborella* is possibly the 'basal' angiosperm, i.e. sister to the rest of the group, and is of special phylogenetic interest (Soltis & Soltis, 2004; Qiu *et al.*, 2006). One feature of its biogeography (Fig. 13c) has remained unnoticed: not only is *Amborella* absent from the ultramafics, as Jaffré *et al.* (1987) and Lowry (1998) observed, it is almost entirely restricted to the basement terranes. The map in the flora includes one early (queried) record in the north-east (not shown on Fig. 13c), and one anomalous record in western Grande Terre (not accepted on the map at http://www.endemia.nc/), but the main pattern is clear.

Many other taxa are restricted to the basement terranes. For example, in *Acropogon* (Malvaceae), five of the seven new species described by Morat (1988) and Morat & Chalopin (2003) (*Acropogon aoupiniensis*, *Acropogon domatifer*, *Acropogon grandiflorus*, *Acropogon macrocarpus* and *Acropogon merytifolius* – the last a remarkable pachycaul) are endemic to the basement.

Bocquillonia lucidula (Euphorbiaceae *sensu lato*; Fig. 13d) is a basement endemic. It is keyed out in Aubréville *et al.* (1967–present) with the *Bocquillonia nervosa*/*Bocquillonia longipes*/*Bocquillonia spicata* complex, widespread on Grande Terre but notably absent from the basement. The biogeography of the group as a whole is typical and illustrates several of the main patterns discussed here, including a standard West Caledonian fault disjunction (*Bocquillonia spicata*).

Baloghia balansae (Euphorbiaceae *sensu lato*) (surrounded by *Baloghia buchholzii* which is in the north and south but notably absent from the basement) and the orchid *Chamaeanthus aymardii* illustrate the two main centres occupied by *Amborella* (Fig. 14a). The disjunct sister pair *Pittosporum mackeei*–*Pittosporum bernardi nardii* (Fig. 14b) occupy the same two areas. These areas correspond with the Central Chain volcano–sedimentary terrane, the product of a Jurassic island arc.

Within the basement, Mount Aoupinié (Fig. 15a; Central Chain terrane) is a centre of endemism for lizards and plants. North-west of Mount Aoupinié, the Plateau de Tango is another centre of local endemism on the basement (e.g. for *Pittosporum bouletii* and *Phyllanthus tangoensis*). *Phyllanthus aoupiniensis* is endemic to Mount Aoupinié and related to *Phyllanthus cherrierei* of Mount Arago, to the east (Fig. 15a). Both localities are on the Central Chain terrane. Other *Phyllanthus* species (Fig. 15b) illustrate independent connections of Mount Aoupinié and Mount Arago with the HP terrane in the north-eastern Grande Terre via parallel arcs.

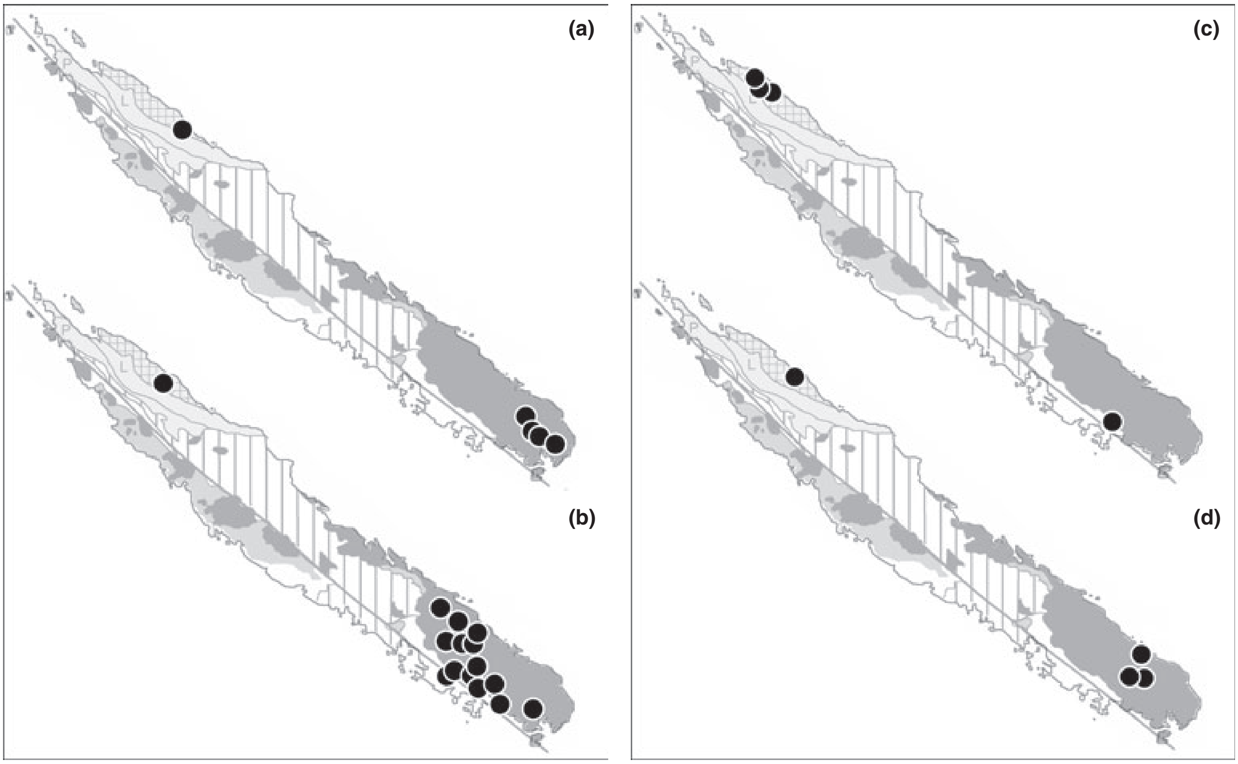

Figure 10 Southern Grande Terre–north-eastern Grande Terre disjunction. (a) *Podocarpus lucienii* (Podocarpaceae). (b) The monotypic New Caledonia endemic *Beaupreopsis* (Proteaceae). (c) *Symplocos gracilis* (symplocaceae). (d) *Bulbophyllum pachyanthum* (Orchidaceae).

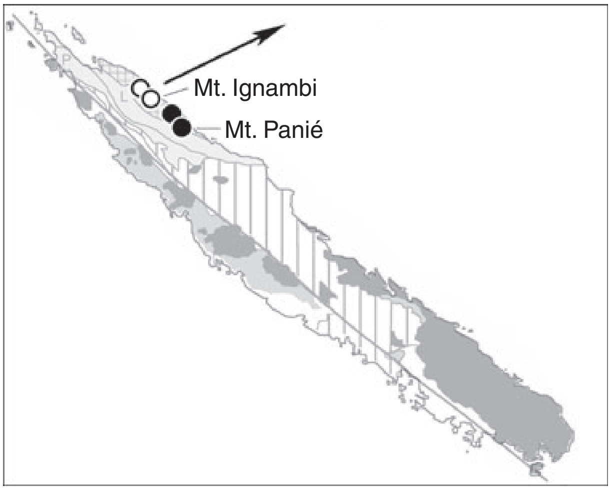

Figure 11 North-eastern Grande Terre. *Araucaria schmidi* (Araucar.) (dots Mount Panié and Mount Colnette), *Agathis montana* (Araucariaceae) (Mount Panié and Mount Colnette), *Spathoglottis petri* (Orchidaceae) (circles, also in Vanuatu). Mount Ignambi is the only known locality of *Hooglandia* (Cunoniaceae).

This may indicate early biogeographical connections between the Central Chain island arcs and precursors of the HP terrane island arcs, long before the terranes derived from these arcs were eventually juxtaposed.

Similar patterns occur in animals, such as the cockroach *Lauraesilpha*, a Grande Terre endemic (Murienne *et al.*, 2008). It has a basal clade on Mount Aoupinié. Its sister group surrounds it, with one component in the south and the other disjunct in the north-east, as in pattern 7 above. As Murienne *et al.* (2008) emphasized, the pattern is not correlated with either rainfall or soil type.

Judging from the distribution map in the Flora, *Amborella* has a small number of populations growing on ultramafic terrane in the southern part of its range where the basement terrane meets the ultramafic rocks. Several other taxa (*Syzygium brachycalyx*, *Syzygium propinquum*, Myrtaceae; *Pleurocalyptus austrocaledonicus*, Myrtaceae; *Salaciopsis megaphylla*, Celastraceae; *Pittosporum letocartiorum*, Pittosporaceae) are restricted to the central third or so of the island, and are found mainly but not exclusively on basement. Again, this probably means that the area of endemism is due to geographical aspects of phylogeny rather than edaphic or climatic factors.

Taxa notably absent or very rare on the basement include *Hunga* (Chrysobalanaceae). The eight New Caledonian species are widespread in Grande Terre but are almost totally absent from the basement (three records of *Hunga rhamnoides* are from there).

Biogeographical patterns within New Caledonia and regional patterns

Several of the taxa referred to show interesting relationships between their distribution within New Caledonia and their distribution outside the country. For example, *Hunga* is found

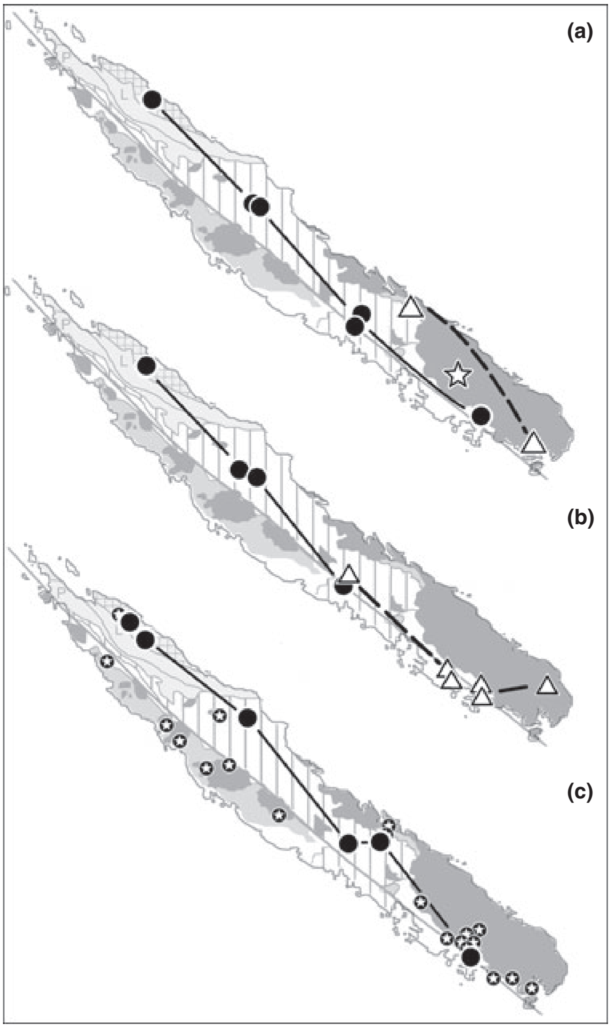

Figure 12 North-eastern–south-western Grande Terre. (a) *Cryptocarya aristata* (dots), *Cryptocarya longifolia* (triangles) and *Cryptocarya bitriplinervia* (star) (Lauraceae). (b) *Cryptocarya velutinosa* (dots) and *Cryptocarya macrocarpa* (triangles). (c) The two species of *Knightia* (Proteaceae) in New Caledonia: *Knightia strobilina* (dots) and the widespread *Knightia deplanchei* (smaller dots).

in New Caledonia but not on the basement, only on accreted terrane, and in eastern PNG, again, not on the cratonic basement of the island, only on accreted terrane. There are also important biogeographical connections between north-eastern Grande Terre and Vanuatu/Fiji, and between the southern ultramafic massif of Grande Terre and New Zealand.

DISCUSSION

Terrane accretion

Aspects of terrane tectonics other than the rifting of Gondwana are often overlooked. Sanmartín & Ronquist (2004) compared the phylogenies of Southern Hemisphere taxa with the break-up sequence of Gondwana and found much incongruence, at least for plants. The authors suggested this could be because the plant taxa they studied are too young to have been affected by break-up (the possibility of their being too old was not considered) or because of long-distance dispersal after the break-up of Gondwana, which they favoured. However, the terminal areas in their cladograms, including New Zealand and New Caledonia, are all biogeographically and geologically composite, and the analyses are thus compromised (cf. Heads, 1999; Ladiges & Cantrill, 2007). Sanmartín & Ronquist (2004) treated New Zealand as a single area simply because it was 'one unit' at the time of break-up of Gondwana, but geologists and panbiogeographers stress that the New Zealand region was already diverse. A large terrane that is critical for New Zealand biodiversity, the Northland–East Coast Allochthon (including the Northland Ophiolite), accreted in the Oligocene, long after the break-up of Gondwana (Whattam *et al.*, 2004). New Caledonia, which Sanmartín & Ronquist (2004) also accepted as an area, is largely the result of terrane amalgamation and associated metamorphism and orogeny which took place both before break-up of Gondwana (for example, in the Jurassic/Early Cretaceous) and after break-up (in the Eocene).

The amalgamation of New Caledonia terranes in the two orogenies involved the metamorphism of rocks, landscapes and living communities, and may be just as significant for evolution and biogeography in the region as classic vicariance by seafloor spreading and basin formation. Phases of modernization for geography and biogeography occurred about the same time in other areas, for example in the western Americas and the Caribbean. The Greater Antilles show many parallels with New Caledonia and New Zealand. A synthesis of ecology and evolution in Caribbean *Anolis* lizards stressed the importance of plate tectonics and terrane accretion (Roughgarden, 1995). Fossil *Anolis* material 20 and possibly even 40 Myr old from Hispaniola is 'indistinguishable' from extant species there, and so the *Anolis* lizards may serve as 'living strata'. The assemblage of large communities, such as those on Cuba and Hispaniola, probably results from combining packages of species when tectonic blocks fuse to form a single island, rather than from the addition of single species one by one, as in chance dispersal. Roughgarden (1995, p. 185) concluded: 'An overall implication of plate tectonics for terrestrial ecology is that relatively fast-acting ecological interactions such as competition and predation are far from sufficient to explain the structure and composition of ecological communities. Instead, ecological communities are fashioned as much by relatively slow geologic processes as by fast species interactions'.

Terranes and age of taxa

In traditional work on ecology and evolution, chronology is based on the age of oldest fossils and the Mesozoic–Cenozoic tectonics discussed here would be considered too old to be

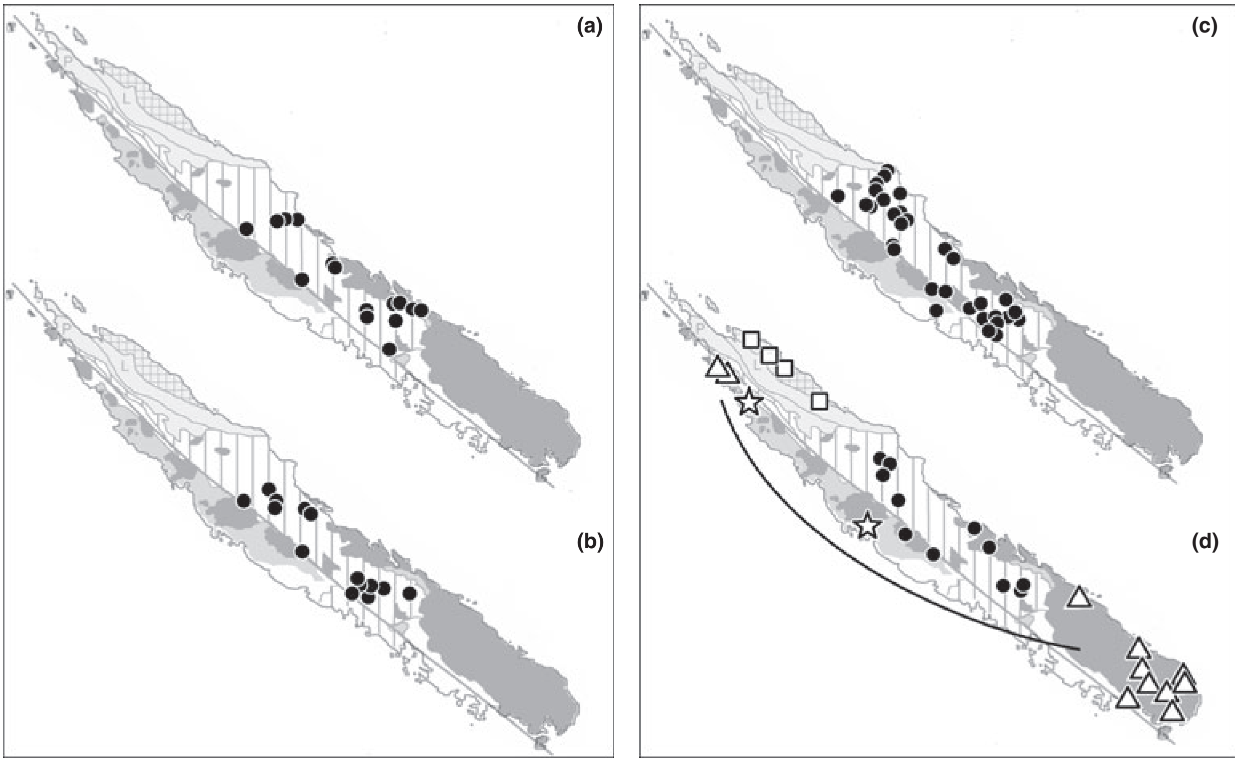

Figure 13 New Caledonia basement endemics. (a) *Pittosporum malaxanii*. (b) *Pittosporum morierei* (Pittosporaceae). (c) *Amborella trichopoda* (Amborellaceae). (d) *Bocquillonia lucidula* (dots, Euphorbiaceae) and the related group *Bocquillonia nervosa* (squares), *Bocquillonia longipes* (stars) and *Bocquillonia spicata* (triangles, disjunct).

relevant to modern species. Species distributions have been assumed to reflect present-day ecology, even when the species themselves might be accepted as (slightly) older. However, much recent molecular work indicates that taxa and their distributions have evolved together, and that both can be much older than usually accepted. A critique of the use of a clock model in evolution and the usual fossil-calibrated molecular clocks suggested that spatial correlation of molecular clades with tectonics is a more reliable method (Heads, 2005b). A recent study using this approach found that the distribution of clades (haplotypes) of the Mediterranean oak *Quercus suber* shows 'remarkable conformity' with terrane rifting and dispersion in the Oligocene and subsequent accretion around the margins of the western Mediterranean (Magri *et al.*, 2007). The authors inferred an early Cenozoic origin for the species and subsequent displacement on the terranes. For at least 15 Myr the populations have persisted in each terrane without detectable modifications of chloroplast DNA and Magri *et al.* (2007) cited this as an example of 'long-term permanence in situ and prolonged evolutionary standstill'. They also compared the biogeographical pattern of the oak with a similar one in *Pinus pinaster*. Hampe & Petit (2007) discussed the *Quercus suber* work and noted that examples of great antiquity of lineages in this region are starting to accumulate. Hampe & Petit (2007) emphasized that Magri and colleagues' innovation lay in their new interpretation, which rejected the idea of long-distance colonizations and showed that genetic patterns instead reflect tectonic history. This conclusion was reached because, first, the distributions are 'extremely clear-cut' and, second, Magri *et al.* (2007) introduced a simple but very effective methodological improvement – using oldest fossils (in this case Miocene) to set a minimum limit for age, not a maximum limit as in many clock studies.

For the diverse New Caledonia palms, Pintaud *et al.* (2001, p. 453) argued that 'It is unlikely that the local endemism of the New Caledonia at specific and generic level in putative refuge zones can be explained by Pleistocene allopatric speciation'. Pintaud *et al.* suggested that the taxa and their distributions, including several north-eastern Grande Terre–southern Grande Terre disjunctions, are instead the result of earlier Cenozoic events.

The oak and palm species cited here may be early Cenozoic, but groups like *Amborella*, the basal angiosperm endemic to the New Caledonian basement terrane, could be much older.

Ultramafic terranes: ophiolite obduction, serpentine soils and biogeography

Ultramafic endemism has fascinated botanists since the first systematists and biogeographers observed it in 16th century Italy (Heads, 2005a). The ultramafic terranes are parts of ophiolites or obducted slices of ocean floor crust and upper mantle and so they are distinctive in both their geochemistry and their tectonic history. The evolutionary relationship

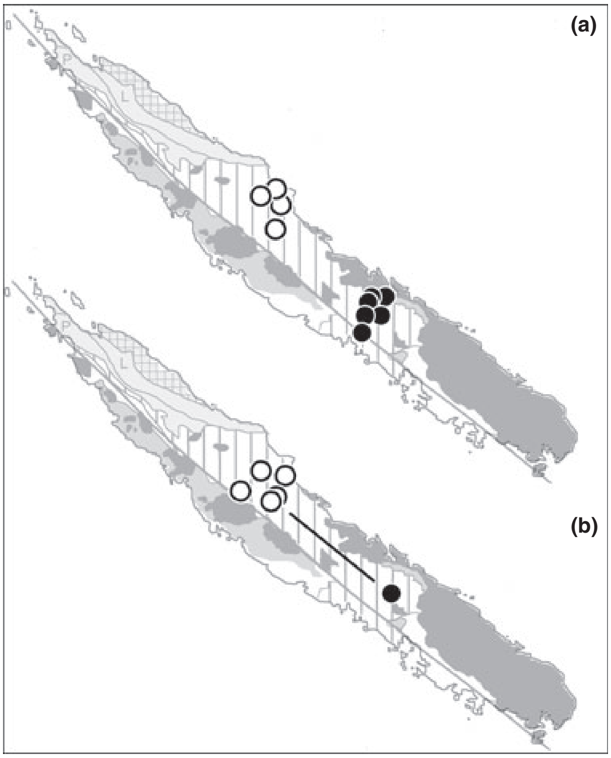

Figure 14 Basement distribution. (a) *Baloghia balansae* (Euphorbiaceae; dots) and *Chamaeanthus aymardii* (Orchidaceae; circles). (b) *Pittosporum mackeei* and *Pittosporum bernardii* (Pittosporaceae).

between the ultramafic terranes and the endemism they host remains controversial and a new approach is suggested here.

Ultramafic-limestone (base-rich) endemism

A classic 'calcareous riddle' (Ewald, 2003) – why are there so many calciphilic species in the central European flora? – has a counterpart in the 'ultramafic riddle' of places like New Caledonia. Both riddles are related by the New Caledonian taxa which occupy both ultramafic and limestone sites. Plants such as *Bocquillonia sessiliflora*, *Balanops vieillardii* and *Syzygium pseudopinnatum* grow on ultramafics on Grande Terre but on calcareous substrate on the Loyalty Islands and Ile des Pins. Santalaceae in New Caledonia have 'zones de prédilection' on ultramafic and calcareous soils (Aubréville *et al.*, 1967–present). The five *Euphorbia* species in New Caledonia are all on calcareous substrate (Morat *et al.*, 2001) while the closely related *Neoguillauminia*, an endemic genus, is restricted to ultramafics. This is a common pattern; plant taxa known only from ultramafic rock and limestone occur in Tuscany (Selvi, 2007), the Balkan Peninsula (Papanicolaou *et al.*, 1983; Stevanović *et al.*, 2003), the Greater Antilles (Judd *et al.*, 1988; Graham, 2002; Hong *et al.*, 2004; Barker & Hickey, 2006; Grose & Olmstead, 2007; Vorontsova *et al.*, 2007), Malesia (Heads, 2003) and New Zealand (Heenan & Molloy, 2006). In both habitats the soil shows high base saturation, but in limestone soils the exchange complex is dominated by calcium, in ultramafic habitats by magnesium. The New Caledonian *Normandia* (Rubiaceae) is a pioneer plant on young and rocky soils on the ultramafic massifs and is also unusual in having relatively high levels of calcium in its leaf tissue (http://www.endemia.nc/).

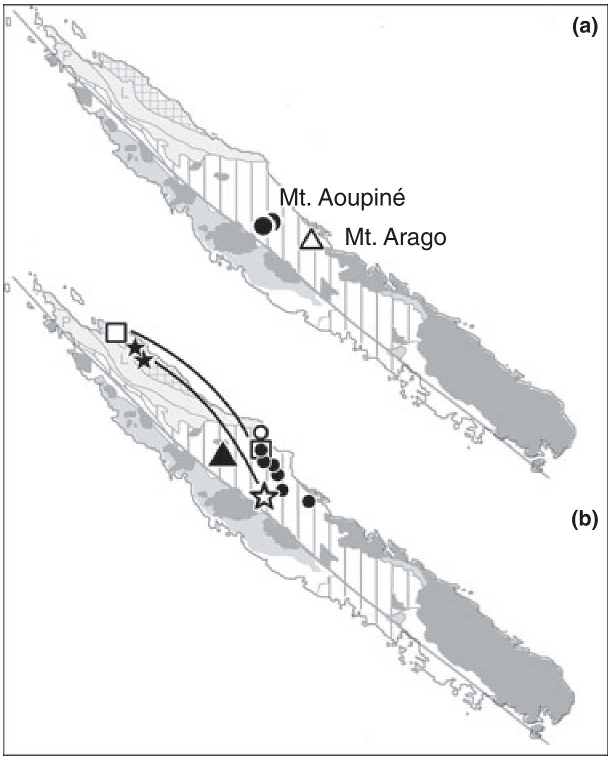

Figure 15 Basement–HP terrane distribution. (a) *Phyllanthus aoupiniensis* (Euphorbiaceae) (Mount Aoupinié) and *Phyllanthus cherrieri* (Mount Arago). (b) *Phyllanthus moratii* (triangle), *Phyllanthus margaretae* (white star), related to *Phyllanthus mandjeliaensis* (black stars), *Phyllanthus vespertilio* (squares), *Phyllanthus pseudotrichopodus* (dots), *Phyllanthus trichopodus* (circle).

Taxa that are able to survive on ultramafics and limestone will automatically thrive around zones of subduction and obduction and will be able to persist there indefinitely as metapopulations surviving on the ephemeral volcanic islands and obducted ophiolites.

Evolution of ultramafic flora

Pole (1994, p. 629) wrote that 'Much of New Caledonia's unique or otherwise interesting plant life at the specific level is restricted to, and presumably a result of, soils developed on its widespread ultramafic rocks. However, some genera are restricted to this substrate, and since the ultramafics were emplaced as an obducted slice of ocean floor in the Late Eocene…, it requires an element of special pleading to argue that these lineages date back to the Cretaceous, 40 million years earlier, as most biogeographers have'. Pole's (1994) interpretation assumes that taxa have stayed in place, not just in the region but even on the same substrate they evolved on.

In this static view, taxa endemic to ocean-floor strata obducted at 40 Ma cannot be any older than the obduction. However, this is unlikely as the ultramafic nappe would have been colonized by the local flora and fauna as it (or the whole ophiolite sequence) was emerging from the sea. It would have inherited its biota from other terranes already in the region, such as the mafic Poya terrane (largely covered by the ultramafic nappe) or limestone strata subsequently removed by erosion. As the upper, mafic, strata of the ophiolite sequence were removed by erosion or tectonic movement, taxa were redeposited onto the lower, ultramafic, strata.

As indicated, the ultramafic flora in New Caledonia shows many affinities with the limestone flora, and the ultramafic nappe was probably emplaced near island arcs. In fact ophiolites in general may be tectonically associated with arcs. Thus, there is no need for the flora currently preserved on the New Caledonian ultramafics to have actually originated on these or indeed any other ultramafics. The biota is one of former island arcs, redeposited onto the ophiolite nappe and eventually onto its peridotite base where plants still survive by means of various morphological and physiological pre-adaptations (such as possession of lignotubers and tolerance of nickel).

Fiedler (1985, p. 1716) argued in a similar way, suggesting that heavy metal tolerance in North American *Calochortus* (Liliaceae) 'is an exaptation in the sense that it may be a character evolved for another use (or no other function), which presently is coopted for its current role for life on ultramafic substrates. [It] may be a plesiomorphic character that perhaps has been repeatedly lost throughout the clade, rather than an apomorphy derived through selection for ultramafic substrates. Thus, tolerance of trace metal accumulation…is a feature that enhances plant fitness but not necessarily one that evolved repeatedly and specifically for life on ultramafic substrates'.

De Kok (2002) concluded likewise, arguing that the occurrence of New Caledonian species on ultramafic soils is a homoplasious character in the respective genera and the result of either pre-adaptation or frequent shifts. He also observed that 'In the minds of some botanists serpentine soils seem to possess almost magical properties. Not only are they said to preserve in isolation so called "primitive" taxa, they can at the same time act as an evolutionary laboratory [producing "derived" taxa]' (De Kok, 2002, p. 235). There does seem to be a problem understanding just how ultramafic endemism evolves. This is probably because the focus has been on soil chemistry and current ecology rather than tectonics and biogeography. As Proctor (2003, p. 105) wrote, in New Caledonia 'The variation in species richness on the ultramafics is difficult to explain. The degree of endemism varies too; it is probably less dependent on soil characteristics than on historical factors'.

Botanists in New Guinea have known for years that the ultramafics there were strong foci of endemism, but as usual it was felt that this endemism was due to edaphic rather than historical factors. However, Polhemus (1996) pointed out that many animals show similar patterns and this greatly weakens the edaphic hypothesis. Instead, Polhemus (1996) recognized that the ultramafics are biogeographically significant because they indicate the location of prior arc terranes and their collision with continental crust. Older collisions are preserved as arc fragments now deeply embedded in the basement terranes of New Caledonia, New Zealand and New Guinea. The remnants of all the accreted arc systems have been crushed between even older arcs or continental crust fragments but have left a biological signature in the disjunct distributions of living taxa.

Many authors have argued that the diversity of rock types in New Caledonia is a fundamental cause of the high floristic diversity. Lithological diversity may have permitted the survival of diverse flora. However, it is suggested here that the diversity of substrates is not the original cause of the biodiversity. This is more likely due to the separate tectonic history and accretion of the component terranes in the Jurassic/Cretaceous and the Eocene.

The conspicuous absences in the New Caledonia flora and the presence of endemic groups could both result from the prior location of the component terranes and floras, rather than soil chemistry. It is sometimes suggested that the extensive ultramafic outcrops in New Caledonia have discouraged the establishment of certain groups there, but this conclusion is not well founded; apart from anything else, most of the land in New Caledonia does not consist of ultramafic rock. In addition, some groups that are typically diverse in ultramafic areas, such as grasses (cf. their high diversity in Cuba) are notably depauperate in New Caledonia; Dawson (1981) described this as 'puzzling'. Indigenous grasses are also depauperate in Fiji (*Lepturus*, with two species, is possibly the only genus there with more than one good species; cf. Heads, 2006) and so the situation in New Caledonia may reflect a regional low-diversity anomaly, also seen in groups such as bees.

CONCLUSIONS

There are clear relationships between the New Caledonian terranes and centres of endemism. The basement terranes together constitute an important centre of endemism not previously recognized. Of the individual basement terranes, the Central Chain volcanics have many local endemics which may represent accreted island arc relics. The Poya terrane outcrops around the margins of the ultramafic terrane. The two are closely associated spatially and it has not been possible to distinguish them biogeographically. The ultramafic terrane is well known as a centre of endemism. It is suggested here that its biota was inherited from the mafic Poya terrane and from limestones of prior arc terranes. The HP terrane, like many orogens, is a major centre of endemism. The Loyalty Ridge has a very different tectonic history from Grande Terre and there are also major differences between the biotas of the two, with old taxa endemic to the Loyalty Islands surviving on the young islands. In addition to these centres, the disjunctions between them may also reflect aspects of palaeogeography.

Correlation of accreted terranes and biogeographical patterns is evident in New Caledonia and also in New Zealand, New Guinea and Borneo (Heads, 1990, 2001, 2003) and in the western Mediterranean (Magri *et al.*, 2007). New Caledonia is composed of seven or eight geological terranes, whereas the much larger New Guinea is made up of 32 and New Zealand of about nine (Mortimer, 2004). The large number of terranes in New Caledonia in relation to its size may have been responsible for the high diversity, endemism and far-flung geographical affinities of the biota.

For the especially diverse New Caledonian groups, Morat *et al.* (1984) cited 'surprisingly active speciation in view of the small surface of the island', but all the component terranes of New Caledonia are now much smaller than they were originally. Likewise, several of the terranes in New Zealand are represented by mere slivers, remnants of formerly much larger structures. Other terranes have probably disappeared entirely within ancestral New Zealand and New Caledonia, leaving only some flora and fauna as a trace of their former existence.

Many authors have assumed that vicariance associated with the rifting of Gondwana and long-distance dispersal are the only possible explanations for Southern Hemisphere biogeography, but this overlooks a great deal of relevant geology. Many taxa have not always existed on the terrane they currently occupy. For example, old endemics can survive *in situ* more or less indefinitely as metapopulations on the individually ephemeral volcanic islands around centres and belts of volcanism. In another example, a slice of seafloor ramped up onto land may inherit taxa from island arcs in the locality that have themselves subsequently been destroyed. The taxa that currently occupy it as local endemics could have colonized the terrane by normal ecological dispersal as it emerged from the sea.

There are clear biogeographical parallels among the Loyalty Islands, the Lau Group in eastern Fiji and Rennell Island in the south-western Solomon Islands. All are young, volcanic/limestone islands on submarine ridges that are much older. They each preserve a biota that is different from that of the older mainland in the respective island groups, and includes many endemics and biogeographical affinities with other, distant archipelagos. Because of this, the bird fauna of Rennell represents a 'paradox' for dispersalist biogeography (Mayr & Diamond, 2001) and the biota of the Loyalty Islands is an 'enigma' (Virot, 1956). It is suggested here that the biogeography of all these islands reflects Palaeogene tectonics and *in situ* survival of endemic 'subduction weeds' as metapopulations around the active margins.

Biologists were quick to appreciate that divergent plate margins could lead to vicariance. However, sister taxa may also occur at convergent margins. This may be the result of juxtaposition during terrane accretion, with the original evolutionary divergence of the groups caused by earlier events. Accretion of terranes and biotas, as suggested for New Caledonia, has occurred widely around the Pacific rim in Japan, New Guinea, east Australia and New Zealand, and from Peru to Alaska. New Caledonia and its extraordinary biodiversity have developed in a context of backarc basin formation, terrane accretion, obduction and orogeny, and the biogeographical patterns of differentiation, deformation and juxtaposition reflect this dynamic history.

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SUPPORTING INFORMATION

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

Appendix S1 Additional information on New Caledonia terranes and endemism.

BIOSKETCH

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