

Ancient islands acted as refugia and pumps for conifer diversity

Fabien L. Condamine^{a,b,c,*}, Andrew B. Leslie^d and Alexandre Antonelli^{a,e}

^aDepartment of Biological and Environmental Sciences, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden; ^bDepartment of Biological Sciences, University of Alberta, Edmonton T6G 2E9, AB, Canada; ^cCNRS, UMR 5554 Institut des Sciences de l'Evolution, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier, France; ^dDepartment of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA; ^eGothenburg Botanical Garden, Carl Skottsbergs gata 22A, 413 19 Gothenburg, Sweden

Accepted 27 January 2016

Abstract

Island species are thought to be extinction-prone because of small population sizes, restricted geographical distribution and limited dispersal ability. However, the topographical and environmental heterogeneity, geographical isolation and stability of islands over long timescales could create refugia for taxa whose source area is threatened by environmental changes. We address this possibility by inferring the evolution of the New Caledonia (NC) and New Zealand (NZ) conifer diversity, which represents over 10% of the world's diversity for this group. We estimate speciation and extinction rates in relation to the presence/absence on these islands, and dispersal rates between the islands and surrounding areas. We also test the Eocene submersion of NC and the Oligocene drowning of NZ by comparing the fit of biogeographical scenarios using ancestral area estimations. We find that extinction rates were significantly lower for island species, and dispersal “out of islands” was higher. A model including a diversification shift when NC emerged better explains the diversification dynamics. Biogeographical analyses corroborate that conifers experienced high continental extinctions, but survived on islands. NC and NZ have thus contributed to the world's conifer diversity as “island refugia”, by maintaining early-diverging lineages from continents during environmental changes on continents. These ancient islands also acted as “species pumps”, providing species into adjacent areas. Our study highlights the important but neglected role of islands in promoting the evolution and conservation of biodiversity.

© The Willi Hennig Society 2016.

“It seems the unlikeliest place on Earth to come to and look for conifers. That impression is wrong. New Caledonia is something like Mecca for conifer enthusiasts ...” Aljos Farjon (2008, p. 154)

Islands have fascinated evolutionary biologists since Darwin and Wallace revealed their value as model systems for understanding biological processes (Losos and Ricklefs, 2009). Because of their isolation, islands exemplify the mechanisms of species colonization and radiation because biodiversity develops as a dynamic between age, dispersal, speciation and extinction (MacArthur and Wilson, 1967; Warren et al., 2015). Although biological radiations have been identified and studied in detail for several

groups on different island systems (e.g. Losos et al., 1998; Gillespie, 2004; Kreft et al., 2008; Fritz et al., 2009; Jönsson et al., 2012), we are just beginning to understand the evolutionary processes governing the generation and maintenance of island biodiversity and their contribution to global diversity (Losos and Ricklefs, 2009; Weigelt et al., 2013; Warren et al., 2015). This is especially true for geologically old and isolated islands originally derived from continental landmasses (Yoder and Nowak, 2006; Weigelt and Kreft, 2013). Such islands are thought to contain an initial biota at the time of their separation from their source, which would then become mixed with the arrival of new taxa by long-distance colonization events. This mosaic composition of old lineages and new arrivals often makes them unique and markedly different from biotas occurring on oceanic islands (Yoder and Nowak, 2006).

*Corresponding author:

E-mail address: fabien.condamine@gmail.com

During periods of drastic environmental changes on mainland areas, it is possible that islands act as refugia for biodiversity. Islands are often topographically and environmentally heterogeneous, and therefore species may not have to move far during periods of climate change to maintain their optimal environment (Sandel et al., 2011). In addition, islands will tend to have more stable climates relative to mainland environments, which may further buffer against the effects of climate changes (Weigelt et al., 2013). By offering a variety of montane and lowland habitats, soil types and relatively stable climates, islands may therefore be able to contribute to protecting species. Some of these species might even at some point re-colonize their source area, and re-establish if suitable environmental and ecological conditions prevail again (Strijk et al., 2012). Although the role of refugia has been extensively acknowledged in temperate ecosystems linked to past climatic changes (Petit et al., 2003; Sahney et al., 2010; Tzedakis et al., 2013), little attention has been paid to the potential role of islands as refugia.

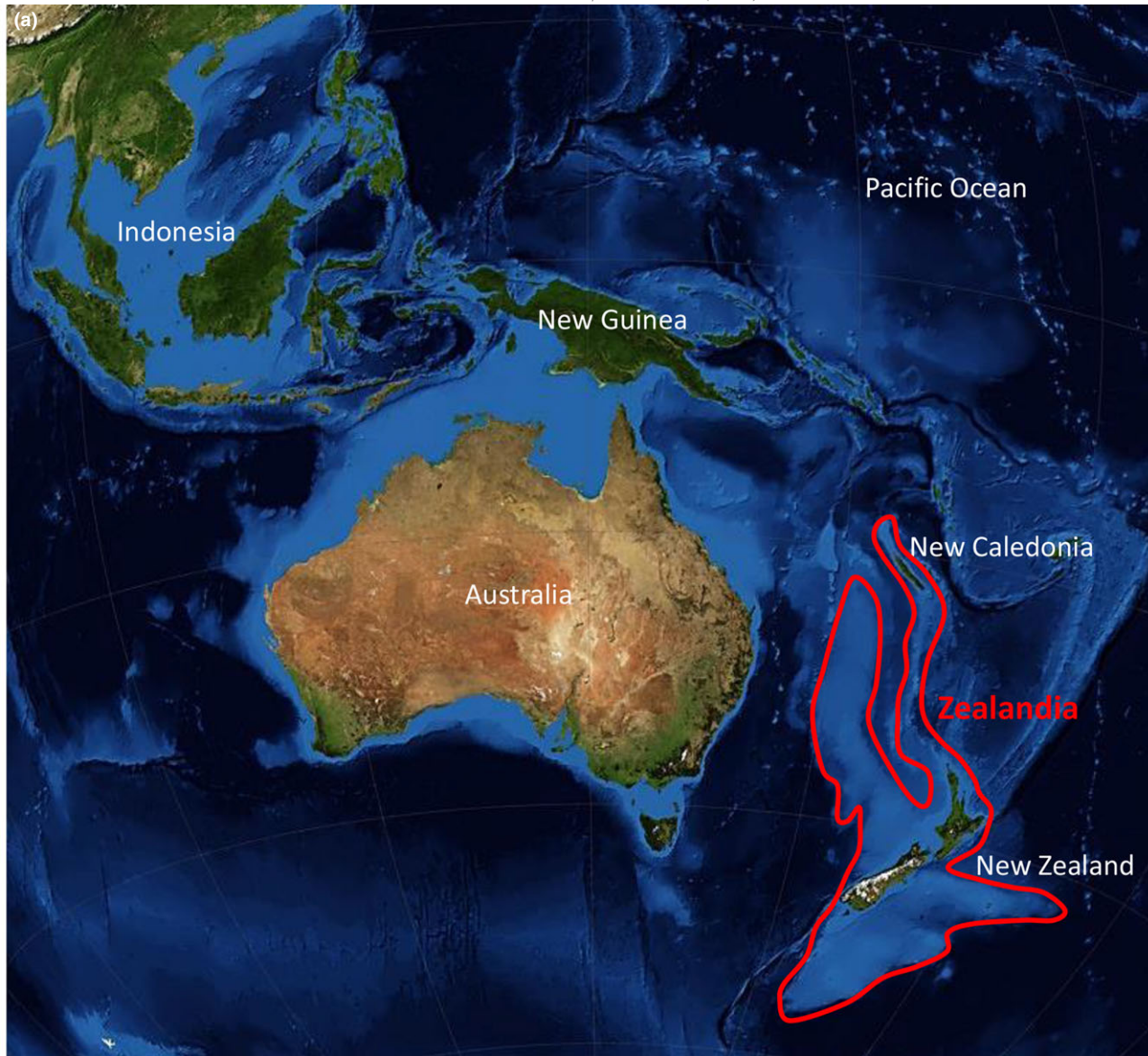
New Caledonia and New Zealand (hereafter jointly called NCNZ) constitute a suitable area for assessing the potential role of islands as biodiversity refugia. Their biodiversity is outstanding, which together with a high level of endemism and threat makes them two biodiversity hotspots (Mittermeier et al., 2004). In NZ, endemism is concentrated at the species level, while NC has a high generic and family endemism. Both islands became isolated in the south-west Pacific Ocean and are today situated more than 1000 km east of the nearest landmass, Australia. NCNZ are remnants of Zealandia, an ancient continent that sank after breaking away from Australia about 60–85 Ma (Gibbs, 2004; Bache et al., 2014). The isolation of Zealandia's remnant islands has been thought to have given rise to a relictual biota (Raven and Axelrod, 1974), although more recent work suggests these islands may be home to more recent radiations or dispersals from other landmasses than traditionally assumed (Trewick et al., 2007; Grandcolas et al., 2008). The NCNZ flora is suggested to comprise many lineages that are survivors of the Cretaceous Gondwanan flora, which once covered large parts of the Southern Hemisphere (Lowry, 1998; Peralta-Medina and Falcon-Lang, 2012). Among these are the conifers (Pinophyta), an ancient clade of seed plants (Leslie et al., 2012) comprising 615 species, of which 43 are endemic to NC and 20 are endemic to NZ. Conifers include many ecologically dominant and well-known species in various families, such as pines in Pinaceae, cypresses in Cupressaceae and araucarias in Araucariaceae. The combined conifer flora of these two islands, despite comprising less than 0.2% of the world's total landmass, is home to more than 10% of the world's conifer diversity (Fig. 1). What explains the high species richness and elevated endemism of

conifers in NCNZ, and which role these islands have played in maintaining or generating conifer diversity, remains unknown.

Competing hypotheses for explaining biodiversity in NCNZ

The geological and evolutionary history of NCNZ is complex (Fig. 2). Over recent decades, three major hypotheses have emerged. The first one postulates that as Zealandia separated from Australia and NZ and NC drifted to their present positions, the newly formed continent carried with it several species. It is important to recognize that Zealandia had a significantly greater land area in the past when it was above water (Gibbs, 2004). Often referred to as the “Gondwanan vicariance” or “Noah's Ark” hypothesis, this scenario is based on the high species diversity observed today in NCNZ, the old age of their geological basement and the presence of supposedly ancient clades with disjunct distribution in the Southern Hemisphere (Lowry, 1998; Heads, 2013). It has also been suggested that descendants from this initial biota have been able to survive in the island's relatively stable climates, while most of their relatives in Australia went extinct due to Cenozoic climatic changes, especially the development of increasingly drier conditions that culminated in the origin of today's semi-arid and desert areas (Byrne et al., 2011).

The second hypothesis posits that the current biotas of NCNZ derive from trans-oceanic dispersals following their separation from Gondwana. This hypothesis formed in response to the development of molecular phylogenies and methods for estimating divergence times, which soon began to challenge the “Gondwanan vicariance” hypothesis. Phylogenetic studies consistently suggest that the current NCNZ biota reached the islands much more recently, apparently by long-distance dispersal from neighbouring islands (Waters and Craw, 2006; Grandcolas et al., 2008; Cruaud et al., 2012; Barrabé et al., 2014; Swenson et al., 2014; Thornhill et al., 2015). In parallel, new geological data indicate that Zealandia was underwater early in the Cenozoic due to thinning of the Australian continental crust and the parallel opening of the Coral and Tasman Seas (Gibbs, 2004; Bache et al., 2014). In particular, some geological data suggest a total submersion of New Caledonia until the “late Eocene re-emergence” ca. 34–37 Ma (Cluzel et al., 2001; Pelletier, 2006; Schellart et al., 2006; Cluzel et al., 2012; Matthews et al., 2015; Fig. 2). There are also conflicting views on whether NZ was completely submerged during the Oligocene (“late Oligocene drowning”, Landis et al., 2006, 2008; Waters and Craw, 2006), or partially remained above sea level (Trewick et al., 2007; Krosch and Cranston, 2013). Evidence from some NZ taxa



(b)

Region	Area size (km ²)	Area of occupancy (km ²)	Number of species	Endemic species
New Caledonia	18 575	1845	43	43
New Zealand	267 000	19 000	20	20
Japan	374 744	13 675	40	30
Caribbean	238 112	5025	16	16
Australia	8 840 000	21 325	41	40
Africa	31 000 000	14 625	34	22
South America	17 850 420	15 100	34	32
Mexico	1 972 545	39 825	80	61

Fig. 1. Geographical context of the now 93% submerged continent Zealandia and the remnant islands (a). The table highlights the species richness pattern of conifers in several regions including New Caledonia and New Zealand, two important biodiversity reservoirs (relative to their area size) of conifer diversity (b).

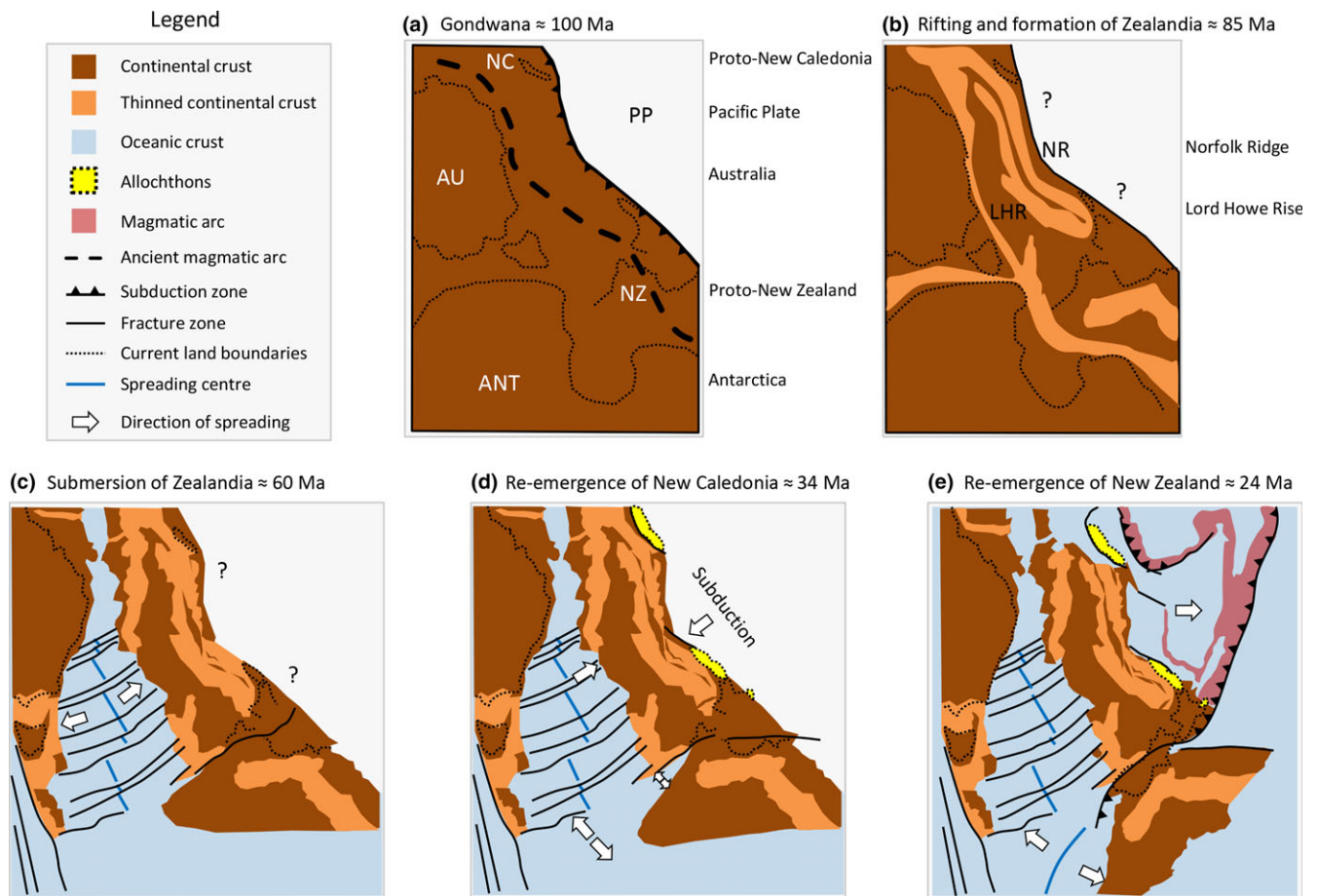


Fig. 2. Tectonic evolution of Zealandia adapted from Bache et al. (2014). In the Early Cretaceous (> 100 Ma), the eastern Gondwanan margin was characterized by a SW-dipping subduction (a). The second phase (100–85 Ma) is characterized by widespread rifting and extension (b). The third phase corresponds to the opening of the Tasman Sea and isolation of Zealandia, starting a progressive submersion due to crustal thinning (c). The fourth and fifth tectonic phases are associated with the Cenozoic initiation and evolution of a subduction event, which led to the re-emergence of New Caledonia (d) and New Zealand (e).

(e.g. Conran et al., 2014), as well as recent geological evidence (e.g. Kamp et al., 2014), suggests that at least some land must have stayed above water (Matthews et al., 2015). Thus for a period of about 20 Myr, terrestrial life would not have been possible on NC, meaning that when it surfaced again the island would have been vacant (Grandcolas et al., 2008). Therefore, NC can be effectively considered as an oceanic island, albeit of great age and of predominantly continental rather than volcanic origin (Grandcolas et al., 2008). The second hypothesis thus implies that the apparently relictual groups endemic to NCNZ must have arrived lately on these islands, and then gone extinct in Australia, for example due to Miocene continental aridification (Byrne et al., 2011). Nonetheless it is challenging to distinguish between old lineages that have dispersed into NCNZ versus old lineages that have persisted and then radiated.

The third hypothesis posits that while Zealandia was at least partially submerged, ephemeral islands

remained and served as refugia for the old Gondwanan biota (Morat et al., 1984; Lowry, 1998; Heads, 2008, 2013). Many attributes of NC's flora, such as its high generic and familial diversity, and the presence of numerous relict groups, would be particularly difficult to explain by invoking long-distance dispersal (Lowry, 1998). This model was notably developed based on the occurrence of many supposedly relictual species from Mesozoic tropical rainforests (such as *Amborella*, conifers, palms, *Nothofagus*), as well as doubts on the geological evidence supporting a complete submersion of NCNZ after their separation from the mainland (Kamp et al., 2014). Under this model, old lineages have persisted over geological time as dynamic meta-populations surviving *in situ* on the ephemeral islands and atolls (Ladiges and Cantrill, 2007; Heads, 2008). These supposed islands may have occurred in the surroundings of NCNZ in the Palaeogene, and were of either continental or volcanic origin (Hackney et al., 2012; Baur et al., 2014) or emerged from low sea levels

(Morat et al., 1984; Lowry, 1998; Heads, 2008, 2013). Alternatively, NZ could have served as a temporary Eocene refuge, while NC was under water, and vice versa once NC re-emerged (assuming a drowning of NZ). Consequently, these islands would have served as biotic sources and a starting point for stepping-stone dispersals. Recent geological evidence underlying this scenario tends to be supportive (Hackney et al., 2012), but the refugia hypothesis remains largely untested in a phylogenetic framework.

Considering the three prevalent biogeographical scenarios proposed thus far, explaining the presence of supposedly relictual groups in NCNZ remains elusive. Given the relatively old age, extreme island endemism and low dispersal ability of conifers (Farjon, 2008), they constitute an excellent model for testing the validity of each scenario (De Laubenfels, 1996). We pursue this using a well-sampled time-calibrated phylogeny combined with distributional data and birth–death models as well as biogeographical analyses to evaluate the diversification processes that shaped the evolution and maintenance of NCNZ diversity.

Materials and methods

Time-calibrated phylogeny and conifer diversity in NC and NZ

We used a recently published time-calibrated conifer phylogeny including 489 out of 615 species, which is approximately 80% of the extant conifer diversity

(Leslie et al., 2012). This phylogeny is built based on a molecular dataset comprising two nuclear genes (18S and a phytochrome gene, PHYP) and two plastid genes (*matK* and *rbcL*). Divergence times were estimated using a Bayesian relaxed clock approach coupled with an uncorrelated lognormal model calibrated with 16 fossils, which were used as minimum age constraints on different nodes (Leslie et al., 2012). We coded each species in the dataset for two binary (1/2) characters: (i) occurring outside NCNZ and (ii) endemic to NCNZ, based on published literature of species distributions (Farjon and Filer, 2013) and thoroughly verified online databases (<http://www.conifers.org/>; <http://herbaria.plants.ox.ac.uk/bol/conifers>).

Hypotheses and predictions

We formulate three testable hypotheses (H_1 – H_3) to explain the origin and diversification of the conifer diversity in NCNZ, which imply different expectations in patterns and processes (summarized in Table 1).

H_1 : Under the “Gondwanan vicariance” hypothesis, we expect: (i) ancient ages for the lineages subtending a clade of endemic species in NCNZ that are congruent with the tectonic history of the region (ca. 80 Ma or more); (ii) low dispersal rates between NCNZ and neighbouring regions after the vicariance event; (iii) high cladogenetic speciation rates implied by the break-up of Australia and Zealandia (i.e. the geographical range of a lineage is split into discontinuous parts, which form two geographically isolated descendant lineages).

H_2 : Under the “late Eocene NC re-emergence” and “late Oligocene NZ drowning” hypothesis, we expect: (i) recent ages

Table 1

Expected macroevolutionary mechanisms under three biogeographical scenarios explaining the conifer diversity in New Caledonia and New Zealand

	Scenario 1 Gondwanan vicariance	Scenario 2 Islands' re-emergence	Scenario 3 Island refugia
Ages of lineages			
Ancient	×		
Recent		×	
Mosaic			×
Dispersal rates			
Low into NCNZ	×		
High into NCNZ		×	
Low out of NCNZ	×		
High out of NCNZ			×
Extinction rates			
Low within NCNZ	×		×
High within NCNZ		×	
Speciation rates			
Low within NCNZ	×		×
High within NCNZ		×	
Ancestral area			
Ancient vicariance	×		
Recent long-distance dispersal		×	
Ephemeral islands			×

for the endemic species of NCNZ, i.e. post-dating the late Eocene for NC, and post-dating the late Oligocene for NZ; (ii) higher dispersal rates into NCNZ after they re-emerged than out of NCNZ, due to a higher rate of colonization events out of the mainland and into the islands as predicted by island biogeography (Warren et al., 2015); and (iii) high speciation rates within NCNZ after the colonization of the islands, due to ecological opportunity (i.e. constituting an evolutionary “cradle” of diversity).

H₃: Under the “island refugia” hypothesis, we expect: (i) a mosaic of ancient and recent clades due to the persistence of Gondwanan lineages and recent diversification of others when NCNZ surfaced again; (ii) higher dispersal rates out of NCNZ than the other way around because refugia provided the biodiversity for colonizing adjacent areas (Petit et al., 2003; Tzedakis et al., 2013); (iii) lower extinction rates in NCNZ than elsewhere due to the general capacity of mountainous islands to withstand environmental changes better than flatter continental areas, in this case Australia (NZ became mountainous in the mid-Miocene, Walcott, 1979).

Macroevolutionary analyses

If there are *a priori* reasons to believe that ecological, geographical or morphological traits influence diversification, the use of trait-dependent diversification models is appropriate to concurrently model trait evolution and its impact on diversification (Maddison et al., 2007). In those models, species are characterized by an evolving trait, and their diversification follows a birth–death process in which speciation and extinction rates may depend on the value of the trait. Some of these models, derived from the Binary State Speciation and Extinction model (BiSSE, Maddison et al., 2007), have been used in biogeographical contexts (e.g. Roldan et al., 2014) but they have been rarely applied to island biogeography. Although recent studies have challenged the use of BiSSE-like models to test hypotheses on trait-based diversification (Maddison and FitzJohn, 2015; Rabosky and Goldberg, 2015), these models remain important and relevant tools to address such hypotheses (Ng and Smith, 2014), and should be less sensitive to biases when applied to well-sampled and large phylogenies such as are available for conifers.

Here we use 500 conifer phylogenies randomly selected from the Bayesian posterior distribution of dating analyses (from Leslie et al., 2012) and combined them with distributional data to fit two trait-dependent diversification models: (i) the BiSSE model with constant diversification rate for a given trait through time, and (ii) the Cladogenetic State change Speciation and Extinction model (ClasSE, Goldberg and Igic, 2012). We did not use the Geographic State change Speciation and Extinction model (GeoSSE, Goldberg et al., 2011) because all NCNZ species are endemic to those islands, whereas GeoSSE is appropri-

ate when dealing with widespread species (occurring in more than one analytical unit). The BiSSE and ClasSE models account for incomplete taxon sampling, which is informed as a sampling fraction of species at present having a given trait (FitzJohn et al., 2009). The main advantage of ClasSE over traditional BiSSE is that characters can change both along a branch independently from the speciation process (i.e. an anagenetic change), as well as during the speciation process (i.e. cladogenetic change; Goldberg and Igic, 2012). Simulation studies have shown that a large, well-sampled tree (which is the case here) is required by these methods, whereas trees containing fewer than 300 species may lack sufficient phylogenetic signal to produce enough statistical power (Davis et al., 2013).

The BiSSE model has six distinct parameters: two speciation rates without character change (i.e. without range shift, or *in situ* speciation) associated with NCNZ (hereafter “N”, λ_N), and species occurring in other places (hereafter “Elsewhere” or “E”, λ_E), two extinction rates associated with NCNZ (μ_N) and Elsewhere (μ_E), and two transition rates (i.e. dispersal or range shift) with one out of NCNZ to Elsewhere (q_{N-E}), and from Elsewhere to NCNZ (q_{E-N}).

The ClasSE model has ten distinct parameters: two cladogenetic speciation rates without range shift associated with NCNZ (λ_{N-N+N}) and Elsewhere (λ_{E-E+E}), four cladogenetic speciation rates with range shift (λ_{N-N+E} , λ_{E-E+N} , λ_{N-E+E} and λ_{E-N+N}), two extinction rates associated with NCNZ (μ_N) and Elsewhere (μ_E), and two transition rates with one out of NCNZ to Elsewhere (q_{N-E}), and one out of Elsewhere to NCNZ (q_{E-N}). For clarity, we called “symmetrical” the speciation rate that produces two daughters from one parent without range shift (λ_{N-N+N} and λ_{E-E+E}), and “asymmetrical” the speciation rate that produces two daughter lineages with range shift (λ_{N-N+E} , λ_{E-E+N} , λ_{N-E+E} and λ_{E-N+N}). An overall speciation rate for a given occupied area is the sum of symmetrical and asymmetrical speciation rates estimated by the ClasSE models.

Analyses were performed using the R-package *diversitree* 0.9-7 (Fitzjohn, 2012) using the functions *make.bisse*, and *make.classe* to construct the likelihood functions for each model based on the data, and the functions *constrain* and *find.mle* to apply different diversification scenarios as described in Appendix S1.

Time-variable trait diversification and the emergence of NCNZ

We assessed the effect of the geographical occurrence and endemism on diversification, while also allowing for rates to change through time, which reduces the bias of using constant rates. For this we used the BiSSE.td model, in which rates are allowed to

vary for each parameter. BiSSE.td uses the same parameters as BiSSE, except that the number is doubled as we introduce a time at which rates are allowed to shift. For instance, the speciation rate associated with NCNZ may undergo a slowdown after the shift time, necessitating two parameters for the speciation rate. This results in 12 parameters in total for the BiSSE.td model. A similar approach cannot be performed with the ClaSSE model, as no time variation has been implemented to date.

The analytical framework designed here is particularly suitable to test the emergence of NC, estimated between ~ 34 and 37 Ma (Schellart et al., 2006), and of NZ at ~ 24 Ma (Landis et al., 2006, 2008). Introducing a shift time around those ages, the model infers speciation, extinction and transition rates before each shift (i.e. from the origin of the group to the shift) and subsequently infers those rates after the shift to the present. We built two scenarios with BiSSE.td models (with the same number of BiSSE models): one scenario with a shift time at 25 Ma (NZ scenario model) and one with a shift time at 35 Ma (NC scenario model). These shift times are initial values that are re-estimated by the models during the likelihood calculation. We also fitted the BiSSE.td models on the posterior trees of conifers to estimate the confidence intervals of parameters and the support and robustness of the selected models.

Model selection

For each BiSSE, BiSSE.td and ClaSSE model, we computed the corrected Akaike Information Criterion (AICc) based on the log-likelihood ($\log L$) and the number of parameters. We checked support for the selected model against all models nested within it using the likelihood ratio test (LRT, significant at $P < 0.05$). The scenario supported by LRT and with the lowest AICc was considered the best. If the model with the lowest AICc was not supported by LRT, the model with fewer parameters was instead considered the best. Net diversification rates [$r = \text{speciation} (\lambda) - \text{extinction} (\mu)$] were then computed. Finally, we used the maximum clade credibility (MCC) tree and a Markov Chain Monte Carlo (MCMC) approach for the best model to examine the confidence interval of the parameter estimates. Following the recommendations from Fitzjohn (2012), we used an exponential prior $1/(2r)$ and started the chain with the parameters obtained by maximum likelihood. We ran 20 000 steps of MCMC and applied a burn-in of 2000 steps.

Biogeographic analyses and the emergence of NCNZ

We followed the study of Rolland et al. (2015), and complemented our diversification approach with

biogeographical analyses to estimate ancestral areas in order to corroborate the inferences of BiSSE-like models. We did not aim at inferring a precise biogeographical history of conifers but instead our purpose was orientated to test biogeographical hypotheses relative to the geological context of NCNZ. We thus examined the fit of two simple biogeographical scenarios in which we built a time-stratified palaeogeographical model as a constraint for the analyses. We used BioGeoBEARS (Matzke, 2014) to estimate ancestral areas for conifers based on four areas: NC, New Caledonia; NZ, New Zealand; AU, Australia; and E, elsewhere. We coded each species as present or absent within each of these regions. We used the Dispersal-Extinction-Cladogenesis (DEC) model (Ree and Smith, 2008) along with the j parameter (for founder-event dispersal or jump dispersal) because founder-event speciation is particularly likely to be important in oceanic island systems (Matzke, 2014).

We then constructed two time-stratified palaeogeographical models with the following time slices: 0 – 24 Ma (re-emergence of NZ), 24 – 37 Ma (re-emergence of NC, and drowning of NZ), 37 – 56 Ma (submersion of NC), 56 – 80 Ma (separation of Zealandia from Australia), 80 – 120 Ma (Zealandia separated from Antarctica) and 120 – 330 Ma (Zealandia did not exist). The first biogeographical scenario, referred to as the “late Eocene re-emergence of NC and Oligocene drowning of NZ”, imposed geological constraints on the absence of NC during the Eocene and of NZ during the Oligocene, according to the most recent geological model (Cluzel et al., 2001, 2012; Pelletier, 2006; Schellart et al., 2006; Bache et al., 2014; Matthews et al., 2015). The second biogeographical scenario, referred to as the “island refugia”, relied on the same model but added a fifth region to model the possible presence of ephemeral islands (either of continental or of volcanic origin) in the region while NC and/or NZ were submerged (Morat et al., 1984; De Laubenfels, 1996; Lowry, 1998; Heads, 2008, 2013; Hackney et al., 2012; Baur et al., 2014). The two models also included the vicariance model, originally invoked, as represented by the separation of Zealandia (NCNZ) from Australia, and the split of NCNZ in the Palaeocene (Gibbs, 2004; Ladiges and Cantrill, 2007; Heads, 2008, 2013). In addition, dispersal constraints between areas were applied to represent the dispersal possibilities to move from one area to another. A key epoch is from the late Eocene to early Miocene when the islands were close enough for plant dispersal, but after the early Miocene dispersal was more hazardous (Segev et al., 2012). We set a value of 1.0 when two areas were geologically connected, and a value of $0.1/0.5$ when an oceanic/marine barrier separated two areas, respectively.

Long-distance dispersal was set with a value of 0.01. A value of 0.0 was set for when the islands were submerged. The same dispersal constraints were used for the two biogeographical models, but we set a dispersal value of 0.1 to disperse into or out of the ephemeral (volcanic) islands in the second model. Thus, the two biogeographical models differed only by the presence or absence of the ephemeral islands. We applied these two models to reconstruct ancestral areas of conifers, and then compared the log-likelihoods and AICc to select the best-fitting model.

Results

Conifers in NC and NZ

In total, NCNZ has 63 endemic conifer species (43 in NC and 20 in NZ), which makes up more than 10% of the global conifer diversity. In the conifer timetree, 58 of the 63 endemic species in NCNZ were included (ca. 92%; see Appendix S2). Examining the distribution of these species in the phylogeny (Fig. 3), there are some evident recent colonizations and

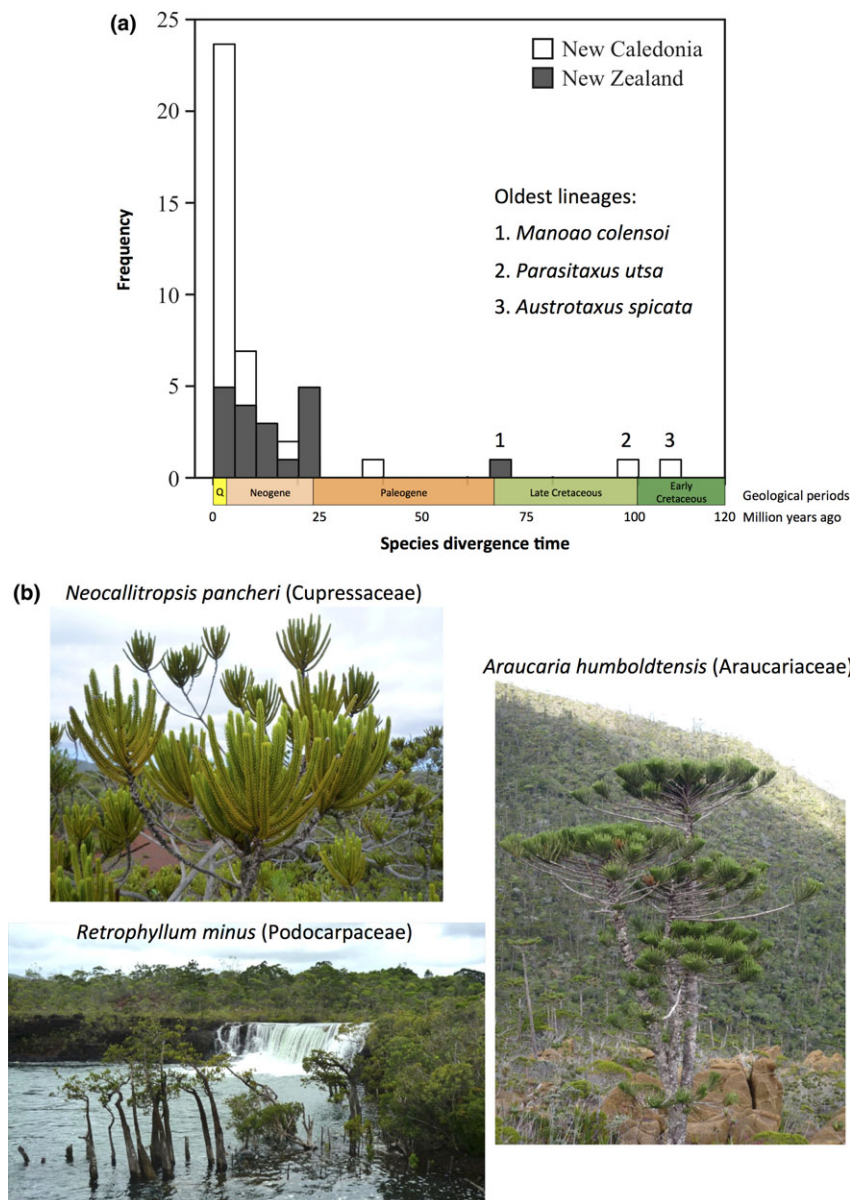


Fig. 3. Histogram of divergence times (a) of island species based on the conifer time-calibrated tree. New Caledonia contains long branched “relictual” taxa (e.g. *Austrotaxus* and *Parasitaxus*), but it also has several more recent radiations (e.g. *Agathis*, *Araucaria*, *Dacrydium* and *Podocarpus*). Similarly, New Zealand experienced both recent speciation events (e.g. *Podocarpus* and *Phyllocladus*) as well as ancient ones (e.g. *Manoao*). Endemic conifer species in New Caledonia (b) are portrayed. Pictures courtesy of Fabien Condamine.

subsequent radiations (e.g. *Araucaria* in NC) as well as ancient isolated lineages that survived in NCNZ (or did not diversify) since the Mesozoic (this pattern may also be interpreted as the survival of old lineages and recent diversification). Both NC and NZ show a mixture of old and more recent lineages, supporting a mosaic of ages as predicted under H_3 .

Macroevolutionary analyses

We found that the best-fitting BiSSE model was the one with occupied area affecting speciation ($\lambda_N \neq \lambda_E$), extinction ($\mu_N \neq \mu_E$) and transition rates ($q_{N-E} \neq q_{E-N}$). Simpler models were not supported ($\Delta AIC = 16.21$ and $P < 0.001$ against the second best model). The results of all the BiSSE models realized over the Bayesian posterior distribution are presented in Table 2. The Bayesian MCMC analysis using the MCC tree and the best-fitting model is shown in Fig. 4 (the model selection is given in Appendix S3). In this model, speciation rate was lower for NCNZ species ($\lambda_N = 0.0795 \pm 0.00055$ events/Myr and $\lambda_E = 0.2309 \pm 0.00107$ events/Myr). Extinction rate was lower for NCNZ species ($\mu_N = 0.0151 \pm 0.00106$ events/Myr and $\mu_E = 0.2348 \pm 0.00126$ events/Myr). Transition rates were much higher out of NCNZ than in the other direction. Speciation, extinction and transition rates between the two geographical traits are significantly different with the Bayesian MCMC analysis (Additional file 4: Fig. S2). Net diversification rates were thus higher for NCNZ species, and are significantly different from the net diversification rates of species in other areas (Appendix S4).

We found that the best-fitting ClaSSE model was the one with occupied area affecting cladogenetic speciation, both without and with range shift ($\lambda_{N-N+N} \neq \lambda_{E-E+E} \neq \lambda_{N-N+E} \neq \lambda_{E-E+N} \neq \lambda_{N-E+-E} \neq \lambda_{E-N+N}$), extinction ($\mu_N \neq \mu_E$) and anagenetic speciation ($q_{N-E} \neq q_{E-N}$). Other models were not supported ($\Delta AIC = 2.864$ and $P = 0.0261$ against the second best model that has one fewer parameter). The results of all the ClaSSE models performed over the Bayesian posterior distribution are presented in Table 2. The Bayesian MCMC analysis of the best-fitting model with the MCC tree is portrayed in Fig. 5; the model selection is given in Appendix S1. In the best-fitting model, inferred parameters are of the same order as for the BiSSE, and most importantly they show the same evolutionary pattern: speciation rates without range shift were also lower for NCNZ species ($\lambda_{E-E+E} > \lambda_{N-N+N}$). Moreover, speciation rates with range shift were higher for NCNZ ($\lambda_{N-N+E} > \lambda_{N-E+E} > \lambda_{E-N+N} > \lambda_{E-E+N}$), and speciation rates with range shift change were lower than speciation rates without range shift. Extinction rates were also

lower for NCNZ species ($\mu_E > \mu_N$). Transition rates were higher from NCNZ to elsewhere ($q_{N-E} > q_{E-N}$). While over 500 posterior trees, speciation, extinction and transition rates are significantly different (Table 2), the Bayesian MCMC analysis on the MCC tree does not show significant differences for speciation rates with range shift (Appendix S5). As for BiSSE, the net diversification rates were thus higher for the NCNZ species and significantly different from the net diversification rates of other species (Appendix S5).

Overall the best-fitting models and the estimated parameters are very similar for BiSSE and ClaSSE (i.e. lower cladogenetic speciation without range shift, lower extinction in NCNZ than elsewhere, and higher anagenetic speciation rate dispersing away from NCNZ). The best-fit BiSSE model has six free parameters ($\log L = -1893.878$) and the best-fit ClaSSE model has ten free parameters ($\log L = -1901.087$), which gives support to the BiSSE model ($\Delta AIC = 22.704$ and $P = 0.0061$ against the ClaSSE model that has four more parameters). This suggests that accounting for the effect of cladogenetic range shift did not improve the fit of the models, and indicates that our results are robust to the choice of diversification method used.

Time-variable trait diversification

We found that the best-fitting BiSSE.td model with a shift time at 35 Ma (NC re-emergence) was the model in which all parameters are allowed to vary. Simpler models were not supported ($\Delta AIC = 22.447$ and $P < 0.001$ against the second best model). We found that the best-fitting BiSSE.td model with a shift time at 25 Ma (NZ re-emergence) was also the model in which all parameters are allowed to vary. Simpler models were not supported ($\Delta AIC = 2.096$ and $P = 0.0427$ against the second best model).

The results of all the BiSSE.td models realized over the Bayesian posterior distribution are presented in Table 3. We compared both BiSSE.td models: the best-fit BiSSE.td for the NC scenario model has 13 free parameters ($\log L = -1875.211$) and the best-fit BiSSE.td model for the NZ scenario has also 13 free parameters ($\log L = -1880.632$), which gives support to the BiSSE.td model with the NC scenario ($\Delta AIC = 10.841$ and $P < 0.0001$). The Bayesian MCMC analysis using the MCC tree and the best-fitting model is shown in Fig. 6 (the model selection is given in Appendix S6). In this model, we found that initial speciation, extinction and transition rates were essentially similar between NCNZ and elsewhere. After the shift of diversification, estimated at 31.7 Ma, we found that both speciation and (in particular) extinction rates decreased for NCNZ species, and dispersal (transition) rates increased out of NCNZ. Speciation,

Table 2

Comparison of models for the global conifer phylogeny, using 500 random Bayesian posterior trees for the BiSSE (a) and the ClaSSE models (b). These results correspond to all models considered in this study. For each model, the maximum-likelihood estimates of the mean and standard error for all parameters are summarized over the posterior distribution of the dating analysis. The best model is indicated in bold. We denote log L, the log-likelihood; AICc, the corrected Akaike Information Criterion; $\Delta AICc$, the difference between AICc of the model and the best model. In BiSSE the parameters are λ_E , the speciation rate for continental species; λ_N , the speciation rate for species living in NCNZ; μ_E , the extinction rate for continental species; μ_N , the extinction rate for species living in NCNZ; q_{E-N} , the transition rate from continents to NCNZ; q_{N-E} , the transition rate from NCNZ to continents

Model	d.f.	log L	AICc	$\Delta AICc$	λ_E	λ_N	μ_E	μ_N	q_{E-N}	q_{N-E}
(a) BiSSE										
Null model	3	-1918.780 ± 1.5574	3843.609 ± 3.1148	43.679	0.1978 ± 0.00085		0.1912 ± 0.00088		0.0037 ± 0.00001	
$(\lambda_E = \lambda_N, \mu_E = \mu_N, q_{E-N} = q_{N-E})$										
$\lambda_E \neq \lambda_N, \mu_E = \mu_N, q_{E-N} = q_{N-E}$	4	-1909.028 ± 1.5912	3826.138 ± 3.1825	26.208	0.2021 ± 0.00088	0.1575 ± 0.00070	0.1904 ± 0.00089		0.0064 ± 0.00003	
$\lambda_E = \lambda_N, \mu_E \neq \mu_N, q_{E-N} = q_{N-E}$	4	-1910.164 ± 1.5949	3828.410 ± 3.1897	28.479	0.1963 ± 0.00083		0.1842 ± 0.00083	0.2253 ± 0.00105	0.0069 ± 0.00003	
$\lambda_E = \lambda_N, \mu_E = \mu_N, q_{E-N} \neq q_{N-E}$	4	-1904.028 ± 1.5927	3816.140 ± 3.1855	16.209	0.1976 ± 0.00084		0.1909 ± 0.00087		0.0035 ± 0.00003	0.0218 ± 0.00021
$\lambda_E \neq \lambda_N, \mu_E \neq \mu_N, q_{E-N} = q_{N-E}$	5	-1908.762 ± 1.5892	3827.647 ± 3.1785	27.717	0.2069 ± 0.00087	0.1408 ± 0.00104	0.1958 ± 0.00088	0.1721 ± 0.00124		
$\lambda_E \neq \lambda_N, \mu_E = \mu_N, q_{E-N} \neq q_{N-E}$	5	-1903.874 ± 1.5932	3817.872 ± 3.1863	17.941	0.1975 ± 0.00084	0.1908 ± 0.00098	0.1901 ± 0.00087		0.0039 ± 0.00007	0.0215 ± 0.00018
$\lambda_E = \lambda_N, \mu_E \neq \mu_N, q_{E-N} \neq q_{N-E}$	5	-1903.163 ± 1.5952	3816.451 ± 3.1904	16.520	0.1998 ± 0.00088		0.1990 ± 0.00102	0.1773 ± 0.00081	0.0019 ± 0.00005	0.0267 ± 0.00035
All free										
$(\lambda_E \neq \lambda_N, \mu_E \neq \mu_N, q_{E-N} \neq q_{N-E})$	6	-1893.878 ± 1.5915	3799.931 ± 3.1830	0	0.2309 ± 0.00107	0.0795 ± 0.00055	0.2348 ± 0.00126	0.0151 ± 0.00106	0.0004 ± 0.00002	0.0632 ± 0.00082
(b) ClaSSE										
$(\lambda_{E-EE} = \lambda_{N-NN} = \lambda_{E-EN} = \lambda_{N-NE} = \lambda_{E-NN} = \lambda_{N-EE}, \mu_E = \mu_N, q_{E-N} = q_{N-E})$	3	-2144.707 ± 1.8284	4295.464 ± 3.6567	472.829	0.0586 ± 0.00028					
$\lambda_{E-EE} \neq \lambda_{N-NN} \neq \lambda_{E-EN} \neq \lambda_{N-NE} \neq \lambda_{E-NN} \neq \lambda_{N-EE}, \mu_E = \mu_N, q_{E-N} = q_{N-E}$	8	-1908.199 ± 2.2937	3832.698 ± 4.5875	10.063	0.1758 ± 0.00346	0.0014 ± 0.00005	0.0676 ± 0.01011	0.1681 ± 0.00150	0.0075 ± 0.00166	
$\lambda_{E-EE} \neq \lambda_{N-NN}, \lambda_{E-EN} \neq \lambda_{N-NE} = \lambda_{E-NN} \neq \lambda_{N-EE}, \mu_E = \mu_N, q_{E-N} = q_{N-E}$	5	-1911.497 ± 1.8310	3833.119 ± 3.6621	10.484	0.1989 ± 0.00098	0.0013 ± 0.00005	0.1532 ± 0.00077	0.1895 ± 0.0010	0.0028 ± 0.00012	
$\lambda_{E-EE} = \lambda_{N-NN}, \lambda_{E-EN} \neq \lambda_{N-NE} = \lambda_{E-NN} = \lambda_{N-EE}, \mu_E = \mu_N, q_{E-N} = q_{N-E}$	7	-1933.215 ± 2.5945	3880.662 ± 5.1889	58.027	0.1197 ± 0.00522	0.0000 ± 0.00000	0.3307 ± 0.02229	0.1197 ± 0.00522	0.0367 ± 0.00274	

Table 2
(Continued)

Model	d.f.	log L	AICc	$\Delta AICc$	λ_{E-EE}	λ_{E-EN}	λ_{E-NN}	λ_{N-EE}	λ_{N-NE}	λ_{N-NN}	μ_E	μ_N	q_{EN}	q_{NE}
$\lambda_{E-EE} = \lambda_{N-NN} =$ $\lambda_{E-EN} = \lambda_{N-NE} =$ $\lambda_{E-NN} = \lambda_{N-EE},$ $\mu_E = \mu_N, q_{EN} \neq$ q_{NE}	4	-1980.951 ± 1.8362	3969.984 ± 3.6725	147.349	0.0668 ± 0.00064						0.1939 ± 0.00200		0.02931 ± 0.00082	0.1255 ± 0.00683
$\lambda_{E-EE} = \lambda_{N-NN} =$ $\lambda_{E-EN} = \lambda_{N-NE} =$ $\lambda_{E-NN} = \lambda_{N-EE},$ $\mu_E \neq \mu_N, q_{EN} =$ q_{NE}	4	-2001.438 ± 1.8256	4010.958 ± 3.6512	188.323	0.1282 ± 0.00064						0.0000 ± 0.00000	2.5274 ± 0.01558	0.0746 ± 0.00044	
$\lambda_{E-EE} \neq \lambda_{N-NN} \neq$ $\lambda_{E-EN} \neq \lambda_{N-NE} \neq$ $\lambda_{E-NN} \neq \lambda_{N-EE},$ $\mu_E \neq \mu_N, q_{EN} =$ q_{NE}	9	-1903.561 ± 2.8447	3825.499 ± 5.6894	2.864	0.1873 ± 0.00476	0.0000 ± 0.00000	0.0003 ± 0.00001	0.0659 ± 0.01121	0.0945 ± 0.00971	0.0827 ± 0.00131	0.2047 ± 0.00175	0.0642 ± 0.00204	0.0075 ± 0.00132	
$\lambda_{E-EE} = \lambda_{N-NN} =$ $\lambda_{E-EN} = \lambda_{N-NE} =$ $\lambda_{E-NN} = \lambda_{N-EE},$ $\mu_E \neq \mu_N, q_{EN} =$ q_{NE}	5	-1980.136 ± 1.8278	3970.395 ± 3.6556	147.760	0.0669 ± 0.00046						0.1085 ± 0.00574	0.9211 ± 0.05404	0.0504 ± 0.00678	0.14310 ± 0.00052
$\lambda_{E-EE} \neq \lambda_{N-NN} \neq$ $\lambda_{E-EN} \neq \lambda_{N-NE} \neq$ $\lambda_{E-NN} \neq \lambda_{N-EE},$ $\mu_E = \mu_N, q_{EN} \neq$ q_{NE}	9	-1911.792 ± 2.5755	3841.959 ± 5.1510	19.324	0.1664 ± 0.00422	0.0004 ± 0.00037	0.0011 ± 0.00005	0.0697 ± 0.01168	0.0936 ± 0.01170	0.1653 ± 0.00170	0.1810 ± 0.00139		0.0261 ± 0.00158	0.1369 ± 0.00016
All free ($\lambda_{E-EE} \neq \lambda_{N-NN} \neq$ $\lambda_{E-EN} \neq \lambda_{N-NE} \neq$ $\lambda_{E-NN} \neq \lambda_{N-EE},$ $\mu_E \neq \mu_N, q_{EN} \neq$ q_{NE})	10	-1901.087 ± 2.6120	3822.635 ± 5.2241	0	0.1945 ± 0.00459	0.0000 ± 0.00000	0.0003 ± 0.00001	0.0584 ± 0.01120	0.0783 ± 0.00957	0.0771 ± 0.00118	0.2094 ± 0.00177	0.0512 ± 0.00164	0.0061 ± 0.00122	0.0119 ± 0.00066

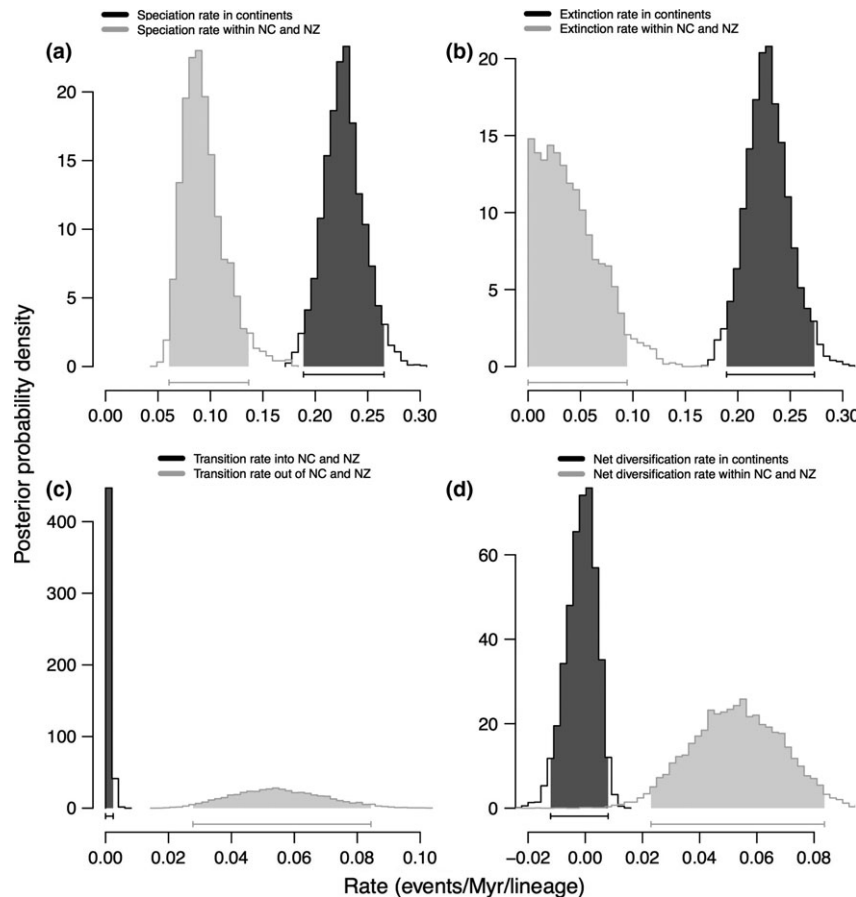


Fig. 4. Diversification patterns (inferred with BiSSE) of speciation (a), extinction (b), transition (c) and net diversification (d) rates for conifer species living outside or inside New Caledonia and New Zealand. Results show lower rates of species extinction in the islands and higher transition rates “out of the islands”. Bayesian posterior distributions were computed using MCMC analyses with the best-fitting model on the MCC tree (Table 2a). Bars below each distribution correspond to the shaded area and represent the 95% credibility interval of each estimated parameter.

extinction and transition rates between the two geographical traits are significantly different with the Bayesian MCMC analysis (Fig. 6).

We further compared both BiSSE and BiSSE.td approaches: the best-fit BiSSE model has six free parameters ($\log L = -1893.878$) and the best-fit BiSSE.td model has 13 free parameters ($\log L = -1875.211$), which gives support to the BiSSE.td model ($\Delta AIC = 22.743$ and $P < 0.0001$ against the BiSSE model). The BiSSE.td models are significantly more likely than the BiSSE and ClaSSE models. This suggests that accounting for time variation of rates improved the fit of the models. Importantly, the overall results for the time-variable trait diversification remained the same, regardless of the method used.

Methodological pitfalls and robustness of the results

Our results rely on several assumptions, such as (i) the quality and accuracy of the phylogeny, (ii) the size

of the tree and the character state ratio (Davis et al., 2013), (iii) the homogeneity of rates across lineages (Morlon et al., 2011), (iv) the constancy of diversification rates through time and (v) the possible effect of diversity-dependence in diversification rates (Etienne et al., 2012).

Diversification analyses depend on the topological and dating quality of the phylogeny used. The conifer phylogeny of Leslie et al. (2012) is the most up-to-date phylogeny of conifers and comprises 80% of all described species, but it can be seen as provisional because not all species are included and conifers have not always been found as a monophyletic group (e.g. Ruhfel et al., 2014). Together, these aspects can cause phylogenetic and dating biases leading to poor estimates of diversification rates. We have accounted for dating uncertainties by running BiSSE and ClaSSE analyses on 500 trees taken randomly from the Bayesian posterior distribution, and found consistent results with the MCC tree (Table 1). To take into account the

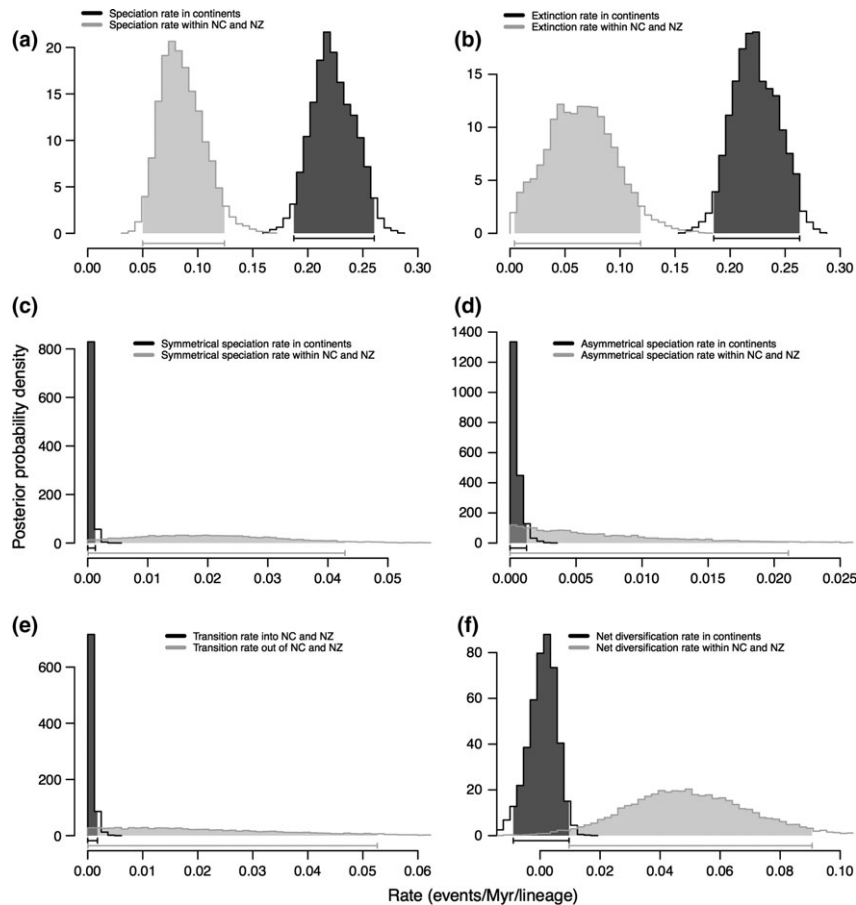


Fig. 5. Diversification patterns (inferred with ClaSSE) of speciation (a), extinction (b), symmetrical (c) and asymmetrical (d) speciation, transition (e) and net diversification (f) rates for conifer species living outside or inside New Caledonia and New Zealand. Results are congruent with BiSSE by inferring lower rates of extinction on the islands and higher transition rates “out of the islands”. The extra ClaSSE parameters are not significantly different from each other, meaning that taking into account cladogenetic changes does not improve the likelihood of the model. Bayesian posterior distributions were computed using MCMC analyses with the best-fitting model on the MCC tree (Table 2b).

non-monophyly of conifers inferred by some studies (e.g. Ruhfel et al., 2014), we also ran independent analyses for all diversification models pruning out the family Pinaceae, and found similar results to those reported here (Appendices S7–S9). These assessments suggest that our results and the main conclusions we derive from them are robust to phylogenetic and dating uncertainty.

Simulations have demonstrated that the power of BiSSE models (and probably also of ClaSSE) is sensitive to tree size and character state ratio (Davis et al., 2013). As a result, the potential for type II errors (failing to reject the null hypothesis when the alternative hypothesis is true) is high. Here the conifer tree is probably large enough (489 species sampled out of 615 known) to have acceptable type II error rates. However, the NCNZ species represent only 10.2% (63/615) of all conifer species and 11.9% (58/489) when considering the full phylogeny. This low ratio may have an impact on the estimation of diversification rates. Removing the Pinaceae

(231 species of which none is endemic to NCNZ) increases the ratio to 16.4% (63/384), and to 19.2% (58/302) in the phylogeny. The BiSSE and ClaSSE models without Pinaceae are essentially similar to estimated rates of diversification of the whole tree (Appendices S7–S9). These results further suggest that our analyses are unlikely to be systematically biased by incomplete phylogenetic sampling.

Clades may have heterogeneous diversification rates for many reasons, including differences in ecological features, occupied areas or morphological traits (Drummond et al., 2012). To reduce the bias introduced by this heterogeneity in our global-scale analyses, we ran the various models for the primarily Southern Hemisphere and tropical/warm temperate families Araucariaceae and Podocarpaceae, where 51.4% and 20.6% of their species are endemic to NCNZ, respectively. In this case, the BiSSE and ClaSSE models did not yield significant differences between NCNZ and taxa living elsewhere

Table 3

Comparison of models for the global phylogeny, using 500 random Bayesian posterior trees for the BiSSE time-dependent models with a shift inferred around the re-emergence of New Caledonia (a) and another one around the re-emergence of New Zealand (b). These results correspond to all models considered in the article. For each model, the maximum-likelihood estimates of the mean and standard error for all parameters are summarized over the posterior distribution of the dating analysis. The best model is indicated in bold. We denote the headers as in Table 1. The difference from non-time-variable BiSSE is the introduction of a shift time (s.t.) thus making a time variation of the rates, denoted as $\lambda_{E,1}$ for the speciation rate of continental species between present and the shift time, and $\lambda_{E,2}$ for the speciation rate of continental species between the shift time and the origin of conifers. The same rationale applies to all parameters.

Model	d.f.	log L	AICc	$\Delta AICc$	$\lambda_{E,1}$	$\lambda_{N,1}$	$\mu_{E,1}$	$\mu_{N,1}$
(a)								
Null model ($\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$)	7	-1912.514 ± 1.728	3839.261 ± 3.457	62.072	0.1993 ± 0.0010		0.1931 ± 0.0012	
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	9	-1904.715 ± 1.723	3827.806 ± 3.446	50.617	0.2029 ± 0.0011	0.1435 ± 0.0011	0.1850 ± 0.0016	
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	9	-1903.475 ± 1.695	3825.326 ± 3.390	48.138	0.1919 ± 0.0010		0.1680 ± 0.0013	0.2401 ± 0.0014
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	9	-1895.879 ± 1.795	3810.134 ± 3.590	32.946	0.2041 ± 0.0021		0.1947 ± 0.0025	
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	11	-1903.420 ± 1.691	3829.394 ± 3.381	52.206	0.1941 ± 0.0012	0.1664 ± 0.0020	0.1651 ± 0.0021	0.2277 ± 0.0034
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	11	-1888.541 ± 1.707	3799.635 ± 3.414	22.447	0.1874 ± 0.0010	0.1398 ± 0.0015	0.1476 ± 0.0019	
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	11	-1890.685 ± 1.679	3803.924 ± 3.358	26.735	0.1885 ± 0.0010			0.1624 ± 0.0017
All free ($\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$)	13	-1875.211 ± 11.609	3777.188 ± 23.218	0	0.2038 ± 0.0014	0.0971 ± 0.0034	0.1784 ± 0.0056	0.0656 ± 0.0061
(b)								
Null model ($\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$)	7	-1906.698 ± 1.779	3827.628 ± 3.558	39.599	0.1886 ± 0.0011		0.1665 ± 0.0015	
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	9	-1900.507 ± 1.762	3819.390 ± 3.523	31.360	0.1949 ± 0.0011	0.1288 ± 0.0009	0.1614 ± 0.0015	
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	9	-1900.154 ± 1.755	3818.683 ± 3.510	30.654	0.1840 ± 0.0010		0.1445 ± 0.0014	0.2378 ± 0.0015
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	9	-1890.699 ± 1.972	3799.774 ± 3.943	11.745	0.1974 ± 0.0025		0.1765 ± 0.0031	
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} = q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} = q_{NE,2}$	11	-1899.764 ± 1.753	3822.082 ± 3.507	34.053	0.1898 ± 0.0012	0.1499 ± 0.0025	0.1523 ± 0.0017	0.1896 ± 0.0056
$\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} = \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} = \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	11	-1883.786 ± 1.738	3790.125 ± 3.477	2.096	0.1845 ± 0.0010	0.1288 ± 0.0012	0.1347 ± 0.0015	
$\lambda_{E,1} = \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} = \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$	11	-1885.024 ± 1.698	3792.602 ± 3.396	4.573	0.1826 ± 0.0010		0.1425 ± 0.0016	0.1986 ± 0.0015
All free ($\lambda_{E,1} \neq \lambda_{N,1}$, $\mu_{E,1} \neq \mu_{N,1}$, $q_{EN,1} \neq q_{NE,1}$, s.t., $\lambda_{E,2} \neq \lambda_{N,2}$, $\mu_{E,2} \neq \mu_{N,2}$, $q_{EN,2} \neq q_{NE,2}$)	13	-1880.632 ± 1.734	3788.029 ± 3.467	0	0.1994 ± 0.0012	0.0916 ± 0.0009	0.1589 ± 0.0019	0.0509 ± 0.0025

(Appendix S10). These results suggest that NCNZ conifer diversification is different from elsewhere only when analysed at a global scale.

Diversification rates may also vary due to variations in the abiotic and biotic environment. In particular, there is considerable evidence for slowdowns in

$q_{EN.1}$	$q_{NE.1}$	s.t.	$\lambda_{E.2}$	$\lambda_{N.2}$	$\mu_{E.2}$	$\mu_{N.2}$	$q_{EN.2}$	$q_{NE.2}$
$0.0052 \pm 5.85E-05$		84.1 ± 7.2	0.1932 ± 0.0127		0.1380 ± 0.0083		0.0414 ± 0.00238	
$0.0065 \pm 3.66E-05$		53.2 ± 3.8	0.1711 ± 0.0298	0.1396 ± 0.0147	0.1542 ± 0.0254		0.00711 ± 0.0015	
$0.0076 \pm 3.74E-05$		34.2 ± 0.1	0.0908 ± 0.0018		0.0798 ± 0.0029	0.0239 ± 0.0014	0.01474 ± 0.0075	
0.00087 ± 0.00015	0.0423 ± 0.0010	65.9 ± 7.0	0.1697 ± 0.0176		0.0767 ± 0.0021		0.0112 ± 0.0021	0.0058 ± 0.0016
0.2277 ± 0.0034		34.7 ± 0.3	0.2366 ± 0.0491	0.1664 ± 0.0118	0.0512 ± 0.0025	0.0254 ± 0.0083	0.0016 ± 0.003	
$0.00015 \pm 2.47E-05$	0.0432 ± 0.0007	30.3 ± 0.5	0.0897 ± 0.0142	0.0770 ± 0.0016	0.0658 ± 0.0014		0.0441 ± 0.0011	0.0018 ± 0.0042
0.1994 ± 0.0012	0.0357 ± 0.0003	33.0 ± 0.2	0.0952 ± 0.0013		0.12596 ± 0.0151	0.0784 ± 0.0014	0.0016 ± 0.00042	0.0001 ± 0.0002
$5.80E-05 \pm 2.80E-05$	0.074 ± 0.0054	31.7 ± 0.3	0.1161 ± 0.0135	0.0405 ± 0.0074	0.1023 ± 183245.0	0.0527 ± 0.0208	0.00196 ± 0.0003	0.00001 ± 0.0000
$0.0062 \pm 4.23E-05$		34.9 ± 4.1	0.0961 ± 0.0054		0.0758 ± 0.0017		0.0150 ± 0.0133	
$0.0069 \pm 3.77E-05$		24.4 ± 0.1	0.0781 ± 0.0010	0.0732 ± 0.0020	0.0661 ± 0.0011		0.0023 ± 0.0003	
$0.0085 \pm 3.85E-05$		24.6 ± 0.5	0.0824 ± 0.0011		0.0687 ± 0.0014	0.0327 ± 0.0039	0.0034 ± 0.0004	
0.0008 ± 0.0002	0.0518 ± 0.0015	34.9 ± 4.1	0.1127 ± 0.0117		0.0728 ± 0.0018		0.012 ± 0.0019	0.0586 ± 0.0017
0.1896 ± 0.0056		24.2 ± 0.2	0.0908 ± 0.0043	0.0470 ± 0.0068	0.0512 ± 0.0025	0.0254 ± 0.0083	0.0013 ± 0.002	
$0.0000 \pm 7.73E-06$	0.0488 ± 0.0005	23.9 ± 0.2	3.6651 ± 2.64	0.0725 ± 0.0012	0.0622 ± 0.0011		0.0541 ± 0.0011	0.0018 ± 0.0042
$0.0000 \pm 7.73E-06$	0.0395 ± 0.0003	24.5 ± 0.1	0.0936 ± 0.0012		0.1057 ± 0.0222	0.0804 ± 0.0015	0.0559 ± 0.0046	0.0208 ± 0.0012
$0.0000 \pm 8.88E-06$	0.0726 ± 0.0006	24.3 ± 0.1	0.1851 ± 0.0218	0.0477 ± 0.0025	0.1906 ± 0.0108	0.0320 ± 0.0018	0.0644 ± 0.0018	0.0135 ± 0.0075

diversification rates over time, which has often been attributed as evidence for diversity-dependent processes (Etienne et al., 2012). We considered it unlikely

that such processes would govern conifer diversity, because diversity-dependence is unlikely to operate at the large taxonomic scales considered here. Notwith-

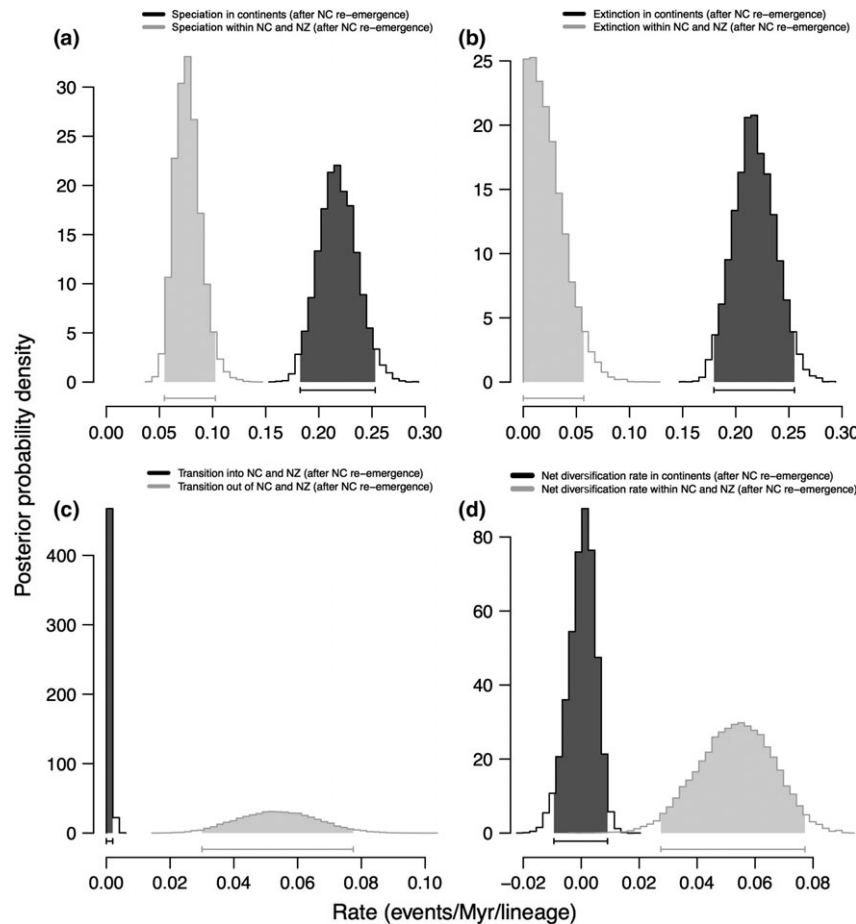


Fig. 6. Diversification patterns through time (inferred with BiSSE.td) of speciation (a), extinction (b), transition (c) and net diversification (d) rates (after the re-emergence of New Caledonia) for conifer species living outside or inside New Caledonia and New Zealand. The rates prior to NC re-emergence (i.e. 32 Ma to the origin of the clade) were estimated to be equal between continents and NCNZ (Table 2). Results are congruent with BiSSE and ClaSSE by inferring lower rates of species extinction in the islands and higher transition rates ‘out of the islands’ after the estimated re-emergence of New Caledonia at ca. 32 Ma. Bayesian posterior distributions were computed using MCMC analyses with the best-fitting model on the MCC tree (Table 3).

standing, to further address this possibility we ran diversity-dependent analyses on the whole phylogeny and the phylogeny without Pinaceae using Etienne et al.’s (2012) approach. The analyses estimated that current conifer diversity is far from being at equilibrium (i.e. it has not reached a potential “carrying capacity”): for the whole phylogeny the carrying capacity approaches infinity, and for the phylogeny excluding Pinaceae it is close to 6320 species (to be compared with the currently known 384 species). We conclude that diversity-dependent processes are unlikely to bias our results at such geographical and taxonomic scales.

Biogeographical analyses

The two time-stratified biogeographical models applied with DEC+J in BioGeoBEARS indicated that Australia is the main source of NCNZ conifer diver-

sity, as expected. However, this was not always the case as the genera *Austrotaxus*, *Dacrycarpus*, *Dacrydium*, *Libocedrus* and *Retrophyllum* have their most recent common ancestors estimated to other regions (Fig. 7; Appendix S11). Nonetheless, we acknowledge that this result does not take into account the fossil record, which could potentially bias the biogeographical inference for those taxa (Crisp et al., 2011). For instance, *Dacrycarpus* and *Dacrydium* have today most of their diversity in NCNZ, but both occurred in Australia since the Eocene (Carpenter and Pole, 1995). The analyses also suggested numerous local extinctions in Australia, but with lineage survivals in NCNZ. In several clades (e.g. *Phyllocladus*, *Podocarpus*), we found that NCNZ was the source area for the neighbouring regions. The maximum-likelihood estimates of the DEC+J parameters for each model are as follows: dispersal = $0.0013/8 \times 10^{-4}$, extinction = $8 \times 10^{-4}/5 \times 10^{-4}$, and jump dispersal = $0.0368/0.0349$. While

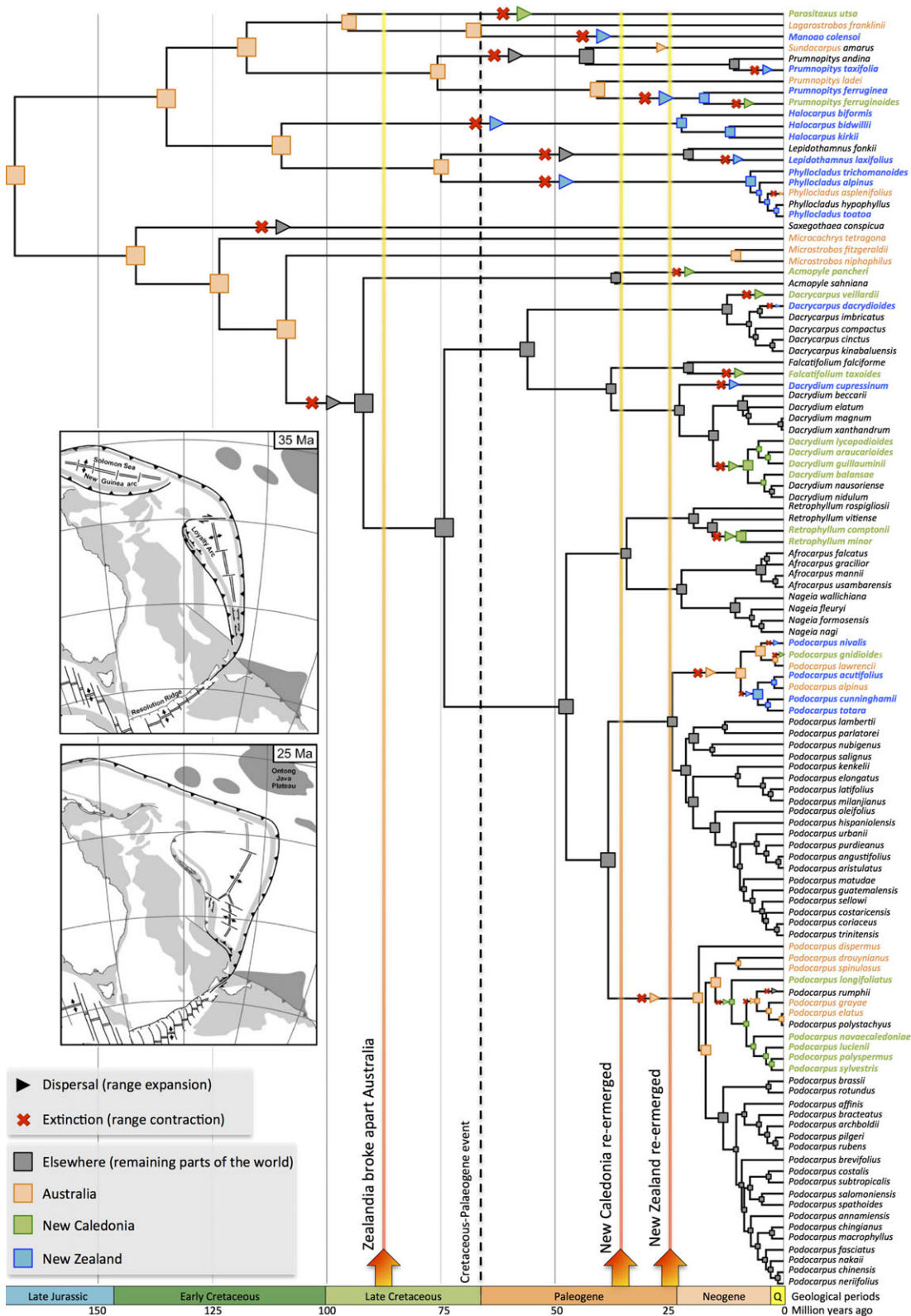


Fig. 7. Biogeographical estimations of ancestral areas for Podocarpaceae as inferred with the “island refugia” scenario, which relies on a time-stratified model taking into account the submersion of NC and drowning of NZ as well as a region to represent the possible presence of ephemeral (now sunken) islands in the region while NC and/or NZ were submerged. The global ancestral area estimations are presented in Appendix S11 for all conifers.

taking into account the geological context with the vicariance events between Australia and Zealandia, the founder-event speciation was the dominant biogeographical process of the two DEC+J models, as expected in an island system (Appendix S11). The jump dispersal is 28- and 43-fold higher than the dispersal by range extension, respectively. After applying DEC+J to each biogeographical model, we compared both scenarios: the first DEC+J model has three free parameters and a log L = −423.48 (AICc = 853.009) and the second DEC+J model has also three free parameters and a log L = −397.91 (AICc = 801.869), which gives support to the second biogeographical model ($\Delta\text{AIC} = 51.14$ and $P < 0.0001$ against the first model). This suggests that accounting for the possible presence of ephemeral (volcanic) islands in the region improved the fit of the models. For instance, we evidence the role of these islands for the colonization of *Prumnopitys* in NCNZ (Fig. 7). Importantly, the overall results for both biogeographical models were essentially similar (Appendix S11).

Discussion

Explaining conifer diversity in NC and NZ

Considering the three biogeographical scenarios explaining the presence of supposedly relictual groups and the stunning biodiversity in NCNZ, our study brings new insights into this old debate. Altogether, our results rule out the “Gondwanan vicariance” hypothesis (H_1), as we found that models including allopatric speciation (with ClaSSE) were not supported (knowing the time-calibrated phylogenies provides a minimum age estimate, Heads, 2005). Also biogeographical models taking into account the past tectonic evolution of the region did not infer vicariant events within conifers. In addition, our results did not provide convincing evidence for the “late Eocene NC re-emergence” nor the “late Oligocene NZ drowning” hypothesis (H_2). Although we found phylogenetic evidence in the diversification of conifers supporting a scenario with a diversification rate shift around 32 Ma (close to the supposed late Eocene re-emergence), we estimated low dispersal rates into NCNZ, and did not detect high speciation rates following the islands’ colonizations (once NC surfaced again). Before this shift, diversification did not differ among species within and outside Zealandia, probably because Zealandia was part of the Australian plate for most of the evolutionary history of conifers.

Instead, our data and analyses favour the “island refugia” hypothesis (H_3). We found several lines of evidence supporting this scenario. First, the estimated timing for the origin of NCNZ conifers exceeds the

geological ages of the extant emerged islands (at least for NC, as there is conflicting evidence for a total drowning of NZ; Landis et al., 2006, 2008; Kamp et al., 2014). The conifer molecular ages might be overestimated, however, because the branching between the island and continental lineages represents the upper limit of island colonization, as the closest relative might have gone extinct. Nonetheless, the age of an island radiation at its crown age might be an underestimation, marking the lower bound, as island colonization might have occurred well before. The time-calibrated tree of conifers represents minimum divergence times due to fossil calibrations, which may lead to a potential underestimate of the true ages (ages might be older). Second, we estimated high dispersal rates “out of NCNZ”, in opposition to the expected island colonization rate. Third, contrary to expectations of the theory of island biogeography, we found that the extinction rate was much lower within the islands, corroborated by the results obtained with BiSSE, BiSSE.td and ClaSSE. Fourth, an explicit time-stratified biogeographical model including island refugia while NCNZ were underwater or submerged fit better than a model reflecting only the submersion and re-emergence of NCNZ. Taking this evidence together, we favour the scenario that today’s submerged islands in the vicinity of NCNZ existed above sea level, while NCNZ were underwater or drowned, and probably allowed conifers to survive.

Although the scenario of today’s submerged islands may be difficult to validate given the lack of definitive support for the presence of ancient islands, several recent phylogenetic studies have also suggested the presence of ancient (now sunken) islands in different archipelagos as temporary refugia for biodiversity (e.g. Canaries: Fernández-Palacios et al., 2011; Patiño et al., 2015; Galápagos: Torres-Carvajal et al., 2014; Hawaii: Haines et al., 2014; and Mascarene Islands: Bradler et al., 2015). Palaeo-islands acted as refugia against extinction, and as cradles and sources of genetic diversity to other areas within the archipelago (Mairal et al., 2015; Patiño et al., 2015). Thus, one cannot rule out the possibility that ancient (now sunken) islands may have existed in the Coral and/or Tasman Seas during the Oligocene and Miocene periods. In particular, the D’Entrecasteaux Islands that are located midway between Australia and NC are of volcanic origin, representing a stage of continental breakup (Baldwin et al., 1993). Finally, the idea of NC as a refugium has been recently emphasized with a meta-analysis over 60 relict angiosperm taxa that survived from the persistence of rainforests in the island despite global fluctuations in climate during the Quaternary that affected floras in the region (Pouéteau et al., 2015).

Our results suggest that NC had a greater role in the conifer diversity of the region than NZ. Yet, the

emergence of NC makes the island “younger” than NZ (Baur et al., 2014; Conran et al., 2014); this means that time-for-speciation cannot be invoked to explain the greater standing diversity of NC. Instead NC was a more dynamic geological entity at the front of an obduction zone and so the emergence of NC would see significant topographic changes as can be seen in New Guinea in the last 5 Ma (similar tectonic setting). In comparison, NZ was low lying with little topographic diversity and therefore less climatic buffering (the uplift of the Southern Alps occurred in the mid-Miocene, Walcott, 1979). Our results also bring further light into this essentially geological debate as we do not support a model incorporating a drowning of NZ. It is also possible that the change of diversification we found at ca. 32 Ma can be explained by global climate change. The late Eocene cooling event (33.9 Ma, Liu et al., 2009) has been proposed as a major historical event that triggered important macroevolutionary changes worldwide (e.g. Pearson et al., 2008; Erwin, 2009), and has been evoked as period of extinction in gymnosperms (Crisp and Cook, 2011).

Islands as refugia for conifers: low extinction on ancient islands

Island species are often thought to be extinction-prone as a result of smaller population sizes, restricted geographical distribution and limited dispersal ability outside islands (MacArthur and Wilson, 1967; Warren et al., 2015). In this study we found phylogenetic evidence for the opposite pattern. Our results reveal significantly lower extinction for conifer species living in NCNZ than for species living outside these islands. As a consequence, NCNZ are not only areas of high species richness but also areas with low extinction probability, which have preserved ancient lineages and thus acted as “museums” of diversity.

Our diversification analyses indicate that a broad geographical signature is imprinted in the evolutionary history of conifers, and that extinction events impacted conifers globally (i.e. we found no support for models in which NCNZ impacted the diversification of Araucariaceae and Podocarpaceae). Our results suggest that NCNZ are different when compared to conifers globally, but may not be that different from other species-rich areas such as Borneo or New Guinea in terms of diversification dynamics.

Three non-mutually exclusive explanations may explain the patterns recovered: (i) NCNZ is a special case of different diversification dynamics in the Southern Hemisphere, with longer phylogenetic branches and less extinction (or with lower turnover, see Leslie et al., 2012). The Northern Hemisphere continental radiations may also have experienced higher extinction (Peralta-Medina and Falcon-Lang, 2012) or turnover

due to climate shifts, which might explain their greater “stemness” in reconstructed phylogenies. (ii) Both Podocarpaceae and Araucariaceae, whose species diversity is concentrated in island-rich Southeast Asia and Melanesia, may generally be considered as island clades. Thus one would not expect as many differences with NCNZ as comparing them to Cupressaceae or Pinaceae, which have several recent radiations in continental environments, such as *Juniperus* (e.g. Mao et al., 2012), *Abies* (e.g. Aguirre-Planter et al., 2012), *Picea* (e.g. Lockwood et al., 2013) and *Pinus* (e.g. Eckert and Hall, 2006; Hernández-León et al., 2013). Although these groups also include island species, we cannot consider islands as their centre of diversity contrary to southern clades such as *Agathis*, *Araucaria*, *Dacrydium* and *Podocarpus* showing a rich diversity in Borneo, New Guinea and NC (Farjon and Filer, 2013). (iii) NC and NZ do not have the same diversification dynamics (Biffin et al., 2010; Kranitz et al., 2014), and combining them effectively subsamples the whole Southern Hemisphere. Analysing the effect of NCNZ separately would be very complex and not advised in the context of BiSSE models and the requested data. Moreover, NCNZ had a common geological history, long before they separated when Zealandia sank, making it relevant to analyse their common effect on conifer diversification. Despite their stunning biological richness, NCNZ may represent an extrapolation of similar diversification dynamics in Southern Hemisphere groups (Leslie et al., 2012). Since the break-up of Gondwana, the Southern Hemisphere has become an ocean-dominated hemisphere, so it is not surprising that conifers display insular diversification dynamics.

Our results support the idea that islands can retain old lineages as well as harbour new ones. They do not support the idea, however, that island species have higher extinction rates than mainland species (as predicted under the island biogeography theory; Warren et al., 2015). We corroborate this finding with biogeographical models, which show higher local extinction in continents (Australia, and elsewhere) than in islands. Additional information can be gleaned from the fossil record. Araucariaceae and Podocarpaceae, the richest families in those islands, were globally co-dominant in the Early Cretaceous, especially in humid tropical and subtropical biomes, but drastically reduced in numbers and range during the Late Cretaceous (Peralta-Medina and Falcon-Lang, 2012). Their relative abundances dropped from 55% to 25% in the Early Cretaceous, respectively, to as little as 5% for both groups at the end of the Cretaceous (Peralta-Medina and Falcon-Lang, 2012). By the Late Cretaceous, Araucariaceae became extinct in the Northern Hemisphere, and also disappeared from southern Africa and India. This suggests that Araucariaceae and

Podocarpaceae suffered from drastic continental extinctions during the Cretaceous. Still existing in the early Cenozoic in South America, Antarctica and Australasia, the ranges of species continued to contract further when global climate cooled dramatically at the Eocene–Oligocene transition, and Australia turned largely into semi-arid and desert regions (Byrne et al., 2011). Both biogeographical and diversification analyses made from phylogenies are thus congruent with fossil data, together corroborating the continental extinction events that are probably responsible for long stem branches subtending recent radiations (Crisp and Cook, 2011).

Explaining these continental extinctions remains complex. Environmental changes or the migration of new competitors may drive extinction, and can even be global triggers (e.g. temperature and their environmental consequences, Erwin, 2009). The drastic global decline in conifer ecological dominance and diversity may be linked directly to the rise of angiosperms, which increased from 32 to 78% in the mid-Cretaceous and the Late Cretaceous, respectively (de Boer et al., 2012; Chaboureau et al., 2014). Evidence of drastic biome contractions at global scale for the tropical belt under cool climates (Morley, 2007), or more regionally such as in Australia (Byrne et al., 2011), may also explain the decline of conifers (Farjon, 2008). By contrast, NCNZ have always remained at more or less the same latitude and experienced relatively less pronounced climate changes (Lowry, 1998). The numerous ancient but currently species-poor lineages found today in NCNZ, i.e. with long phylogenetic branches containing unique monotypic genera (e.g. *Parasitaxus* in NC, *Manoao* in NZ, Fig. 3, Appendix S1), probably represent the last survivors of a vast diversity of continental conifers. Altogether these results suggest that during periods of drastic environmental changes, these Pacific Islands have provided refugia for Mesozoic plants, whereas their continental relatives more often went extinct.

Role of oceanic islands for the assembly of continental biodiversity

Centres of high species diversity are often considered sources of diversity (also known as species pumps), nourishing surrounding areas with lineages that evolved *in situ*. However, higher species richness does not necessarily mean higher diversification rates (Becerra and Venable, 2008), nor imply directionality of dispersals. Sources and sinks of diversity may be identified on the basis of dispersal “out of” or “into” a region (Hutsemékers et al., 2011). Although NCNZ contains about 10% of the world’s diversity of conifers, we estimated that NCNZ has a higher net diversification rate than elsewhere, suggesting a higher rate of species formation over time. Our results also point

out the role of these ancient islands as sources of biodiversity, by showing that dispersals “out-of-the-refugia” were much more frequent than the other way around (with three models). Together, these results suggest that NCNZ promoted local diversification and acted as a species pump to surrounding regions (including Australia, Melanesia and South America, e.g. Swenson et al., 2014). We thus put forward a potential important role of NCNZ in generating, maintaining and exporting conifer diversity that probably contributed to the extant world’s conifer diversity. Our results also challenge the traditional notion that islands are the “end of the colonization road” and illustrate the significant role of islands as reservoirs of novel biodiversity for the assembly of continental floras (Bellemain and Ricklefs, 2008; Hutsemékers et al., 2011).

Generality of the results

Beyond the Pacific islands, other areas might have played a similar role to NCNZ in conserving ancient lineages and being mainly a source of diversity (Hutsemékers et al., 2011). Madagascar could be a further example, due to its long availability of terrestrial ecosystems, Gondwanan origin, and high degree of topographic, climatic and environmental heterogeneity (Yoder and Nowak, 2006). Indeed, several studies have indicated that lineages originally derived from Africa recolonized that continent, establishing new clades, such as chameleons (Raxworthy et al., 2002), daisy trees (Strijk et al., 2012) and swallowtail butterflies (Condamine et al., 2013). Madagascar has also been recognized as a refuge for biodiversity, at least for arthropods (Wesener et al., 2011). Although Madagascar can be considered of the same age as NCNZ, the island is not outstanding for its species diversity or ancient lineages in conifers. The reason Madagascar is not as species rich as NCNZ is because the source pool (Africa) is not diverse (Farjon and Filer, 2013). Surrounding continental islands, i.e. in the Arctic Ocean, are also depauperate probably because of this African diversity pattern. By contrast, the Japanese Archipelago contains a similar diversity of lineages as NCNZ, and harbours relatively high species richness with high level of endemism (Fig. 1) as well as some ancient lineages (e.g. *Sciadopitys verticillata*). Separated from Asia in the Cenozoic, probably in the Miocene when most of the modern conifer diversity was derived, the Japanese Archipelago might have acted as a source of diversity for the Northern Hemisphere in a similar way that NCNZ did for the Southern Hemisphere.

A key feature of islands in relation to their potential as a source or pump of diversity is not only that they are isolated from the continent, but also that they are often very mountainous and thus have more

heterogeneous landscapes (in soil, climate, precipitation and temperature) within a shorter geographical distance, as compared with the continental areas—e.g. Australia versus NCNZ. NC is thought to have promoted species diversification because of its soil heterogeneity and the presence of ultramafic soils (Pillon et al., 2009, 2014). Such an ecological factor might have triggered the exceptional conifer diversity in NC as most of the species occur on ultramafic soils (Appendix 12). Mountainous islands (e.g. all volcanic ones) are more “protected” in the sense they will have suitable habitats regardless of how much climate changes, as species need to move shorter distances to keep their optimal conditions (Sandel et al., 2011). This, combined with low (or at least different) levels of competition with other species, might offer the key recipe for making islands refuges and sources of biodiversity.

These results are of interest because identifying spatial sources of diversification and combining this information with current diversity may have greater long-term conservation payoff than considering standing diversity alone (Becerra and Venable, 2008). Because many islands and archipelagos are biodiversity hotspots, future studies comparing clades that inhabit biodiversity hotspots with those that do not may be needed to better understand geographical speciation and extinction patterns. Recent findings show that islands (especially atolls or low-lying islands) recognized as biodiversity hotspots may experience an average loss of 31% of their area in the next century (Bellard et al., 2014), suggesting the risk for elevated extinctions. For conifers, Rumeu et al. (2014) showed that 285 out of the 547 studied species have an insular distribution (exclusively or not). A high proportion of the threatened conifers occur on islands (52%), and many of them are insular endemics (72%). Additionally, they suggested that oceanic islands play a key role in catalysing speciation mechanisms, in particular Pacific islands that harbour the greatest diversity levels in the world, and probably constitute a major centre of diversification. Our results provide further insights into understanding the mechanisms maintaining and generating the biodiversity in oceanic-like islands. We not only confirmed that those islands constitute a major centre of diversification but also that they have primarily functioned as a reservoir and source of diversity for neighbouring areas.

Conclusions

Our results shed further light on how islands have impacted and shaped the history of species diversification. NCNZ cover a small land area with disproportionately high levels of taxonomic and phylogenetic conifer diversity. Our results suggest that this diversity was attained in two ways. First, these islands have

served as refugia, conserving ancient lineages with low levels of extinction during global environmental changes. Second, they were primarily a source of lineages, contributing to the world’s conifer diversity. Our results thus challenge the traditional views that oceanic islands confer a higher risk of going extinct, and are at an evolutionary dead end. We illustrate the significant role of oceanic islands as refugia of ancient biodiversity and reservoirs of novel biodiversity for the assembly of continental floras. The size and topographic complexity of islands allow them to act as refugia and to promote speciation that can later be transferred to continents, what has been termed “boomerang events” (Caujapé-Castells, 2004). We also show that coupling BiSSE-like models with biogeographical models constitutes an adequate approach to test biogeographical scenarios underlying species richness patterns, such as those outlined here (see also Rolland et al., 2015 on the latitudinal gradient of Carnivora).

Acknowledgements

We are grateful to José María Fernández-Palacios, an anonymous reviewer and the Associate Editor for their insightful comments and suggestions on the manuscript. We thank Aljos Farjon for providing comments on the project, and for his invaluable work on conifers in general. We also thank Jérôme Munzinger and Yohan Pillon for fieldwork in NC and early discussions on New Caledonian flora. F.L.C. was supported by the Carl Tryggers Stiftelse grant (CTS 12:24). A.A. is supported by grants from the Swedish Research Council (B0569601), the European Research Council under the European Union’s Seventh Framework Programme (FP/2007-2013, ERC Grant Agreement no. 331024), and a Wallenberg Academy Fellowship. This is contribution ISEM 2016-044 of the Institut des Sciences de l’Evolution de Montpellier (UMR 5554 – CNRS).

References

- Aguirre-Planter, E., Jaramillo-Correa, J.P., Gómez-Acevedo, S., Khasa, D.P., Bousquet, J., Eguiarte, L.E., 2012. Phylogeny, diversification rates and species boundaries of Mesoamerican firs (*Abies*, Pinaceae) in a genus-wide context. *Mol. Phylogenet. Evol.* 62, 263–274.
- Bache, F., Mortimer, N., Sutherland, R., Collot, J., Rouillard, P., Stagpoole, V., Nicol, A., 2014. Seismic stratigraphic record of transition from Mesozoic subduction to continental breakup in the Zealandia sector of eastern Gondwana. *Gondwana Res.* 26, 1060–1078.
- Baldwin, S.L., Lister, G.S., Hill, E., Foster, D.A., McDougall, I., 1993. Thermochronologic constraints on the tectonic evolution of active metamorphic core complexes, D’Entrecasteaux Islands, Papua New Guinea. *Tectonics* 12, 611–628.
- Barrabé, L., Maggia, L., Pillon, Y., Rigault, F., Mouly, A., Davis, A.P., Buerki, S., 2014. New Caledonian lineages of *Psychotria* (Rubiaceae) reveal different evolutionary histories and the largest

- documented plant radiation for the archipelago. *Mol. Phylogenet. Evol.* 71, 15–35.
- Baur, J., Sutherland, R., Stern, T., 2014. Anomalous passive subsidence of deep-water sedimentary basins: a prearc basin example, southern New Caledonia Trough and Taranaki Basin, New Zealand. *Basin Res.* 26, 242–268.
- Becerra, J.X., Venable, D.L., 2008. Sources and sinks of diversification and conservation priorities for the Mexican tropical dry forest. *PLoS One* 3, e3436.
- Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. *Glob. Ecol. Biogeogr.* 23, 1376–1386.
- Bellemain, E., Ricklefs, R.E., 2008. Are islands the end of the colonization road? *Trends Ecol. Evol.* 23, 461–468.
- Biffin, E., Hill, R.S., Lowe, A.J., 2010. Did kauri (*Agathis*: Araucariaceae) really survive the Oligocene drowning of New Zealand? *Syst. Biol.* 59, 594–602.
- de Boer, H.J., Eppinga, M.B., Wassen, M.J., Dekker, S.C., 2012. A critical transition in leaf evolution facilitated the Cretaceous angiosperm revolution. *Nat. Commun.* 3, 1221.
- Bradler, S., Cliquenois, N., Buckley, T.R., 2015. Single origin of the Mascarene stick insects: ancient radiation on sunken islands? *BMC Evol. Biol.* 15, 196.
- Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., Weston, P.H., 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *J. Biogeogr.* 38, 1635–1656.
- Carpenter, R.J., Pole, M., 1995. Eocene plant fossils from the Lefroy and Cowan paleodrainages, Western Australia. *Austral. Syst. Bot.* 8, 1107–1154.
- Caujapé-Castells, J., 2004. Boomerangs of biodiversity? The interchange of biodiversity between mainland North Africa and the Canary Islands as inferred from cpDNA RFLPs in genus *Androcymbium*. *Botánica Macaronésica* 25, 53–69.
- Chaboureau, A.C., Sepulchre, P., Donnadiou, Y., Franc, A., 2014. Tectonic-driven climate change and the diversification of angiosperms. *Proc. Natl Acad. Sci. USA* 111, 14066–14070.
- Cluzel, D., Aitchison, J.C., Picard, C., 2001. Tectonic accretion and underplating of mafic terranes in the Late Eocene intraoceanic fore-arc of New Caledonia (Southwest Pacific): geodynamic implications. *Tectonophysics* 340, 23–59.
- Cluzel, D., Maurizot, P., Collot, J., Sevin, B., 2012. An outline of the geology of New Caledonia; from Permian–Mesozoic Southeast Gondwanaland active margin to Cenozoic obduction and supergene evolution. *Episodes – Newsmag. Int. Union Geol. Sci.* 35, 72–86.
- Condamine, F.L., Sperling, F.A.H., Kergoat, G.J., 2013. Global biogeographical pattern of swallowtail diversification demonstrates alternative colonization routes in the Northern and Southern Hemispheres. *J. Biogeogr.* 40, 9–23.
- Conran, J.G., Mildenhall, D.C., Lee, D.E., Lindqvist, J.K., Shepherd, C., Beu, A.G., Bannister, J.M., Stein, J.K., 2014. Subtropical rainforest vegetation from Cosy Dell, Southland: plant fossil evidence for Late Oligocene terrestrial ecosystems. *New Zealand J. Geol. Geophys.* 57, 236–252.
- Crisp, M.D., Cook, L.G., 2011. Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. *New Phytol.* 192, 997–1009.
- Crisp, M.D., Trewick, S.A., Cook, L.G., 2011. Hypothesis testing in biogeography. *Trends Ecol. Evol.* 26, 66–72.
- Cruaud, A., Jabbour-Zahab, R., Genson, G., Ungricht, S., Rasplus, J.-Y., 2012. Testing the emergence of New Caledonia: fig wasp mutualism as a case study and a review of evidence. *PLoS One* 7, e30941.
- Davis, M.P., Midford, P.E., Maddison, W.P., 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol. Biol.* 13, 38.
- De Laubenfels, D.J., 1996. Gondwanan conifers on the Pacific Rim. In: Keast, A., Miller, S.E. (Eds.), *The Origin and Evolution of Pacific Island Biotas, New Guinea to eastern Polynesia: Patterns and Processes*. SPB Academic, Amsterdam, pp. 261–265.
- Drummond, C.S., Eastwood, R.J., Miotto, S.T., Hughes, C.E., 2012. Multiple continental radiations and correlates of diversification in *Lupinus* (Leguminosae): testing for key innovation with incomplete taxon sampling. *Syst. Biol.* 61, 443–460.
- Eckert, A.J., Hall, B.D., 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): phylogenetic tests of fossil-based hypotheses. *Mol. Phylogenet. Evol.* 40, 166–182.
- Erwin, D.H., 2009. Climate as a driver of evolutionary change. *Curr. Biol.* 19, R575–R583.
- Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A., Phillimore, A.B., 2012. Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B* 279, 1300–1309.
- Farjon, A., 2008. *A Natural History of Conifers*. Timber Press, Portland, OR.
- Farjon, A., Filer, D., 2013. *An Atlas of the World's Conifers. An Analysis of their Distribution, Biogeography, Diversity and Conservation Status*. Brill, Leiden, The Netherlands.
- Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García del Rey, E., Arévalo, J.R., Whittaker, R., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *J. Biogeogr.* 38, 226–246.
- Fitzjohn, R.G., 2012. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.* 3, 1084–1092.
- FitzJohn, R.G., Maddison, W.P., Otto, S.P., 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst. Biol.* 58, 595–611.
- Fritz, S.A., Jönsson, K.A., Fjeldsø, J., Rahbek, C., 2009. Diversification and biogeographical patterns in four island radiations of passerine birds. *Evolution* 66, 179–190.
- Gibbs, G., 2004. *Ghosts of Gondwana. The History of Life in New Zealand*. Craig Potton Publishing, Nelson, New Zealand.
- Gillespie, R., 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303, 356–359.
- Goldberg, E.E., Igic, B., 2012. Tempo and mode in plant breeding system evolution. *Evolution* 66, 3701–3709.
- Goldberg, E.E., Lancaster, L.T., Ree, R.H., 2011. Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* 60, 451–465.
- Grandcolas, P., Muriene, J., Robillard, T., DeSutter-Grandcolas, L., Jourdan, H., Guilbert, E., Deharveng, L., 2008. New Caledonia: a very old Darwinian island? *Philos. Trans. R. Soc. B* 363, 3309–3317.
- Hackney, R., Sutherland, R., Collot, J., 2012. Rifting and subduction initiation history of the New Caledonia Trough, southwest Pacific, constrained by process-oriented gravity models. *Geophys. J. Int.* 189, 1293–1305.
- Haines, W.P., Schmitz, P., Rubinoff, D., 2014. Ancient diversification of *Hypomocoma* moths in Hawaii. *Nat. Commun.* 5, 3502.
- Heads, M.J., 2005. Dating nodes on molecular phylogenies: a critique of molecular biogeography. *Cladistics* 21, 62–78.
- Heads, M.J., 2008. 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. *J. Biogeogr.* 35, 2153–2175.
- Heads, M.J., 2013. *Biogeography of Australasia: A Molecular Analysis*. Cambridge University Press, Cambridge, UK.
- Hernández-León, S., Gernandt, D.S., Pérez de la Rosa, J.A., Jardón-Barbolla, L., 2013. Phylogenetic relationships and species delimitation in *Pinus* section *Trifoliae* inferred from plastid DNA. *PLoS One* 8, e70501.
- Hutsemékers, V., Szövényi, P., Shaw, A.J., González-Mancebo, J.-M., Muñoz, J., Vanderpoorten, A., 2011. Oceanic islands are not sinks of biodiversity in spore-producing plants. *Proc. Natl Acad. Sci. USA* 108, 18989–18994.
- Jönsson, K.A., Fabre, P.-H., Fritz, S.A., Etienne, R.S., Ricklefs, R.E., Jørgensen, T.B., Fjeldsø, J., Rahbek, C., Ericson, P.G.,

- Woog, F., Pasquet, E., Irestedt, M., 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proc. Natl Acad. Sci. USA* 109, 6620–6625.
- Kamp, P.J.J., Tripathi, A.R.P., Nelson, C.S., 2014. Paleogeography of Late Eocene to earliest Miocene Te Kuiti Group, central-western North Island, New Zealand. *New Zealand J. Geol. Geophys.* 57, 128–148.
- Kranitz, M.L., Biffin, E., Clark, A., Hollingsworth, M.L., Ruhsam, M., Gardner, M.F., Thomas, P., Mill, R.R., Ennos, R.A., Gaudeul, M., Lowe, A.J., Hollingsworth, P.M., 2014. Evolutionary diversification of New Caledonian *Araucaria*. *PLoS One* 9, e110308.
- Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. *Ecol. Lett.* 11, 116–127.
- Krosch, M., Cranston, P.S., 2013. Not drowning, (hand)waving? Molecular phylogenetics, biogeography and evolutionary tempo of the ‘Gondwanan’ midge *Stictocladus* Edwards (Diptera: Chironomidae) *Mol. Phylogenet. Evol.* 68, 595–603.
- Ladiges, P.Y., Cantrill, D., 2007. New Caledonia–Australian connections: biogeographical patterns and geology. *Austral. Syst. Bot.* 20, 383–389.
- Landis, C.A., Campbell, H.J., Begg, J.G., Paterson, A.M., Trewick, S.A., 2006. The drowning of Zealandia: evidence and implications. *Geol. Soc. New Zeal. Misc. Publ.* 121, 21.
- Landis, C.A., Campbell, H.J., Begg, J.G., Mildenhall, D.C., Paterson, A.M., Trewick, S.A., 2008. The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geol. Mag.* 145, 173–197.
- Leslie, A.B., Beaulieu, J.M., Rai, H.S., Crane, P.R., Donoghue, M.J., Mathews, S., 2012. Hemisphere-scale differences in conifer evolutionary dynamics. *Proc. Natl Acad. Sci. USA* 109, 16217–16221.
- Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M., Pearson, A., 2009. Global cooling during the Eocene–Oligocene climate transition. *Science* 323, 1187–1190.
- Lockwood, J.D., Aleksić, J.M., Zou, J., Wang, J., Liu, J., Renner, S.S., 2013. A new phylogeny for the genus *Picea* from plastid, mitochondrial, and nuclear sequences. *Mol. Phylogenet. Evol.* 69, 717–727.
- Losos, J.B., Ricklefs, R.E., 2009. Adaptation and diversification on islands. *Nature* 457, 830–836.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K., Rodríguez-Schettino, L., 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279, 2115–2118.
- Lowry, P.P. II, 1998. Diversity, endemism, and extinction in the flora of New Caledonia. In: Peng, C.-I., Lowry, P.P. II (Eds.), *Symposium on Rare, Threatened, and Endangered Floras of Asia and the Pacific*. Academia Sinica, Taipei, Taiwan, pp. 181–206.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Maddison, W.P., FitzJohn, R.G., 2015. The unsolved challenge to phylogenetic correlation tests for categorical characters. *Syst. Biol.* 64, 127–136.
- Maddison, W.P., Midford, P.E., Otto, S.P., 2007. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* 56, 701–710.
- Mairal, M., Sanmartín, I., Aldasoro, J.J., Culshaw, V., Manolopoulou, I., Alarcón, M., 2015. Palaeo-islands as refugia and sources of genetic diversity within volcanic archipelagos: the case of the widespread endemic *Canarina canariensis* (Campanulaceae). *Mol. Ecol.* 24, 3944–3963.
- Mao, K., Milne, R.I., Zhang, L., Peng, Y., Liu, J., Thomas, P., Mill, R.R., Renner, S.S., 2012. Distribution of living Cupressaceae reflects the breakup of Pangea. *Proc. Natl. Acad. Sci. USA* 109, 7793–7798.
- Matthews, K.J., Williams, S.E., Whittaker, J.M., Müller, R.D., Seton, M., Clarke, G.L., 2015. Geologic and kinematic constraints on Late Cretaceous to mid Eocene plate boundaries in the southwest Pacific. *Earth-Sci. Rev.* 140, 72–107.
- Matzke, N.J., 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* 63, 951–970.
- Mittermeier, R.A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J.L., da Fonseca, G.A.B., 2004. *Hotspots Revisited: Earths Biologically Richest and most Threatened Ecoregions*. CEMEX, Mexico, Mexico City.
- Morat, P., Veillon, J.-M., MacKee, H.S., 1984. Floristic relationships of New Caledonian rain forest phanerogams. In: Radosky, F.J., Raven, P.H., Sohmer, S.H. (Eds.), *Biogeography of the Tropical Pacific*. Assoc. Syst. Collections, Lawrence, Kansas and Bernice P. Bishop Museum, Honolulu, Hawaii, pp. 71–128.
- Morley, R.J., 2007. Cretaceous and tertiary climate change and the past distribution of megathermal rainforests. In: Bush, M.B., Flenley, J. (Eds.), *Tropical Rainforest Responses to Climatic Changes*. Praxis Publishing, Chichester, pp. 1–31.
- Morlon, H., Parsons, T.L., Plotkin, J.B., 2011. Reconciling molecular phylogenies with the fossil record. *Proc. Natl Acad. Sci. USA* 108, 16327–16332.
- Ng, J., Smith, S.D., 2014. How traits shape trees: new approaches for detecting character state-dependent lineage diversification. *J. Evol. Biol.* 27, 2035–2045.
- Patiño, J., Carine, M., Mardulyn, P., Devos, N., Mateo, R.G., González-Mancebo, J.M., Shaw, A.J., Vanderpoorten, A., 2015. Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. *Syst. Biol.* 64, 579–589.
- Pearson, P.N., McMillan, I.K., Wade, B.S., Dunkley Jones, T., Coxall, H.K., Bown, P.R., Lear, C.H., 2008. Extinction and environmental change across the Eocene–Oligocene boundary in Tanzania. *Geology* 36, 179–182.
- Pelletier, B., 2006. Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity. In: Payri, C., de Richer Forges, B. (Eds.), *Compendium of Marine Species from New Caledonia*. Documents Scientifiques et Techniques de l'IRD I17, Centre IRD de Nouméa, Nouvelle-Calédonie, pp. 19–32.
- Peralta-Medina, E., Falcon-Lang, H.J., 2012. Cretaceous forest composition and productivity inferred from a global fossil wood database. *Geology* 40, 219–222.
- Petit, R., Aguinalde, I., de Beaulieu, J.L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J.P., Rendell, S., Vendramin, G.G., 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. *Science* 300, 1563–1565.
- Pillon, Y., Munzinger, J., Amir, H., Hopkins, H.C., Chase, M.W., 2009. Reticulate evolution on a mosaic of soils: diversification of the New Caledonian endemic genus *Codia* (Cunoniaceae). *Mol. Ecol.* 18, 2263–2275.
- Pillon, Y., Hopkins, H.C., Rigault, F., Jaffré, T., Stacy, E.A., 2014. Cryptic adaptive radiation in tropical forest trees in New Caledonia. *New Phytol.* 202, 521–530.
- Pouteau, R., Trueba, S., Felid, T.S., Isnard, S., 2015. New Caledonia: a Pleistocene refugium for rain forest lineages of relict angiosperms. *J. Biogeogr.* 42, 2062–2077.
- Rabosky, D.L., Goldberg, E.E., 2015. Model inadequacy and mistaken inferences of trait-dependent speciation. *Syst. Biol.* 64, 340–355.
- Raven, P.H., Axelrod, D.I., 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61, 539–673.
- Raxworthy, C.J., Forstner, M.R., Nussbaum, R.A., 2002. Chameleon radiation by oceanic dispersal. *Nature* 415, 784–787.
- Ree, R.H., Smith, S.A., 2008. Maximum-likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57, 4–14.
- Rolland, J., Condamine, F.L., Jiguet, F., Morlon, H., 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.* 12, e1001775.

- Rolland, J., Condamine, F.L., Beeravolu, C.R., Jiguet, F., Morlon, H., 2015. Dispersal is a major driver of the latitudinal diversity gradient of Carnivora. *Glob. Ecol. Biogeogr.* 24, 1059–1071.
- Ruhfel, B.R., Gitzendanner, M.A., Soltis, P.S., Soltis, D.E., Burleigh, J.G., 2014. From algae to angiosperms—inferring the phylogeny of green plants (Viridiplantae) from 360 plastid genomes. *BMC Evol. Biol.* 14, 23.
- Rumeu, B., Afonso, V., Fernández-Palacios, J.M., Nogales, M., 2014. Diversity, distribution and conservation status of island conifers: a global review. *Diversity Distrib.* 20, 272–283.
- Sahney, S., Benton, M.J., Falcon-Lang, H.J., 2010. Rainforest collapse triggered Pennsylvanian tetrapod diversification in Euramerica. *Geology* 38, 1079–1082.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J., Svenning, J.-C., 2011. The influence of Late Quaternary climate-change velocity on species endemism. *Science* 334, 660–664.
- Schellart, W.P., Lister, G.S., Toy, V.G., 2006. A Late Cretaceous and Cenozoic reconstruction of the southwest Pacific region: Tectonics controlled by subduction and slab rollback processes. *Earth-Sci. Rev.* 76, 191–233.
- Segev, A., Rybakov, M., Mortimer, N., 2012. A crustal model for Zealandia and Fiji. *Geophys. J. Int.* 189, 1277–1292.
- Strijk, J.S., Noyes, R.D., Strasberg, D., Cruaud, C., Gavory, F., Chase, M.W., Abbott, R.J., Thébaud, C., 2012. In and out of Madagascar: dispersal to peripheral islands, insular speciation and diversification of Indian Ocean daisy trees (*Psiadia*, Asteraceae). *PLoS One* 7, e42932.
- Swenson, U., Nylinder, S., Muzinger, J., 2014. Sapotaceae biogeography supports New Caledonia being an old Darwinian island. *J. Biogeogr.* 41, 797–808.
- Thornhill, A.H., Ho, S.Y., Külheim, C., Crisp, M.D., 2015. Interpreting the modern distribution of Myrtaceae using a dated molecular phylogeny. *Mol. Phylogenet. Evol.* 93, 29–43.
- Torres-Carvajal, O., Barnes, C.W., Pozo-Andrade, M.J., Tapia, W., Nicholls, G., 2014. Older than the islands: origin and diversification of Galápagos leaf-toed geckos (*Phyllodactylidae*: *Phyllodactylus*) by multiple colonizations. *J. Biogeogr.* 41, 1883–1894.
- Trewick, S.A., Paterson, A.M., Campbell, H.J., 2007. Hello New Zealand. *J. Biogeogr.* 34, 1–6.
- Tzedakis, P.C., Emerson, B.C., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol. Evol.* 28, 696–704.
- Walcott, R.I., 1979. Plate motion and shear strain rates in the vicinity of the Southern Alps. *R. Soc. New Zealand Bull.* 18, 5–12.
- Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-Palacios, J.M., Hengl, T., Norder, S.J., Rijdsdijk, K., Sanmartín, I., Strasberg, D., Triantis, K., Valente, L.M., Whittaker, R.J., Gillespie, R., Emerson, B.C., Thébaud, C., 2015. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecol. Lett.* 18, 200–217.
- Waters, J.M., Craw, D., 2006. Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Syst. Biol.* 55, 351–356.
- Weigelt, P., Kreft, H., 2013. Quantifying island isolation—insights from global patterns of insular plant species richness. *Ecography* 36, 417–429.
- Weigelt, P., Jetz, W., Kreft, H., 2013. Bioclimatic and physical characterization of the world's islands. *Proc. Natl. Acad. Sci. USA* 110, 15307–15312.
- Wesener, T., Raupach, M.J., Decker, P., 2011. Mountain refugia play a role in soil arthropod speciation on Madagascar: a case study of the endemic giant fire-millipede genus *Aphistogoniulus*. *PLoS One* 6, e28035.
- Yoder, A.D., Nowak, M.D., 2006. Has vicariance or dispersal been the predominant biogeographical force in Madagascar? Only time will tell. *Annu. Rev. Ecol. Evol. Syst.* 37, 405–431.

Supporting Information

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

Appendix S1. Macroevolutionary models used for the trait-dependence diversification.

Appendix S2. Time-calibrated tree of conifers showing the species endemic to NC (red branches) and NZ (blue branches).

Appendix S3. Comparison of models for the MCC tree for the BiSSE approach (a) and the ClaSSE approach (b).

Appendix S4. Differences between speciation (a), extinction (b) and transition (c) rates, and net diversification rates (d), computed from the MCMC analyses using the best BiSSE model and the MCC tree.

Appendix S5. Differences between rates of cladogenetic speciation without character change (a), extinction (b), cladogenetic speciation with symmetrical character change (c), cladogenetic speciation with asymmetrical character change (d), and net diversification rates (e), computed from the MCMC analyses using the best ClaSSE model and the MCC tree.

Appendix S6. Comparison of models for the global phylogeny (a) and the phylogeny excluding the Pinaceae (b) using the BiSSE.td approach in which rates vary according to trait and time.

Appendix S7. Comparison of models for the phylogeny excluding the Pinaceae for the BiSSE approach (a) and the ClaSSE approach (b).

Appendix S8. Differences between speciation (a), extinction (b) and transition (c) rates, and net diversification rates (d), computed from the MCMC analyses using the best BiSSE model for the MCC tree *excluding* the Pinaceae.

Appendix S9. Differences between rates of cladogenetic speciation without character change (a), extinction (b), cladogenetic speciation with symmetrical character change (c), cladogenetic speciation with asymmetrical character change (d), and net diversification rates (e), computed from the MCMC analyses using the best ClaSSE model for the MCC tree *excluding* the Pinaceae.

Appendix S10. Comparison of models for the Araucariaceae and Podocarpaceae for the BiSSE approach (a) and the ClaSSE approach (b).

Appendix S11. Estimates of ancestral areas using the DEC+J model under two time-stratified models.

Appendix S12. List NC conifers with information on their geographical range and habitat, and their presence or absence on ultramafic soils (typical of NC).