













New Caledonian rovers and the historical biogeography of a hyper-diverse endemic lineage of South Pacific leaf beetles

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Abstract

South Pacific archipelagos are central in the biogeographic debate on the relative importance of vicariance and dispersal in shaping the distribution of species. However, each taxonomic group was subject to different processes and histories, and here, we reveal the historical biogeography of the diverse Eumolpinae leaf beetles, widely distributed in the region. Extensive taxon sampling focusing on South Pacific Eumolpinae was used to infer the first molecular phylogeny of the group using three single-copy protein-coding nuclear and two mitochondrial markers. Upon assessing the clade of interest for lineage-specific variation in substitution rates, the age of the most recent common ancestors was estimated using out-group calibration and multi-gamma site models (MGSMs). Biogeographic analyses used standard event-based inferences also incorporating phylogenetic uncertainty. Zealandian Eumolpinae are monophyletic and appear to have split

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from their global relatives in the transition from the Cretaceous to the Paleogene. Variation in the rates of molecular evolution affected the in-group stem branch, with a significant drop in the substitution rate, and the MGSM correction recovered the crown age of Zealandian Eumolpinae during the Late Eocene–Oligocene transition. Biogeographic inference resolved the origin of the radiation in New Caledonia, favouring a null model without island age constraints, and repeated dispersal events to the other islands, including three independent but synchronous colonisations of New Zealand during the Miocene. New Caledonia, with a highly diverse Eumolpinae fauna of uncertain origin, acted as a hub and pump of biodiversity of these beetles in the entire South Pacific region, sending migrants to other islands through long-distance dispersal with lineages establishing when land became available.

KEYWORDS

Chrysomelidae-Eumolpinae, heterotachy, long-distance dispersal, New Zealand, Zealandia

INTRODUCTION

The study of island biotas and their assembly has been critical to understanding the way colonisation and establishment processes configure biogeographic patterns (Gillespie & Roderick, 2002; Losos & Ricklefs, 2009). Where the availability of land habitat is unequivocal due to detailed knowledge of volcanic process, as in Hawaii and the Galapagos, inferences of evolutionary history can be made with tight temporal bounds (Cowie & Holland, 2008; Geist et al., 2014; Parent et al., 2008). In contrast, islands of the southwest Pacific including New Zealand (NZ) and New Caledonia (NC), which are associated with continental basement rocks, have presented challenges to biogeographic interpretation because of their relatively deep age and uncertainty about the continuity of terrestrial habitat through time (Giribet & Baker, 2019; Heads, 2017; Landis et al., 2008; Pelletier, 2007; Sutherland et al., 2020; Trewick et al., 2007). Awareness of the tectonic continental origin of the rock strata from which these islands rise has led to the proposition that parts of the terrestrial biota of these islands might be derived from ancestors that survived in situ during the rifting of Zealandia from the eastern margin of Gondwana in the Late Cretaceous (Jolivet & Verma, 2010; Ladiges & Cantrell, 2007; Mortimer et al., 2017; Stevens, 1980). This reflects a wider view that continental drift vicariance could explain most major biogeographic patterns that developed after a tectonic mechanism was recognised (Trewick, 2017). Taxonomic curiosities including *Sphenodon* Gray reptiles in NZ, and the *Amborella* Baillon plant and *Rhynchotos* Verreaux & DesMurs bird in NC (Donoghue, 2019; Grandcolas et al., 2008; Heads, 2008; Maurizot & Campbell, 2020; Waters & Craw, 2006) have been considered relict taxa and cited as supportive of an ancient vicariant origin (Heads, 2008; Sanmartín & Ronquist, 2004). However, these taxa provide no solid evidence for this interpretation (Grandcolas et al., 2014; Grandcolas & Trewick, 2016), and their exclusive presence in these islands could be explained by other evolutionary processes, including extinction elsewhere (Crisp & Cook, 2005; Grandcolas et al., 2014). Understanding the biogeographic history of South Pacific biotas will not be achieved by the

detailed examination of problematic lineages, but expanding the research to new, reasonably well-known lineages with known and robust phylogenetic structure with the potential to inform on the timing of diversification to develop an informed understanding of the way these biotas develop and change over space and time.

Methods that explicitly incorporate potential biogeographic processes and use dated molecular phylogenies have highlighted the importance of rare dispersal in historical biogeography (De Queiroz, 2005). In the region formerly occupied by the disappeared continent of Zealandia, evidence for the emergence of NC at the end of the Eocene (Cluzel et al., 2012; Sevin et al., 2014) and formation of NZ throughout the early to mid Miocene (Trewick et al., 2007) (Supplementary Text S1) predict island biotas that are predominantly derived from colonisation and in situ diversification. Numerous dated molecular phylogenies representing a range of terrestrial animals and plants (reviewed in Nattier et al., 2017; Wallis & Trewick, 2009; Wallis & Jorge, 2018) are consistent with this biological assembly after land emergence and support the model of NC and NZ as islands subject to the evolutionary and biogeographic processes typical of oceanic islands despite having a continental basement (Grandcolas et al., 2008; Wallis & Trewick, 2009). Long-distance dispersal and establishment, evolution in isolation often involving adaptive radiation and extinction provide a viable explanation for the development of their biota. Extinction can erase the spatio-temporal footprint of an evolutionary lineage in a phylogeny (Dowle et al., 2024; Pillon & Buerki, 2017) and, in the South Pacific, the presence of supposed relicts could be linked to the extinction provoked by severe climate changes that affected the southern hemisphere in the last millions of years (Byrne et al., 2011), whereby the islands of the South Pacific could have acted as refugia (Condamine et al., 2017).

The abovementioned processes affected each group of organisms in different ways. Thus, the study of the historical biogeography of different taxa sharing similar distributions in the South Pacific is important to achieve a good understanding of geographic constraints and opportunities for evolution in this region. Specifically, phylogenetic studies of widespread, species-rich taxa are particularly

informative to understand the way biotas evolve, as well as revealing the specific details of lineage relationships in groups of interest. Here, we consider the ecologically and taxonomically diverse leaf beetle subfamily Eumolpinae, a group with many species that are mostly tropical and found on most islands in the South Pacific (Jolivet & Verma, 2008). South Pacific Eumolpinae belong to the tribe Eumolpini, and it was suggested that they are closest relatives (Gómez-Zurita & Pàmies-Harder, 2022; Jolivet et al., 2007). The only exception is *Rhyparida foaensis* (Jolivet, Verma & Mille) in NC, a representative of the tribe Typophorini, most common in Southeast Asia, the Papuan subregion and the island chain from New Guinea to Samoa (Bryant & Gressitt, 1957; Gómez-Zurita, 2011; Gressitt, 1956). The tribe Eumolpini has its highest species diversity in NC, where 119 endemic species are currently known (Platania & Gómez-Zurita, 2023a), presenting the signature of in situ diversification (Papadopoulou et al., 2013). In contrast, NZ has 15 endemic species of Eumolpini in five genera (Gómez-Zurita, 2019, 2020; Nadein & Leschen, 2017). NZ is larger but colder than NC, a potential limitation for a tropical group, and the archipelago shows remarkable faunal disharmony for Chrysomelidae, whereby 7 of the 11 subfamilies of Chrysomelidae are not native (Leschen et al., 2003). Eumolpinae are also present on the small, emerged volcanic Norfolk (NI) and Lord Howe (LH) islands, where at least two species occur on each island (Jolivet et al., 2006).

In this study, we present the first dated molecular phylogeny of the Eumolpinae in the South Pacific in a broader evolutionary context, addressing several issues related to the systematics and biogeography of the group. These comprise (1) establishing the evolutionary relationship of South Pacific Eumolpinae relative to other faunas, with a particular focus on Australia; (2) establishing evolutionary relationships among South Pacific Eumolpinae on different islands; (3) dating phylogenetic events and exploring matches with geological history and (4) deducing the historical biogeography of the group.

MATERIALS AND METHODS

Sampling and DNA sequence data

To study the historical biogeography of the Eumolpini in the South Pacific, we tried to represent several layers of phylogenetic divergence aiming to provide as much phylogenetic context as possible around the group of interest (Table S1). The bulk of data represent 93 specimens of 92 species of Eumolpini from locations in the South Pacific, including Australia (11 of 238 species, 3 of 22 genera [11 mono- or bitypic]), LH (3 of 3 species, 2 of 2 genera), NC (67 of 119 species, 10 of 12 genera), NI (2 of 2 species, 1 of 1 genus) and NZ (9 of 15 species, 4 of 5 genera). Eumolpini from other regions were represented by 13 species mainly from the Neotropical and Oriental regions, and several other tribes of Eumolpinae were represented by 18 species. Finally, five species in three tribes of Cryptocephalinae, the sister group of Eumolpinae (Gómez-Zurita & Cardoso, 2021), were used as out-group to root the trees. Each species was characterised for five phylogenetic markers, comprising partial mitochondrial

cytochrome c oxidase subunit 1 (*cox1*) and small ribosomal subunit gene (*rrnS*) of the mtDNA genome, and intronless fragments of three protein-coding nuclear genes: carbamoylphosphate synthase domain of the CAD gene (*cps*), polyadenylate binding protein 1 (*pabp1*) and wingless (*wg*). Newly obtained DNA sequence data for this study were produced following the same DNA extraction and PCR amplification and sequencing protocols as described in Gómez-Zurita and Cardoso (2021) for *cox1*, *rrnS* and *pabp1*, and Montelongo and Gómez-Zurita (2014) for *cps* and *wg*, and are curated in the GenBank (NCBI, Bethesda MD) under accession numbers PP235333–PP235379 (*cox1*), PP235735–PP235787 (*rrnS*), PP254021–PP252122 (*cps*), PP255379–PP255474 (*pabp1*) and PP255476–PP255565 (*wg*) (Table S1).

Maximum likelihood tree inference

Each gene fragment was aligned individually using MAFFT 7.3 (Katoh & Standley, 2013), specifically with the default options of the G-INS-i algorithm for protein-coding genes and the Q-INS-i algorithm for the ribosomal RNA gene. Individual multiple sequence alignments were initially used to infer gene trees to check for problematic relationships or obvious topological conflict between markers, and in the absence of such issues, they were concatenated for phylogenetic analyses. Maximum likelihood tree inference was performed on data partitioned according to gene and also codon position in the case of protein-coding genes, distinguishing between first + second and third codon positions. Each partition was assigned an independent GTR + G + I substitution model in the parallel pthreads version of RAxML 8.2.12 (Stamatakis, 2014), which was used to estimate both the best tree using a thorough search with multiple runs (algorithm, –f a, 10 initial random topologies) on the original alignment and branch support (BS) based on 500 bootstrap pseudoreplicates. Trees were rooted on the representatives of Cryptocephalinae, used as out-group, and they were visualised using FigTree 1.4.4 (Rambaut, 2018).

Analysis of lineage-specific rates

The optimal maximum likelihood tree showed an interesting feature, namely the relative short branch lengths of the crown group of interest, the large South Pacific island radiation of Eumolpini. Moreover, preliminary dating analyses using relaxed and random clock models with uniform substitution models across the tree tended to accumulate most of the variation occurring in this clade on its long stem branch, consequently producing unrealistically young age estimates for splits in this group (data not shown). We explored whether lineage-specific substitution rates (heterotachy) may be an issue for this dataset using the parallel version of DPPDiv 0.0.1 (Heath et al., 2012). The analysis was run specifying a root age interval between 127 and 166 Ma (see below), a constant Birth-Death tree prior, and 5 million cycles of MCMC, sampling trees and data every 50th cycle.

Changes in the rate of substitution along branches were visualised in FigTree 1.4.4.

Tree calibration and Bayesian molecular dating

Time-constrained analyses were run in BEAST 2.6.6 (Bouckaert et al., 2019) using a Birth-Death tree prior and defining each gene as a separate partition evolving under independent substitution models. The specific models were estimated previously with ModelTest-NG v0.1.7 (Darriba et al., 2020) in raxmlGUI 2.0.5 (Euler et al., 2021), and selected based on the corrected Akaike Information Criterion (AICc). Heterotachy or lineage-specific evolutionary rates affecting this dataset could potentially introduce biases in the inference of relationships and node age estimates, and this problem was tackled in clock-constrained analyses using the multi-gamma site model (MGSM; Bouckaert & Lockhart, 2015) developed to deal with complex situations as described here by modelling branch-specific gamma rate heterogeneity. Tree calibration was based on root dating using published estimates for the age of the sister-group relationship between in-group and out-group, and of the out-group crown age (Gómez-Zurita & Cardoso, 2021). This strategy took into account the absence of fossils compatible with the sample available for this study and explicit avoidance of in-group biogeographic calibration points to prevent circularity in the timing of biogeographic events. Specifically, the root and out-group priors were set as lognormal distributions with respective means = 30 and 18, standard deviations = 0.4 and 0.6, and offsets = 113 and 92, spanning real space intervals of 127–166 and 97.6–132.0 Ma for the root and the out-group ages, respectively. Cross-validation of the dating strategy was based on independent information, including the fit of the estimated ages with known geological events and also the inferred marker-specific substitution rates and their fit to published rates for the same markers (e.g., Papadopoulos et al., 2010). The analysis was run in BEAST for 1000 M generations, sampling parameters and trees every 50 K steps. Mixing and stability of parameter estimates were confirmed by exploring ESS values in Tracer 1.6 (Rambaut et al., 2018), and the maximum clade credibility tree capturing uncertainty in node heights was calculated using TreeAnnotator 1.8.4 (distributed with BEAST) after discarding the initial 10% of data.

Biogeographic analyses

Dated phylogenetic trees from previous steps were used to compare the fit of the data to biogeographic models using the R package BioGeoBEARS 1.1 (Matzke, 2018). The areas considered in the analyses were the four islands where Eumolpini were sampled: LH, NI, NC and NZ. Their availability for colonisation was modelled based on the geological history of the region by considering two alternatives for NZ, available for the entire period of diversification of the group or only in the past 22 Ma, indicating a scenario of complete inundation during

the Oligocene (Supplementary Text S1). Two additional time-slices in these two alternative models included 7 and 3 Ma for the emergence of LH and NI, respectively. Area models thus defined three scenarios: unconstrained, with all areas always available for colonisation (M_0); NZ always available (M_1) or NZ available from the Miocene onwards (M_2). Moreover, even though extant species do not show extended distributions in the region, a maximum occupation of three areas was allowed to relax the possibility of range expansions in the past, and dispersal multipliers were used in every time interval to model the probability of potential transitions between areas, including 0.1 for trans-oceanic dispersal, and 0.00001 to penalise dispersal in disappeared, submerged areas or areas yet to appear. Biogeographic model selection was done in a maximum likelihood framework, choosing the best model according to the AICc, and based on the consensus maximum clade credibility tree topology and dating of the Bayesian analysis. Three main biogeographic models were tested as implemented in BioGeoBEARS: DEC (Ree & Smith, 2008), DIVALIKE (Ronquist, 1997) and BAYAREALIKE (Landis et al., 2013), both without and with the founder-event speciation parameter (+J; Matzke, 2012). Because of the uncertainty and proximity of key dated phylogenetic splits to the boundaries of time-stratified events of the geological model, the historical biogeography of the group was additionally investigated using a pseudo-Bayesian approach accounting for dating uncertainty, which was accomplished by implementing Magalhaes et al.'s (2021) pipeline in the R environment. In this case, 100 random trees from the post-burnin posterior tree file of the BEAST2 dating analysis were selected to run as many individual biogeographic tests in BioGeoBEARS with the same analytical choices as before, under the best models selected in the previous analysis and the three time-stratified geological scenarios (M_0 – M_2), estimating in every case the type and frequency of events for nodes of interest and the most probable ancestral area based on 100 replicates of biogeographic stochastic mapping per tree (BSM; Dupin et al., 2017).

RESULTS

Dataset

Alignment of protein-coding genes was trivial as they included few gaps consisting of isolated missing triplets in the *pabp1* gene of *Geloptera geniculata* Baly [4352] (positions 228–230 of the alignment) and *Myochrous* sp. [478] (positions 121–123), and one extra triplet in positions 68–70 of the *cps* alignment in *Rhabdopterus fulvipes* (Jacoby) [2598] and *Montrouzierella nana* Jolivet, Verma & Mille [NC267], as well as missing triplets in positions 56–61 of the same gene in *Brachyphnoea* Gistel sp. [1399] and *Spintherophyta violaceipennis* (Horn) [3907], and positions 71–76 in *Pachnephorus cylindricus* Lucas [4643]. The final phylogenetic matrix included 129 rows and 3065 aligned characters corresponding to 129 *cox1* (817 nt) and *rrnS* sequences (499–526 nt in 589 aligned positions), 125 *wg* (466 nt), 120 *cps* (748–757 nt in 757 aligned positions) and 114 *pabp1* (436 nt).

Phylogenetic inference

The structure of the maximum likelihood tree (Figure 1), which was topologically mirrored by the clock-constrained Bayesian tree (Figure 2), was compatible with identification of four main, highly supported lineages: clade C, representing the tribes Typophorini, Euryopini and Bromiini; clade B, with Megascelidini; the single representative of the genus *Pachnephorus* Chevrolat (currently in Bromiini); and clade A, with *Myochrous* sp. (also in Bromiini) as sister to all sampled Eumolpini (clade A). In clade A, aside from two basal branches leading to *Myochrous* Erichson and *Tymnes tricolor* (Fabricius), two main lineages were evident: A2, with assorted Eumolpini from different geographic sources, including Australia, South East Asia, Africa and the Americas, together with the Australian endemic *Eboo* Reid, currently in Bromiini, and the NZ endemic *Pilacolaspis* Sharp; and A1, with Eumolpini from south Pacific islands. In clade A2, American Eumolpini appeared segregated (clade A2.2, BS = 100) from other sources (clade A2.1, BS = 92), and in clade A1, two main, highly supported lineages could be distinguished too: clade A1.2 (BS = 85), the NC endemic genera *Taophila* Heller and *Tricholapita* Gómez-Zurita & Cardoso together with Eumolpini from LH; and clade A1.1 (BS = 100), with all the other New Caledonian Eumolpini and relatives from NI and NZ. While outside the scope of this work, this phylogeny, the most complete and information-rich for this group of beetles in the South Pacific to date, illustrates the need for revision of generic boundaries in Australia (challenged monophyly of genera *Edusa* Chevrolat and *Geloptera* Baly), and in NC and LH (with several problematic genera, including *Colaspoides* Laporte, *Dematochroma* Baly, *Dumbea* Jolivet, Verma & Mille, *Montrouzierella* Jolivet, Verma & Mille and *Samuelsonia* Jolivet, Verma & Mille).

Analysis of heterotachy and phylogenetic dating

The analysis of rate classes in the phylogeny of Eumolpinae identified 3–5 rate categories in the tree. These categories represented slight evolutionary rate differences, except in the branch leading to clade A1, where there was a marked drop in the rate inferred for this branch (Figure S1), about half the average branch rates across the phylogeny, while rates within A1 were in the same range as average rates in the phylogeny (Figure 3). The evidence for rate heterogeneity in the data justified the MGSM approximation to molecular dating of the tree.

The substitution patterns in *cox1* and *cps* were consistent with a transversal model, the TN93 substitution model in the case of *rns* and *wg*, and the TPM2uf model for *pabp1*, in all cases including invariant sites (I) and rate heterogeneity (G). Figures 2 and 4 show the time-constrained phylogeny and the South Pacific clade, respectively, with nodes of interest identified, with their inferred ages and time intervals summarised in Tables 1 and 2. According to our sample and dating strategy, the Eumolpinae [node 1] originated in the Early Cretaceous,

which is consistent with current ideas about the age of leaf beetles, and the Eumolpini [node 3] differentiated in the Late Cretaceous. Of interest for the evolution of Eumolpini in the South Pacific, the NZ endemic genus *Pilacolaspis* shared a common ancestor with Australian relatives [node 8] at the end of the Paleogene, when NZ landscape was forming. In turn, the lineage leading to the main South Pacific radiation of Eumolpini split from the rest of Eumolpini [node 4] in the Early Paleogene, consistent with the separation of Zealandia, with this lineage [node 9] starting to diversify during the Oligocene. The separation of lineages that eventually migrated outside of NC occurred in the Early Miocene [nodes 12, 15, 18 and 21], followed by diversification in NZ during the Late Miocene [nodes 16 and 23], Plio-Pleistocene in LH [node 13] and the Loyalty Islands (LI) [node 19], and the Pliocene in the case of NI taxa [node 24].

Historical biogeography

Our phylogenetic hypothesis suggests that all South Pacific Eumolpini had a common ancestor 20–40 Ma ago, and basal splits appear associated with NC. Uplift of Grande Terre in the Late Eocene (37 Ma ago) provides a plausible land surface for this common ancestor to live on, thus a single dispersal followed by radiation would explain this pattern. In contrast, NZ Eumolpini are not monophyletic, but nest within New Caledonian (and Australian) diversity. Predictably, biogeographic model selection based on AICc favoured models incorporating dispersal, modelled by the +J founder-event speciation parameter (Table 3). The tests also identified the null, unconstrained biogeographic scenario as the best option over other alternatives constraining the availability of areas only to certain periods. Finally, among the preferred +J and M_0 alternatives, there were no significant differences among biogeographic models, although the likelihood score for the DEC model ranked highest (Table 3). The proportion and types of biogeographic inferences across major models and sampled topologies were consistent, and concordant with the observed phylogenetic and species distribution patterns. In situ speciation clearly dominated the inferences, with few instances of founder-event speciation, corresponding to transitions between islands (Table 4), which were deduced mainly from NC to NZ, LH and NI, and ambiguity in the particular transition between NZ and NI or vice versa (Table 5). In the latter case, the alternative BSM inferences were nearly identical with a very slight preference for a NZ (51%–54%) over a NC (46%–49%) origin for NI fauna for all three +J models.

A major difference among favoured biogeographic models involved ~33% of inferred ancestral areas for basal nodes considering a single NC + LH area in the DEC + J model (pie charts in Figure 3), while the other models singled out NC as the ancestral area of all transitions, except for the node joining the Eumolpinae from NI and *Euco-laspis* Sharp from NZ. The incorporation of phylogenetic uncertainty through BSM analyses produced a much clearer outcome, with NC as the most probable root area for all +J models (except in 1% of cases picking an NC + LH area under the DEC + J model).

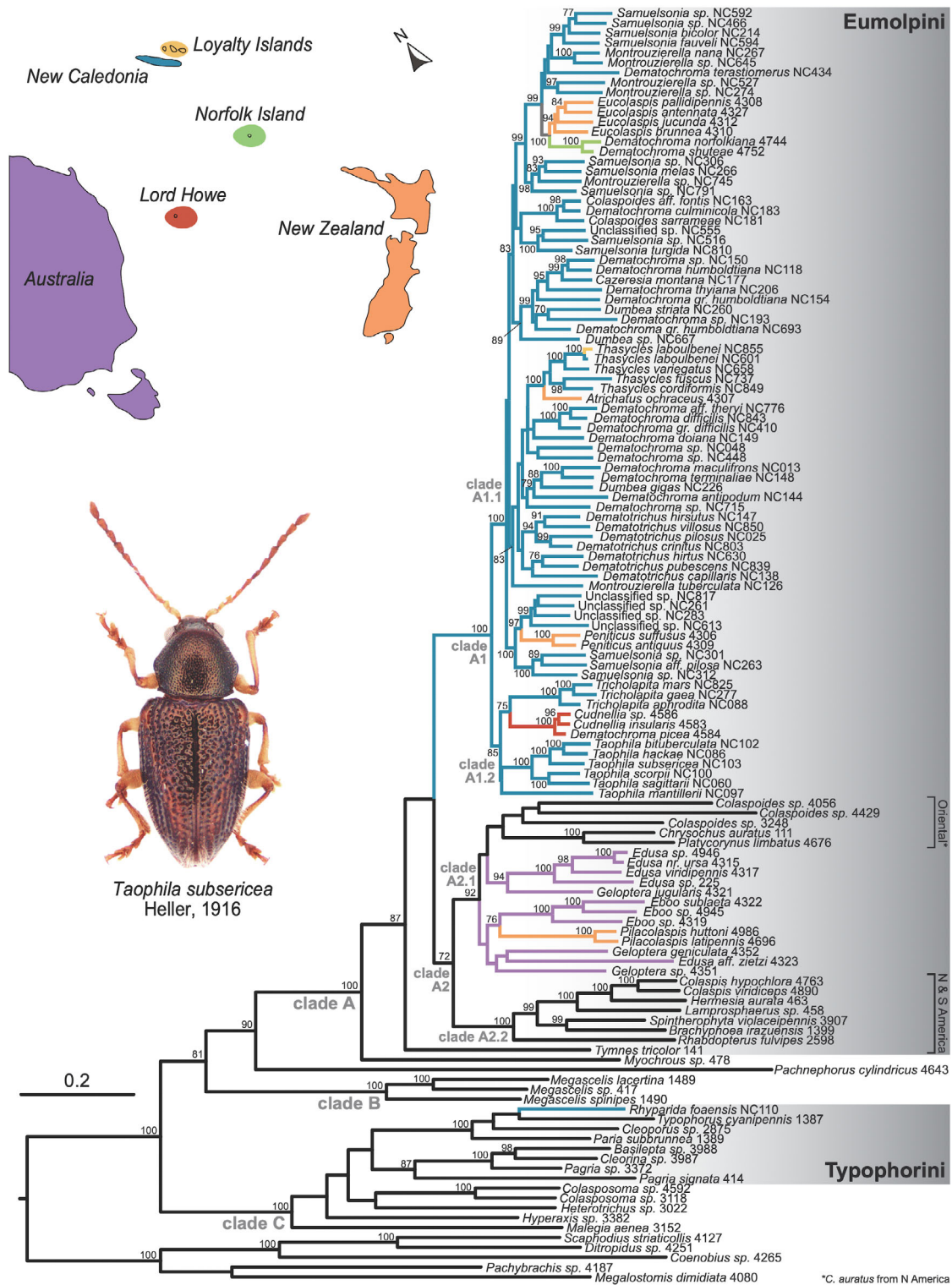


FIGURE 1 Maximum likelihood tree of Eumolpinae leaf beetles based on two mtDNA and three single-copy protein-coding nuclear genes and receiving a final ML optimisation likelihood value = $-93,982.482183$. Clades A–C are described in the **Phylogenetic inference** section of the main text and fundamentally group Eumolpini (A), Megascelidini (B), and Bromiini, Euryopini and Typophorini (C). Other clades of interest include South Pacific Eumolpini (A1), with two main lineages (A1.1 and A1.2), and Eumolpini from other geographic sources (A2), including Old (A2.1) and New (A2.2) World Eumolpini. South Pacific islands and Australian terminals are colour-coded according to the legend and based on the results of BioGeoBEARS.

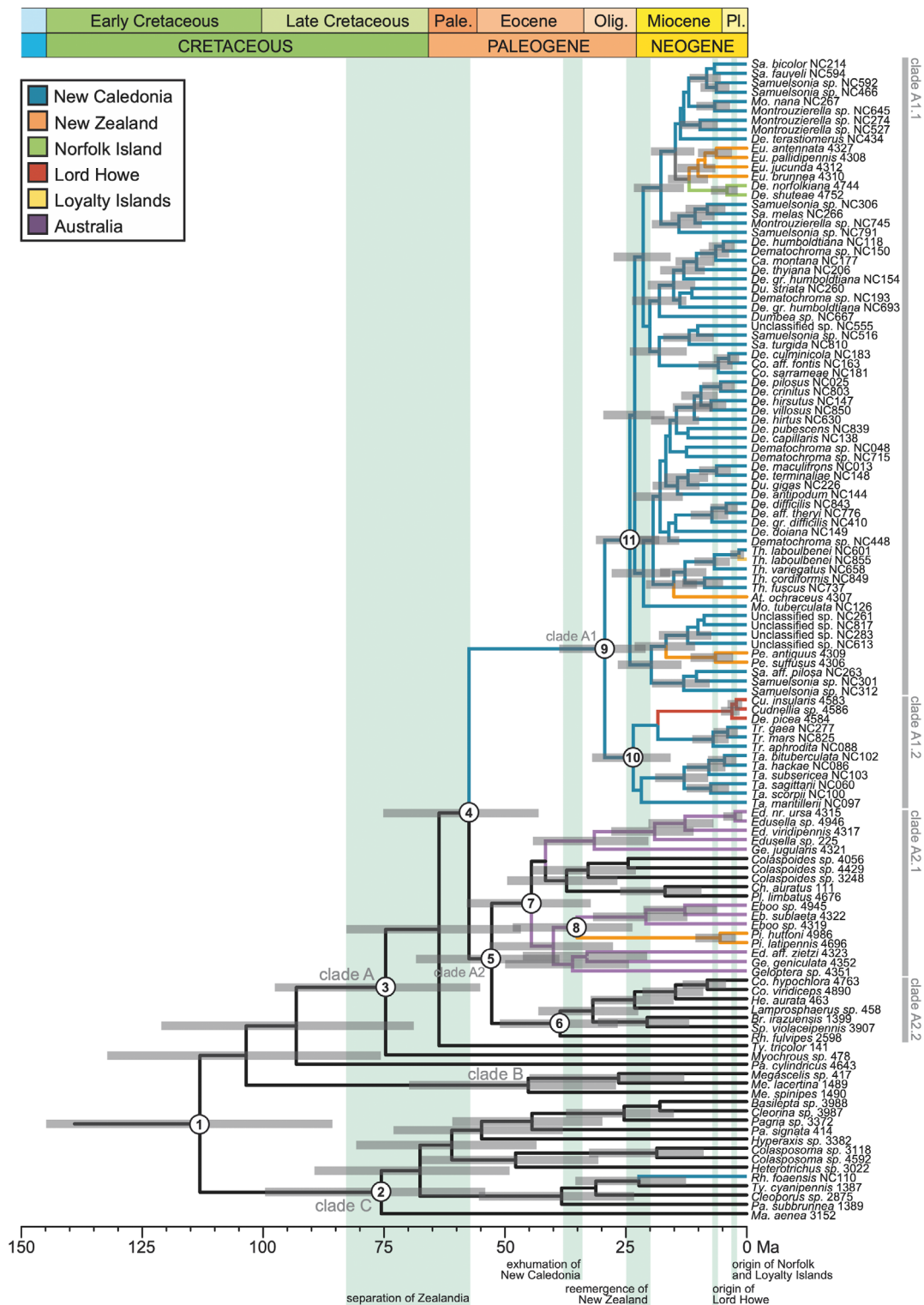


FIGURE 2 Clock-constrained phylogenetic tree of Eumolpinae leaf beetles obtained based on MGSM Bayesian inference and calibrated using out-group dating, with an absolute time framework and geological ages added for reference, and node age 95% highest density intervals shown with grey bars only for nodes with posterior probabilities >0.95. Clades mentioned in the main text and dated nodes of Tables 1 and 2 are labelled, and time intervals for some important events in the evolution of the South Pacific are shown. South Pacific islands and Australian terminals are colour-coded according to the legend and based on the results of BioGeoBEARS.

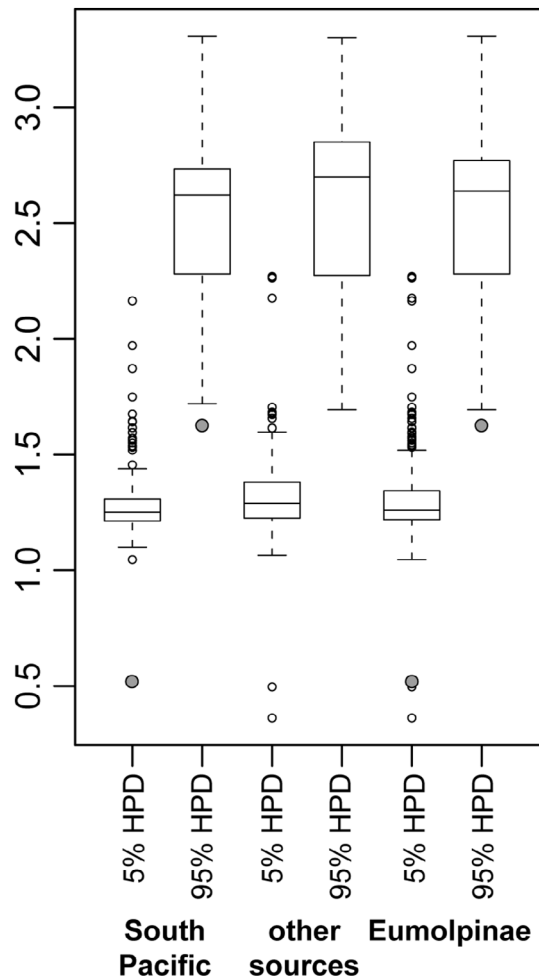


FIGURE 3 Box and whisker plots of the lower and upper boundaries of the relative rates per branch based on the heterotachy analysis using DPPDiv. Results are shown for three subsets of data, including the South Pacific clade (left), the remaining Eumolpinae (centre) or the entire in-group (right). Each plot shows the respective medians, interquartile ranges and potential outliers, and the values corresponding to the branch leading to clade A1 or South Pacific clade are shown as grey circles.

DISCUSSION

Hypotheses on the evolutionary origins of South Pacific Eumolpinae

The separation of the evolutionary branch of Eumolpini currently present in the South Pacific archipelagos does not appear related to Australasian genera of this tribe and the most recent common ancestor of this clade and its sister group was dated at 43.0–75.2 Ma. This inference is compatible with an origin during the initial stages of the fragmentation of eastern Gondwana, matching the entire period since the initial opening of the Tasman Sea well after the definitive opening of the Coral Sea (Mortimer et al., 2017). Given our extensive sampling of Eumolpini diversity, including representatives from both the Old and the New World, we had expected to identify the geographic sister

of South Pacific representatives of the tribe. However, phylogenetic uncertainty associated with the soft basal polytomy of clade A and the lack of supported relationships with current sampling leaves entirely open the evolutionary origin of the lineage on South Pacific Islands. Moreover, the early separation of this group and its apparent single origin of diversification only in the Late Eocene, also add uncertainty about where the ancestor of this radiation was for the ~30 Ma represented by the long stem branch in the phylogeny.

Our data cannot exclude any of the following three interpretations for the exclusive presence and survival of this group in the South Pacific, of which the last one has the highest explanatory power, providing with a plausible extinction process that can explain both the lack of obvious relatives to South Pacific Eumolpinae and their long stem branch. (1) The group could be derived from a Gondwanan ancestor lineage that remained and survived in the region throughout the period when most of Zealandia was submerged through cycles of successful colonisation of available land and extinction of descendant lineages except for one that finally established in NC (Figure 5a). (2) This currently tropical lineage could have dispersed to this region in more recent times from tropical latitudes outside of Zealandia, colonising NC first and subsequently dispersing south (Figure 5b). This origin could be either from Australia, given its geographical proximity (e.g., Buckley et al., 2010; Opell et al., 2016), or stepping stone dispersal from South East Asia (e.g., Colloff & Cameron, 2014; Toussaint et al., 2017; Toussaint & Balke, 2016) and coinciding with the development of tropical and subtropical conditions in South Pacific islands. (3) Finally, dispersal could have followed the opposite route, from Western Antarctica. This plate separated from the continental block Tasmantia in the Late Cretaceous (McLoughlin, 2001), when Eumolpini were in their early stages of diversification, and dispersal could have taken place after this period and before Antarctica became climatically unsuitable at the end of the Eocene (Houben et al., 2019). This model putatively explains the deep split of South Pacific Eumolpini and lack of current living relatives, and has been invoked to explain biogeographic patterns in other leaf beetles, including the Patagonian Mylaxini of the Cryptocephalinae (Gómez-Zurita & Cardoso, 2021) or the Spilopyrinae in the South Pacific and Chile (Verma & Jolivet, 2006). The long branch leading to this radiation could reflect the extinction of Western Antarctic relatives, but also lack of sampling of relevant taxa. However, the latter is not supported by our taxonomic knowledge of extant eumolpines, since the genera of Eumolpini in the South Pacific are endemic of this region (*Dematochroma* was reported, possibly erroneously, from Timor; Jacoby, 1894), and their putative sister group relationship with other genera in nearby regions has not been assessed in the taxonomic literature.

Exceptional colonisation routes of South Pacific Eumolpinae

There are only two exceptions to the monophyly of South Pacific Eumolpinae that are informative about biogeographic dynamics in the region, potentially representing two different phenomena separated

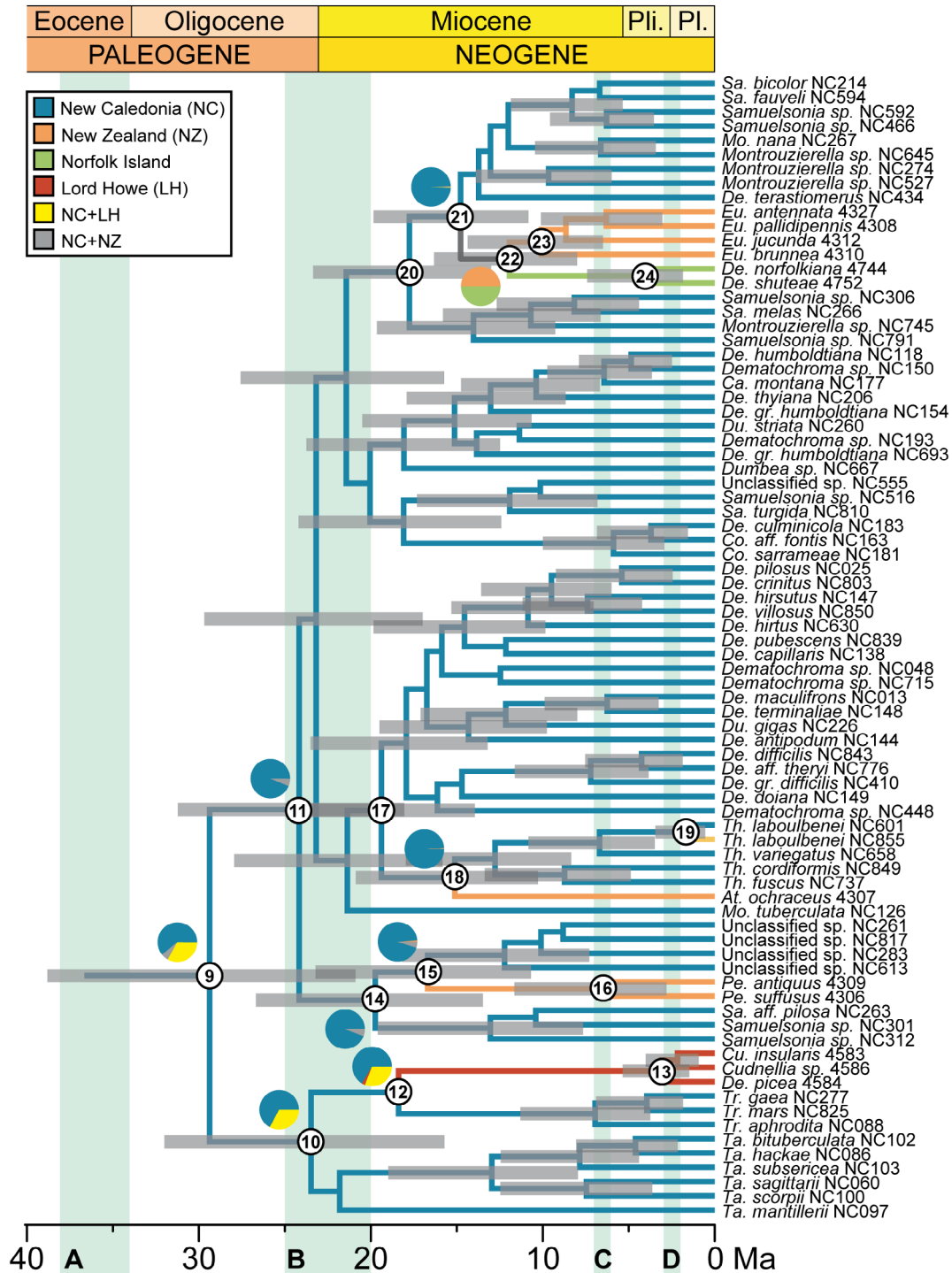


FIGURE 4 Enlargement of clock-constrained clade A1 of Figure 2 showing the phylogenetic relationships of South Pacific Eumolpinae leaf beetles. Information shown is the same as in Figure 2, including time and geological scales, clade names as given in the main text, dated nodes of Table 2, node age uncertainty for branches with posterior probability >0.95, and relevant geological events in the evolution of the South Pacific (A, exhumation of NC; B, reemergence of NZ; C, origin of LH and D, origin of NI and LI). Pie charts at selected nodes represent the inferred area of origin for the corresponding clades based on a DEC + J unconstrained model.

in time. There is phylogenetic support for *Pilacolaspis*, now endemic to South Island of NZ, being relatively close to the Australian endemic genus *Eboo*. They have some morphological similarity including generalised dorsal pubescence and lack of a dorsal groove on the pygidium

(Gómez-Zurita, 2020; Reid, 1993), an atypical combination in Eumolpini, although observed in some species of the Australian genus *Edusa*. However, other than that it is difficult to justify at present their phylogenetic affinity based on morphological traits. The common ancestor

of *Pilacolaspis* with Australian relatives existed between 23.6 and 48.4 Ma, the period of maximum subsidence of Zealandia (Cooper & Cooper, 1995), and this ancestor could have dispersed from Australia to NZ at any time from this period until the most recent common ancestor of the two *Pilacolaspis* species (2.3–10.7 Ma). Although there are no obvious candidates, we cannot rule out the possibility of other Australian Eumolpini nesting within the *Eboo-Pilacolaspis* clade, effectively making the *Pilacolaspis* lineage younger. Unfortunately, we could not study *Tyrannomolpus* Nadein & Leschen, an endemic Eumolpini from Three Kings Island (some 55 km NW of Reinga Cape, NZ), possibly sister to *Pilacolaspis* (Nadein & Leschen, 2017), which would help estimating the crown age of this lineage. The other notable biogeographic exception is *Rhyparida foaensis*, the only non-Eumolpini currently known in the South Pacific archipelagos (Gómez-Zurita, 2011, 2017). In this case, the marked similarity and possible conspecificity of this taxon with one species known from Queensland and allied to *R. limbatipennis* Jacoby, a well-known pest, suggest that its presence in NC could be the result of a recent dispersal of an Australian species, perhaps mediated by human activity.

TABLE 1 Dated deep events in the phylogeny of Eumolpinae leaf beetles (age = median; confidence = 95% HPD interval).

Node	Clade/event	Age	Confidence
1	Eumolpinae	113.1	85.7–144.9
2	Typophorini+Euryopini+Bromiini	75.6	54.1–99.6
3	Eumolpini	74.7	55.1–97.6
4	Split of South Pacific Eumolpini	57.4	43.0–75.2
5	Clade A2	52.7	38.7–68.4
6	Neotropical Eumolpini	38.6	26.7–51.1
7	Clade A2.1	44.5	32.2–57.9
9	Crown age of South Pacific Eumolpini	29.4	20.9–38.8
10	Clade A1.2	23.5	15.7–32.0
11	Clade A1.1	24.2	18.1–31.2

TABLE 2 Estimated time intervals (median age and 95% HPD) for the colonisation of the South Pacific by Eumolpinae leaf beetles, considering that effective colonisation had to happen necessarily between the split of the corresponding lineage (stem) and the diversification of the group in situ (crown).

Colonisation event	Stem node	Age	Crown node	Age
South Pacific	4	57.4 (43.0–75.2)	9	29.4 (20.9–38.8)
Lord Howe	12	18.4 (11.4–26.4)	13	3.1 (1.5–5.3)
Loyalty Islands	19	1.6 (0.6–3.5)	-	0
New Zealand				
<i>Atrichatus</i>	18	15.1 (10.3–20.9)	-	0
<i>Eucolaspis</i> ^a	21	14.8 (10.8–19.8)	23	10.1 (6.5–14.4)
<i>Peniticus</i>	15	16.7 (10.7–23.2)	16	6.5 (2.8–11.7)
<i>Pilacolaspis</i>	8	35.1 (23.6–48.4)	-	5.5 (2.3–10.7)
Norfolk Island ^a	22	11.9 (8.0–16.3)	24	4.1 (1.8–7.4)

Note: Node numbers as in Figures 2 and 4.

^aStem and crown defined considering a favoured scenario where Norfolk Island was colonised from New Zealand.

New Caledonia as South Pacific biodiversity hub

Of the 139 currently valid taxa of Eumolpini in the South Pacific, the vast majority (86.3%) occur in NC (Platania & Gómez-Zurita, 2023a). This large radiation, considering the size of the island, evolved in situ as confirmed with the new phylogenetic evidence produced here, validating one of the hypotheses originally proposed by Papadopoulou et al. (2013). Biogeographic analyses capture the high frequency of in situ speciation events where NC sympatry represents about 87% of the inferred processes for the entire region (Table 4), also inferring NC as the likeliest ancestral area of this clade.

There are several potential and non-exclusive explanations for the strong biogeographic bias in speciation and species distributions in this particular system, including some that have been proposed for other organisms (e.g., Smith et al., 2007). The age of NC, which was the first permanently emerged land in the region since the generalised subsidence of Zealandia during the Eocene (Sutherland et al., 2020), renders it an obvious candidate for initial colonisation and our results support that Eumolpini had successfully colonised (or alternatively, survived; Figure 5b) the island by the end of the Eocene (Papadopoulou et al., 2013; this work). Consequently, time alone offered a significant advantage for the accumulation of speciation events in NC. In addition, the tectonic migration of NC towards the tropics (Figure 5c–f), maintained a tropical climate for at least 25 Ma (Garrouste et al., 2021). Rates of diversification in the tropics are typically higher than in upper latitudes for most organisms (Hillebrand, 2004), and this may be relevant for Eumolpini, a group highly diverse in the tropics worldwide, with relatively few species in temperate regions (Jolivet & Verma, 2008). From the Late Eocene onwards, NC could have been a refuge of biodiversity due to the combination of land availability and inferred climate stability. This contrasts with other parts of the region, lost to submergence in the Oligocene, with consequent losses of terrestrial diversity. Massive extinction may have affected NZ in particular, where a large part of the archipelago may have drowned at the end of the Oligocene (Landis et al., 2008). Moreover, a climatic

TABLE 3 Biogeographic model selection for the diversification of South Pacific Eumolpini.

Model	FES	Scenario	k	Likelihood	AICc
DEC	+J	M ₀	3	-26.37271289	59.06121526
DIVALIKE	+J	M ₀	3	-26.85242162	60.02063271
BAYAREALIKE	+J	M ₀	3	-26.85837056	60.0325306
DIVALIKE	-	M ₀	2	-32.95728481	70.07041377
DEC	+J	M ₁	3	-33.01290564	72.34160075
DEC	+J	M ₂	3	-33.79571588	73.90722123
DIVALIKE	+J	M ₁	3	-34.59380089	75.50339126
BAYAREALIKE	+J	M ₁	3	-34.59399262	75.50377472
DEC	-	M ₀	2	-35.93824094	76.03232603
DEC	-	M ₁	2	-40.1620918	84.48002776
DIVALIKE	-	M ₁	2	-41.53026198	87.21636811
DEC	-	M ₂	2	-43.76104422	91.6779326
BAYAREALIKE	+J	M ₂	3	-45.01929298	96.35437544
DIVALIKE	+J	M ₂	3	-45.25918602	96.83416152
DIVALIKE	-	M ₂	2	-46.61986242	97.39556899
BAYAREALIKE	-	M ₀	2	-49.2170198	102.5898838
BAYAREALIKE	-	M ₁	2	-56.86792111	117.8916864
BAYAREALIKE	-	M ₂	2	-58.4118089	120.979462

Note: Models, including or not the founder-event speciation parameter (FES) and for alternative biogeographic scenarios (M₀-M₂) are ranked from best to worst according to AICc, estimated taking into consideration the likelihood of the model and the number (k) of parameters.

TABLE 4 Mean and standard deviation (SD) ranges of the number of inferred biogeographic events in 100 randomly selected topologies of the pseudo-Bayesian biogeographic analysis for each of the three preferred biogeographic models for South Pacific Eumolpini.

	ISS	FES	ALL	SSY
DEC + J				
Mean range	150.46-151.62	4.28-4.92	0.40-1.48	1.10-2.02
SD range	1.567-2.710	0.386-0.580	0.804-1.003	1.172-2.412
DIVALIKE + J				
Mean range	152.12-153.00	5.00-5.10	0-0.86	0
SD range	0-0.302	0-0.302	0-0.995	0
BAYAREALIKE + J				
Mean range	152.90-153.00	5.00-5.10	0	0
SD range	0-0.302	0-0.302	0	0

Note: Models did not recognise any case of dispersal or extinction. Events considered are in situ speciation (ISS), founder-event speciation (FES), allopatry (ALL) and subset sympatry (SSY).

TABLE 5 Frequency of inferred area transitions consistent with founder-event speciation in South Pacific Eumolpini.

From	To	DEC + J	DIVALIKE + J	BAYAREALIKE + J
NC	NZ	2.44 ± 0.554	2.52 ± 0.500	2.52 ± 0.500
NC	LH	0.67 ± 0.471	1.00 ± 0.065	1.00 ± 0
NZ	NI	0.52 ± 0.500	0.52 ± 0.500	0.52 ± 0.500
NC	NI	0.48 ± 0.500	0.48 ± 0.500	0.48 ± 0.500
NI	NZ	0.48 ± 0.500	0.48 ± 0.500	0.48 ± 0.500

Abbreviations: LH, Lord Howe Island; NC, New Caledonia; NI, Norfolk Island; NZ, New Zealand.

setback for the diversification and survival of tropical groups in this region took place during the transition from the Oligocene to the Miocene (Beddow et al., 2016), followed by gradual cooling down from the middle Miocene onwards (Herbert et al., 2016; Sosdian & Lear, 2020). The environmental and geological dynamism of NC throughout the Oligocene and Miocene (Chevillotte et al., 2006; Maurizot & Campbell, 2020) likely affected rainforest range and connectivity (Pillon, 2012; Pinaud et al., 2001), and these processes are potentially linked to intense cycles of allopatric speciation of New Caledonian Eumolpinae (Platania & Gómez-Zurita, 2023b). This dynamism and its effects on soil pattern and variegation have been

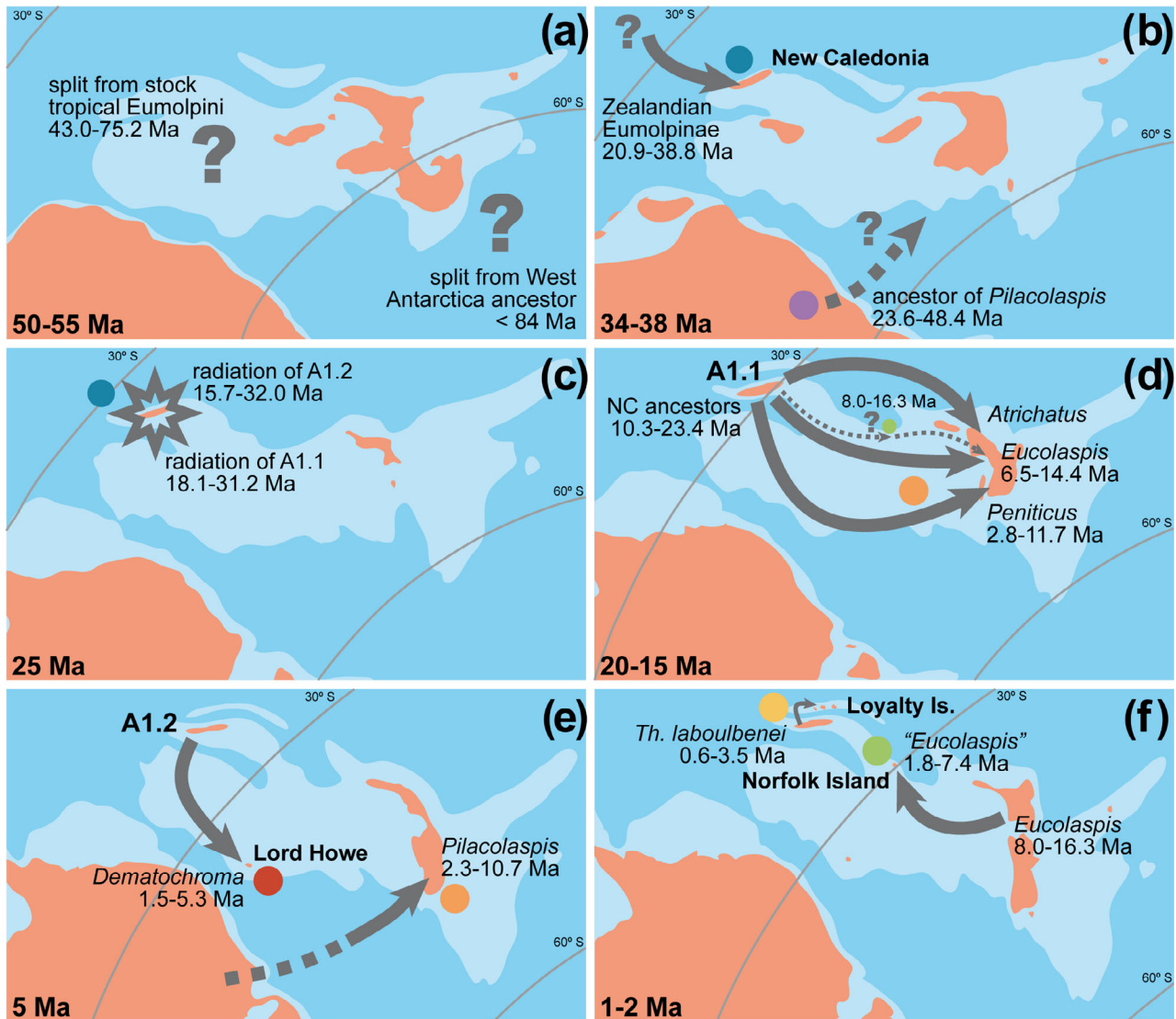


FIGURE 5 Time-stamped cartoon summarising the main biogeographic events in the colonisation of the South Pacific by Eumolpinae against the backdrop of the evolution of the area originally occupied by the continent Zealandia. The geological reconstruction of the South Pacific was based on the GPlates Geological Information Model (Müller et al., 2018) with refinements based on King et al. (1999).

suggested as important in shaping the island diversity for many organisms, also the Eumolpinae (Bauer et al., 2006; Espeland & Johanson, 2010; Isnard et al., 2016; Nattier et al., 2012; Platania et al., 2020). Linked to this, NC is associated with an extensive and singular botanical diversity (e.g., Condamine et al., 2017; Morat et al., 2011). Eumolpinae are herbivores with various levels of trophic specialisation, and their diversification could be interlinked with host plant diversification or responding to similar evolutionary pressures as them (Farrell & Mitter, 1994).

New Caledonia as South Pacific biodiversity pump

The prominence of NC boosting diversity in the South Pacific is well established for many organisms (Grandcolas, 2017). In general, NC is

considered the first receptor of Australian or Asian lineages, subsequently acting as centre of diversification and dispersal to other islands in the Pacific (Keppel et al., 2009; Smith et al., 2007). This role of islands as biodiversity pumps has been recognised for example in mountainous islands of the Papuan region (Toussaint et al., 2013). NC was suggested to behave in a similar fashion, serving as refuge but, most notably, as a source of biodiversity (e.g., conifers; Condamine et al., 2017). The Eumolpinae would be clearly another important example showing that NC, besides harbouring an impressive endemic diversity, also acted as the primary source of evolutionary lineages found in other archipelagos of the region.

When inferring the history of the distribution of Eumolpinae in the South Pacific, biogeographic model selection was not affected by decisions on the geological history of the region, most likely because the main splits fitted perfectly and actually post-dated the age of the

areas involved, at the cost of unnecessary parameters compared with the null model. Moreover, biogeographic models possibly lost support because of the inferred splits to LH (max. 15.7–32.0 Ma) and NI (8.0–16.3 Ma) being much older than the actual age of the islands (6.4–6.9 and 2.3–3.0 Ma, respectively; Jones and McDougall, 1973; McDougall et al., 1981), defining lower theoretical boundaries for putative dispersal events inconsistent with the specifications of the M_1 – M_2 models for most of the phylogenetic trajectory of LH and NI lineages. Nonetheless, the lack of shared species between areas, the exceptional clean-cut biogeographic pattern relating areas, and the timing of crown diversification in each island compatible with their age, facilitate the narrative of events identified as founder-event speciation, thus the result of dispersal, in the analyses.

The colonisation of the small, geologically young LI and LH was from ancestors of lineages now only present in NC, or in the case of NI ambiguously resolved as from NZ or NC. Dispersal from NC to LI is canonical regarding taxonomy (Gómez-Zurita & Pàmies-Harder, 2022) and known age of the islands (Maurizot et al., 2020). The estimated age of the split between representatives of *Thasycles laboulbenei* (Montrouzier) from Grande Terre and the LI fits nicely with the age of the latter, suggesting dispersal to these islands some 0.6–3.5 Ma ago (Figure 5f). The inferred ages of diversification on LH and NI also fit perfectly within the age of the islands themselves. These are accurately dated volcanic islands with ensuing atoll architecture and there are no doubts about their recent, post-Messinian ages, and by sampling two or three species from each island we provide additional evidence that our phylogenetic analyses calibrated with out-group dating are reliable. The apparent age discordance when considering the age of lineages leading to LH and NI most likely reflects the ongoing extinction of relatives in the region. Non-random extinction in NC of all descendants from the same ancestor of these island clades would generate the observed outcome (Pillon & Buerki, 2017), although it is not impossible, as shown for the dispersal of flightless crickets to sub-antarctic islands without close relatives in NZ (Dowle et al., 2024). Missed sampling in the phylogeny of closer living relatives of the island clades would yield the same result. The unambiguous origin of the LH clade in NC is an interesting result, since the most common biogeographic origins of LH biota are Australia or NZ (e.g., Colloff, 2010; Perrie et al., 2003; Shaw & Solodovnikov, 2016), and only exceptionally NC (e.g., Lillemets & Wilson, 2002). Our relatively dense taxonomic sampling in NC makes the idea of sampling bias unlikely in this case. However, in the case of NI this hypothesis deserves some consideration. An origin in NZ is entirely plausible for the Eumolpinae in NI and supported by taxonomic information. These beetles share morphological traits with and should be transferred to the NZ genus *Eucolaspis*, and they are particularly akin to the species *E. kotatou* Gómez-Zurita, described recently from the northernmost tip of the North Island in NZ (Gómez-Zurita, 2019), although unfortunately missing in our dataset. Moreover, the relationship between NI and NZ has been proposed already for other groups (e.g., Arensburger et al., 2004; Colloff, 2011).

The most important long-distance colonisation route in this system, at least in terms of recurrence of the process, was the dispersal from NC to NZ. This long-distance dispersal route occurred at least

three times independently for South Pacific Eumolpinae, during the Early Miocene, founding three of the NZ genera in this subfamily. The biogeographic connection between these two archipelagos is well established in the literature (e.g., Buckley et al., 2010; Heads, 2017), including for the Chrysomelidae (Gressitt, 1956). However, for most organisms, NZ acted as source, and more rarely as receiver of immigrant species (reviewed in Wallis & Trewick, 2009). The predominant source of organisms reaching NZ seems to be Australia (Sanmartín & Ronquist, 2004; Wallis & Trewick, 2009), as we proposed for the endemic genus *Pilacolaspis*. Thus, our finding that NZ genera of Eumolpinae originated from NC is interesting, adding to other examples of this colonisation route, including geckos, cicadas and flax snails, among others (Wallis & Trewick, 2009). It appears that this biogeographic pattern and colonisation route may be relatively consistent for largely tropical groups with lineages with the potential to adapt to cooler conditions (e.g., Buckley et al., 2010; Chapple et al., 2009), since at the inferred time of colonisation the latitudinal climatic gradient was already established (Zhang et al., 2019). The inferred timing of these independent colonisation events (Figure 5d) is interesting as well since they seemingly postdate the supposed period of maximum drowning of NZ (Cooper & Cooper, 1995; Mildenhall et al., 2014). These data do not bear any information for the actual drowning debate of NZ (reviewed in Wallis & Jorge, 2018), but indicate that the Eumolpinae from this evolutionary lineage were not present or did not survive in the NZ area during the critical geological periods.

The fact that colonisation from NC to NZ appears to have been successful at least three times in this system raises the question of the actual mechanism that allowed for such an outcome. Most probable are passive factors that have been invoked for transoceanic dispersal of other insects (Andújar et al., 2016; Chiu et al., 2021; Goldberg & Trewick, 2011; Trewick, 2000). These include aerial dispersal through high wind currents or occasional storms, which in the case of Eumolpinae, mostly winged and relatively small, could be an effective mean of passive dispersal (Nilssen, 1984; Peck, 1994). Insect-trapping studies on ships and airplanes crossing the Pacific frequently recovered Coleoptera (Holzapfel & Gressitt, 1965; Wise, 1983), including occasionally Chrysomelidae (e.g., Holzapfel & Harrell, 1968; Yoshimoto & Gressitt, 1960). Also, the larvae of Eumolpinae are subterranean, thus it is entirely possible that they could disperse rafting on tree stumps carrying big lumps of soil in their roots (Holzapfel & Harrell, 1968; Letsch et al., 2020; Nikula et al., 2013; Tänzler et al., 2016). The potential adaptability of these Eumolpini to new niches, ecological tolerance or opportunism, particularly their ability to exploit new hosts, may have given them an advantage to settle down on new islands upon their arrival. The acquisition of pest status on exotic hosts of several species of *Eucolaspis* in NZ (Doddala et al., 2016; Rogers et al., 2006) could give support to this idea. NC clearly acted as a source of biodiversity of these beetles, which although diversifying in the tropics, were able to successfully colonise cooler regions of the South Pacific via long-distance dispersal.

AUTHOR CONTRIBUTIONS

Leonardo Platania: Formal analysis; writing – original draft; writing – review and editing. **Anabela Cardoso:** Data curation; formal

analysis; investigation; resources; writing – review and editing. **Mark Anderson:** Resources. **Martin Fikáček:** Resources. **Jérémy Gauthier:** Formal analysis. **Lars Hendrich:** Resources. **Christian Mille:** Resources. **Yuta MORII:** Resources. **Chris A. M. Reid:** Resources. **Matthias SEIDEL:** Resources. **Mary Morgan-Richards:** Resources; writing – review and editing. **Steven A. Trewick:** Writing – review and editing; resources. **Emmanuel F. A. Toussaint:** Conceptualization; writing – review and editing. **Jesús Gómez-Zurita:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Sequence data generated for this study has been accessed to GenBank under accession numbers PP235333–PP235379 (*cox1*), PP235735–PP235787 (*rrnS*), PP254021–PP252122 (*cps*), PP255379–PP255474 (*pabp1*) and PP255476–PP255565 (*wg*). The DNA sequence alignment (PHYLIP format) used for likelihood analysis in RAxML together with the resulting optimal tree, and the XML code for BEAST2 MGSM analysis and the input files used in BioGeoBEARS are publicly available on the Zenodo DOI: 10.5281/zenodo.10610285.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

Supplementary Text S1. Geological framework for the historical biogeography of the South Pacific islands.

Table S1. Sampling available for phylogenetic and biogeographic study of the Eumolpini leaf beetles in South Pacific islands.

Figure S1. Summary tree of Eumolpinae leaf beetles with median branch-specific rates estimated from the MCMC run in DPPDiv and color-coded according to their absolute magnitudes. The branch leading to the South Pacific clade (highlighted) presents the lowest

absolute rate, less than half the average rate in the rest of the tree. Several clades are labeled as in the tree shown in Fig. 1 of the main article for reference.

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