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PERSPECTIVE

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Further discussion on the Eocene drowning of New Caledonia: Discordances from the point of view of zoology

Abstract

We discuss the fauna of New Caledonia in the context of the prolonged submergence of Grande Terre until its re-emergence around 37 million years ago and whether the resulting fauna can be entirely explained by over-water dispersal. The current literature discussing the predominant neoendemism in New Caledonia is reviewed, questioning some of the discourse about how the fact that most animal and plant lineages are neoendemics should weigh in to disregard the fewer cases of paleoendemism (clades that have persisted and diversified in New Caledonia for over 37 million years). We argue that many of the examples used in the literature, selected for other purposes, were not chosen to test this particular hypothesis, but several old lineages of non-vagile animals show that a non-trivial number of clades have a history that predates the supposed emergence of New Caledonia. We conclude by posing the question of how much additional evidence should be needed to demonstrate a discordance between the geological history of the archipelago and the evolutionary history of its biota.

1 | INTRODUCTION

A chief biogeographic question is understanding the biotic assemblage of New Caledonia, a series of islands dominated by Grande Terre at the northernmost edge of Zealandia. New Caledonia is home to a large number of endemic plant and animal species, many of which have very narrow ranges (Caesar, Grandcolas, & Pellens, 2017; Wulff et al., 2013). Due to the high level of endemism and the rapid degradation of many of its habitats, it has been considered an important hotspot for biodiversity conservation priorities (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). New Caledonia has a complex geological history with connections to Australia from the time of Gondwana (Campbell et al., 2018) and with deep submergence episodes that lasted millions of years until its re-emergence around 37 million years ago (Cluzel, Maurizot, Collot, & Sevin, 2012). Because a series of supposedly relictual taxa (see Grandcolas, Nattier, & Trewick, 2014; Grandcolas & Trewick, 2016) remain in this island, a number of authors have provided ad hoc explanations for the permanence of such taxa throughout the deep submergence of Grande Terre. Nonetheless, the geological evidence for this submergence is uncontestable, and the biogeographic implications of such a profound marine transgression have been elegantly summarized in a series of papers by Grandcolas and colleagues (e.g. Murienne et al., 2005; Grandcolas et al., 2008; Grandcolas, 2017), among others. A consequence of this major drowning episode is that a large proportion of the island biota is now the result of neoendemism—most clades in New Caledonia are more recent than the geological age of the "oceanic" New Caledonia (as opposed to the pre-submerged "continental" New Caledonia), and published results on dated phylogenies have suggested that these groups evolved according to a diversity-dependent model of diversification in New Caledonia (Espeland & Murienne, 2011). This may imply that after the re-emergence of New Caledonia, open and empty ecological space became available, facilitating evolutionary radiations. A thorough compilation of this neoendemism has been provided in a recent article by Nattier et al. (2017). While many other examples of endemic New Caledonian clades are also known (e.g. the endemic snail genus *Monomphalus* [Figure 2c]), the timing of diversification of these endemic groups remains unstudied (see Harvey et al., 2017). However, another view put forward—although not based on analyses of actual data—in a series of papers mostly led by Heads (Heads, 2008a, 2008b, 2010; see also Ladiges & Cantrill, 2007) postulates a series of emerged landmasses that have been continuously above water, acting as time-stepping stones and thereby facilitating the persistence of the Gondwanan relicts still present in New Caledonia.

Without questioning the ample available scientific data explaining the deep and long submersion of today's Grande Terre, as put forward by multiple sources of geological and biological evidence (summarized in Murienne et al., 2005; Pelletier, 2006; Grandcolas et al., 2008), we continue to be perplexed by the existence of paleoendemism in New Caledonia, and we do not refer here to so-called single-species relicts—as is the case of *Amborella trichopoda*, the sister group to all other flowering plants (Qiu et al., 1999)—as it is not possible to disentangle the origin from the diversification of such monotypic groups, and thus is not informative (i.e. irrelevant) in the context of deciphering the biogeographical history of New Caledonia. We also understand that the presence of *Amborella* in modern New Caledonia does not justify that Amboreales originated there—a common mistake in related discussions. Phylogenetic debate must therefore necessarily use information other than monotypic endemics, as eloquently outlined by Murienne (2009) and Sharma and Wheeler (2013). In the latter paper, in the context of the Oligocene marine transgression of another part of Zealandia, New Zealand, the authors distinguish between neoendemics (which can reject pre-drowning history),

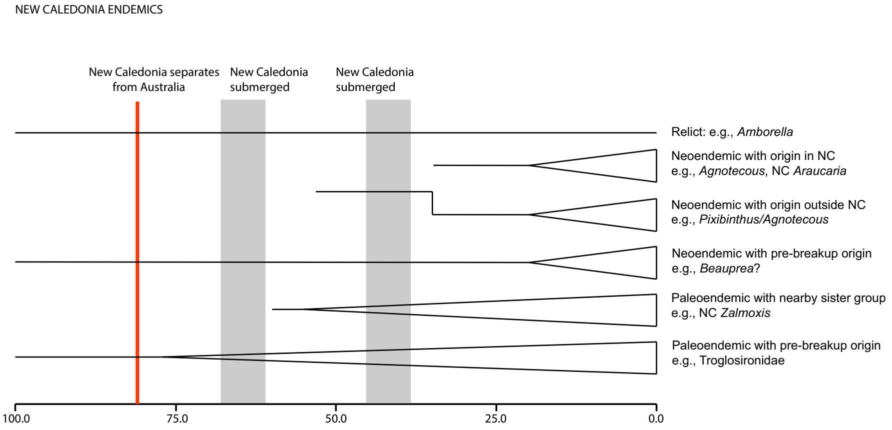

FIGURE 1 New Caledonian taxa, their status as neoendemic or paleoendemic (with respect to the submergence of Grande Terre) and origin of the clades with respect to the breakup of Zealandia from Australia [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Selected New Caledonian endemic species relevant to the biogeographical history of the New Caledonian biota, including neoendemics and paleoendemics: (a) the centipede *Parascutigera* sp. (Myriapoda, Chilopoda, Scutigeromorpha, Scutigeridae); (b) the neanurid springtail *Caledonimeria* sp. (Hexapoda, Collembola, Poduromorpha, Neanuridae); (c) a land snail in the endemic genus *Monomphalus* (Mollusca, Gastropoda, Heterobranchia, Eupulmonata, Charopidae); (d) an undescribed species of mite harvestman *Troglosiro* (Arachnida, Opiliones, Cyphophthalmi, Troglosironidae); (e) the armoured harvestman, *Zalmoxis princeps* (Arachnida, Opiliones, Laniatores, Zalmoxidae); (f) the armoured harvestman *Triconobunus horridus* (Arachnida, Opiliones, Laniatores, Triaenonychidae)

relicts and revenant clades (which cannot reject hypotheses of pre-drowning history) and paleoendemics (which can reject the hypothesis of complete drowning) (Figure 1). It is our opinion that only the latter could shed light onto the debate of the history of New Caledonia during the Eocene. It is now well understood that multiple of these classes of clades (neoendemics, relicts, revenant clades and paleoendemics) coexist today in New Caledonia (e.g. Anso et al., 2016; Condamine, Leslie, & Antonelli, 2017; Nattier et al., 2017), but it is our belief that not all have been given their deserved place in discussions about the evolutionary and biogeographic history of the archipelago.

Ecologically, the debate on the New Caledonian biota has centred on whether the emerged landmass (Grande Terre) is a museum (given its continental origin) or a cradle (given its post-submersion phase) of biodiversity. Assuming that any given landmass must be either a museum or a cradle is, however, unnecessary, as biotic assemblages are often composed of clades that originate at different times and that diversify following a multitude of modes and patterns. Not all clades in New Caledonia are equally old (as shown by Nattier et al., 2017) and not all organisms have the same dispersal ability. Indeed, New Caledonia has been shown to have acted both as a refuge for old lineages and as a source of new lineages of conifers (Condamine et al., 2017). There should also be a relationship between environmental factors and the dispersal ability of particular taxa and the capacity to establish new lineages in a disjunct landmass—whether appearing de novo or not—as shown in the classical meta-analysis of southern hemisphere biogeography by Sanmartín and Ronquist (2004), where plants and animals showed very different patterns of dispersal. In addition, volant animals or species with dispersal phases (e.g. seeds or fruits) are better than saproxylic animals or plants, often with low dispersal capacities, at colonizing new landmasses. Biogeography is not all about *vicariance* nor all about *dispersal*; different groups of organisms fit better one pattern or the other, according to their dispersal capacities.

Because we consider that some *biological* data are in conflict with the evidence for the drowning of New Caledonia, but without necessarily proposing ad hoc mechanisms that could explain the presence of putative paleoendemics in New Caledonia, we feel that some of the arguments put forward for favouring the submergence *based on biological data* are not entirely justified. It is our intention to revisit some of these issues here.

2 | HOW PRECISE ARE THE PHYLOGENIES USED TO ESTIMATE BIOGEOGRAPHIC EVENTS IN NEW CALEDONIA?

Two conditions are strictly necessary to test a biogeographic hypothesis of total submergence, (a) a phylogenetic hypothesis of an endemic clade (note that a clade does not need to be a specific taxonomic rank; it could be a group of species within a genus or any other rank) and (b) a dated phylogeny. Even if the mathematical methods for estimating and dating phylogenies were accurate and precise—a discussion we avoid here—there are many factors that may have an influence on these results.

The existence of relevant fossils (and their precise dating) is a fundamental limitation in many studies on biogeography, perhaps exacerbated by the poor fossil record of New Caledonia. Grandcolas (2017) emphasizes the importance of studying the New Caledonian fossil record, but it remains sparse and poorly documented, if at all, especially for animals relevant to the present biogeographical debate. From published studies dating New Caledonian animal and plant lineages, none use fossils from New Caledonia for dating their trees. Other methods (e.g. using tectonic dating) tend to be unsatisfactory for their circular reasoning (Kodandaramaiah, 2011; but see Landis, 2017), especially within a biogeographic context.

Taxon sampling is another fundamental aspect of phylogenetic reconstruction. While ideally all extant species could be incorporated into a phylogeny, in reality, sampling is constrained by many factors, including accessibility to specimens. This is illustrated in a recent study on *Pixibinthus*/*Agnotecous* crickets, that, by sampling an additional species (which happened to be the sister group to the remaining members of the clade), extended the median age of a neoendemic clade by 13 Ma, placing it closer to the re-emergence of New Caledonia, with the error bar pre-dating such re-emergence (Anso et al., 2016). In the context of New Caledonia, sampling of many groups has maximized efforts in the more accessible southern part of Grande Terre, but at least in one published case (the mite harvestmen of the endemic genus *Troglosiro* [Figure 2d]), a published phylogeny follows a north-to-south cladogenetic pattern, with the earliest diverging lineages being in the north (Sharma & Giribet, 2009a). The age of the crown *Troglosiro* would therefore be very different if the northern species had not been included in a phylogeny of the group. Therefore, maximizing taxonomic diversity of a clade (as in the *Pixibinthus*/*Agnotecous* example) and geographic coverage (as in the *Troglosiro* example) can have a drastic influence on accurately providing the age of an endemic clade. A similar case, although not as clear, is observed for the snails of the family Tateidae, which have been sampled more intensely in the south, yet most of the northern samples belong to the first clade splitting off in a recently published phylogeny (Zielske & Haase, 2015). The point here is that one can easily underestimate the age of a clade by using deficient or geographically restricted extant taxon sampling and that in New Caledonia, this is often the case for many groups, which are often poorly sampled in the North.

Finally, certain New Caledonian taxa are restricted by other environmental parameters. For example, the largely Gondwanan harvestman taxon Triaenonychidae (found in Australia, New Zealand, Madagascar, southern Africa and southern South America, with a genus in North America) includes two monotypic genera in New Caledonia (Figure 2f), but these are found only at high elevation, mostly restricted to the highest mountains of Grande Terre (Mt. Panié, Mt. Humboldt, Mt. Canala, Plateau de Dogny, Me Maoya and Mt. Koghi). While a connection to New Zealand has been inferred (authors' unpublished data), no published phylogenetic analysis has yet tested the relationships and origin of these New Caledonian species. Likewise, another harvestman family, Neopilionidae, is known from most temperate Gondwanan landmasses (southern South America, South Africa, Australia and New Zealand). Despite not having been previously recorded from New Caledonia, we recently found a new species of Neopilionidae in high elevation in Me Maoya and Plateau de Dogny. Unlike triaenonychids, the undescribed neopilionid from New Caledonia does not seem to be closely related to the many clades inhabiting New Zealand and instead is related to a Tasmanian clade (authors' unpublished data). Elucidating the complete biogeographic history of the New Caledonian Triaenonychidae and Neopilionidae is still in the works, but their putative relictual (high elevation) habitats in Grand Terre may provide additional evidence for the biogeography of Zealandia.

3 | NEOENDEMICS AND PALEOENDEMICS: HOW CAN WE REALLY TEST THE EOCENE SUBMERGENCE?

Most of the work on New Caledonia has focused on neoendemics—lineages that have diversified in New Caledonia after arriving there via dispersal, such as the emblematic *Araucaria* radiation

(Kranitz et al., 2014), once thought to be a Gondwanan paleoendemic (i.e. *Araucaria* is still a Gondwanan taxon, but the radiation of New Caledonia was achieved by recent dispersal). Neoendemics are abundant among plants and insects and are wonderful systems to understand the origins and maintenance of the New Caledonian biota. However, they cannot provide much information about what happened in New Caledonia before their arrival. For this, we need to look at putative paleoendemics.

Within arachnids, Opiliones have often been used to study biogeography and are relatively well sampled for New Caledonia (Sharma, 2012; Sharma & Giribet, 2009b; Sharma, Kury, & Giribet, 2011). The genus *Zalmoxis* (Figure 2e) has radiated in the South Pacific, and New Caledonia includes a diverse clade of these animals, with its sister group found in Fiji (Sharma & Giribet, 2012); *Zalmoxis* is well known to have dispersed from the Neotropics to the South Pacific. The persistence of this genus in New Caledonia is however older than 37 Ma (Nattier et al., 2017), and thus, this taxon may require further explanation. But the fact that the group is known to have dispersed to oceanic islands, like Fiji, and that the closest relatives to the New Caledonian clade are in nearby islands may easily lead to ad hoc explanations about persistence in the area through time by stepping from emerged landmass to emerged landmass.

A very different case is that of the New Caledonian Opiliones endemic family Troglosironidae, which includes thirteen named species in the genus *Troglosiro* (see Sharma & Giribet, 2009b) and a few additional undescribed ones (Figure 2d). Troglosironidae perfectly fits the definition of a paleoendemic. It diverged from its sister group before the formation of New Caledonia (before it broke off from Australia), it is endemic to Grande Terre, and it has been diversifying for about 60 Ma (40–73 Ma) (Giribet et al., 2012; Nattier et al., 2017; Oberski et al., 2018). Unlike Zalmoxidae, the harvestmen in the suborder Cyphophthalmi are poor dispersers and have emerged as a model system to study vicariance biogeography (e.g. Giribet & Boyer, 2002; Boyer et al., 2007; Clouse & Giribet, 2010; Giribet et al., 2012). Interestingly, the sister group of the New Caledonian Cyphophthalmi is not among its geographical neighbours; the family Pettalidae is found, among other places in New Zealand and Queensland (Boyer & Giribet, 2007; Giribet et al., 2016; Oberski et al., 2018), and Stylocellidae is found across Southeast Asia (Clouse & Giribet, 2010). Instead, Troglosironidae's closest relatives are the members of the families Ogoveidae (from tropical West Africa) and Neogoveidae (from tropical West Africa and the Neotropics)—a Paleozoic divergence and a biogeographic conundrum for which a satisfactory explanation remains elusive. But because Troglosironidae contains multiple species, one can actually infer the clade's diversification dynamics within Grande Terre, differentiating it from the monotypic *Amborella* (though it is possible that an old radiation of *Amborella*, prior to large-scale extinction, could have looked similar to what we see in *Troglosiro*). However, these minute mite harvestmen are often ignored, or mentioned in passing, in the debate about New Caledonian biogeography despite having achieved more prominence in biogeographical debates of other islands, especially Sulawesi (Stelbrink, Albrecht, Hall, & Rintelen, 2012).

Not all purported paleoendemics may be so. Additional examination of results may be required for some published phylogenies. For example, He, Lamont, and Fogliani (2016) propose a pre-breakup origin of the proteacean genus *Beauprea*, with an extensive palynological fossil record across temperate Gondwana but nowadays restricted to New Caledonia. Their conclusions are, however, derived from a somewhat unorthodox supertree, which combines a dated molecular phylogeny with a distance tree derived from 11 morphological palynological characters (many of them are discretized quantitative characters). Interpretation of this tree is not straightforward given the poor resolution of distance methods in phylogenetic analysis of discrete character data.

Many other patterns are not always crystal clear. For example, the three New Caledonian scutigeromorph centipedes in the genus *Parascutigera* (Figure 2a) are not always resolved as monophyletic, but when including species from Queensland (Australia), the origin of the group seems to at least support some post-breakup dispersal between Australia and New Caledonia (Giribet & Edgecombe, 2013). It also seems that two lineages of the blind scolopendromorph centipede *Cryptops* have colonized New Caledonia independently in recent times (Murienne, Edgecombe, & Giribet, 2011), questioning the low vagility of some of these groups. However, our knowledge of the phylogeny and dating of most other New Caledonian myriapods, including its many species of millipedes (Diplopoda), is virtually non-existent. Given the potential for studying old biogeographic questions (e.g. Wesener & Vandenspiegel, 2009), several groups of Diplopoda from New Caledonia could constitute additional examples of paleoendemic species. The same goes for the many terrestrial snail clades (Solem, 1961) which have received virtually no phylogenetic attention to date.

4 | WHAT IS NEEDED (FROM BIOLOGY) TO REJECT A HYPOTHESIS? OR HOW MUCH IS ENOUGH?

Corroboration for the geological data on the submergence of Grande Terre has been often claimed from the diversity of studies existing for New Caledonian taxa. The elegant study of Nattier et al. (2017) compiled 40 data sets that date regional clades. The authors showed that 34 clades were younger than 37 Ma, while “Only a few inclusive Pacific clades (6 out of 40) were older than the oldest existing island”. They then suggest that “these clades could have extinct members either on vanished islands or nearby continents, emphasizing the role of dispersal and extinction in shaping the present-day biota”.

The great philosopher Karl Popper has been “abused” enough in the systematics literature, but it seems relevant to bring back here his falsificationism. A hypothesis is rejected when falsified by additional data. Should not one unambiguous case be enough to reject (or at least seek an alternative to) the submergence of New Caledonia? Are six cases out of 40 not enough? Or would Popper's falsificationism not be applicable to hypotheses like the total submersion of an island?

Irrespective of our point of view, not all examples seem equal to answer a given biogeographic question. Authors tend to select examples that are appropriate to their relevant study systems—for example spiders in oceanic islands (e.g. Gillespie, 2004) and harvestmen in continental ones (e.g. Clouse & Giribet, 2010). The selection of studies in Nattier et al. (2017) was most certainly not biased, as they selected *all* the available published studies which included a dated phylogeny for a New Caledonian clade. But how about the selection of taxa by the original authors? Most of the examples come from plants and insects, and while botanists and entomologists may be more diligent than other specialists, their study subjects include mostly groups of organisms with high dispersal abilities (although others, like the *Lauraesipha* cockroaches, are considered poor dispersers). This is why studies on crickets or beetles are abundant in the literature of oceanic islands (e.g. Hawaii, Galapagos, Canaries). Without questioning the validity of these studies, would their authors have chosen the same study groups had they been charged with answering the question debated here? Or would have they chosen non-volant hexapods such as Collembola (Figure 2b), Protura or Diplura instead of flying insects? Taxon choice cannot be agnostic to the question one is asking, and thus, a phylogeny of one species of centipede versus one family of mite harvestmen cannot weigh in equally in this debate.

Under our point of view, the question should not be *"are there more taxa supporting hypothesis A or hypothesis B?"* nor *"is group A younger than age X?"*. Instead, the most appropriate questions should be *"is endemic group A older than age X?"*, as it is the only question able to falsify the drowning hypothesis. Simply put, the fact that many groups are neoendemic to New Caledonia should not be able to falsify anything. It is finding endemic groups older than 37 Ma that may bring light to the debate (not finding any should be the corroboration favouring the submergence hypothesis). Such informative biogeographical models tend to be old lineages with low vagility (the fact than many insect island endemics are wingless did not preclude their winged ancestors from dispersing). Short-range endemics (SREs; Harvey, 2002) with saproxylic and leaf-litter habits (e.g. Daniels, Picker, Cowlin, & Hamer, 2009) tend to satisfy these criteria better than any other organisms (as discussed by Giribet & Boyer, 2010 for New Zealand), and many of these SRE taxa (also called micro-endemics) are abundant in New Caledonia (Caesar et al., 2017). Let us hope that future studies are also able to focus on organisms that are old enough to continue testing further the drowning of New Caledonia from the point of view of its biota, but some examples do already exist that may contradict such evidence and instead suggest that some sort of emerged land must have been available.

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CONFLICT OF INTEREST

There are no conflict of interests to report.

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