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Ten false ideas about New Caledonia biogeography

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Abstract

The biogeographical paradigm of New Caledonia has recently changed. Although this island is now considered by many as oceanic, its study is still often impeded by some old misconceptions concerning either regional geology or phylogenetic analysis of evolution and biogeography. I discuss ten points that I feel are especially detrimental, to help focus on the real debate and the real questions: (1) its geological history cannot be understood from the basement only; (2) the island submergence was not due simply to sea-level variation; (3) Zealandia/Tasmantis is not a lost continent; (4) short-distance dispersal is not equivalent to permanence on land; (5) long-distance dispersal is not the sole event opposing vicariance, but short-distance dispersal as well; (6) the occurrence of relicts does not prove biota permanence; (7) a major fault system was not observed in New Caledonia; (8) terranes are not rafts; (9) forest climatic refuges do not necessarily equate to centres of endemism or centres of diversity; and (10) New Caledonia is not only a sink but also a source. Study of New Caledonia will need to focus on old and non-relict clades and there is a need to improve the local fossil record.

Islands have always fascinated biogeographers and their study has seen the emergence of several paradigms (Darwin, 1859; Wallace, 1881; Darlington, 1957; MacArthur and Wilson, 1967; Nelson and Platnick, 1981). These authors traditionally distinguished oceanic islands that were never connected to continents and emerged in the middle of oceans, as opposed to continental islands. The biotas of oceanic islands were necessarily formed entirely by dispersal. In this context, opinions regarding New Caledonia have varied considerably. In early studies, New Caledonia was considered as an island intermediate between continental and oceanic and its biota was assumed to have resulted from both vicariance and dispersal (Darwin, 1859; Wallace, 1881; Jeannel, 1942; Faivre et al., 1955; Darlington, 1957; Wilson, 1961). In the second half of the twentieth century, some scientists came back to the idea of a continental island by presenting New Caledonia as a stunning Gondwanan refuge, based on its continental geological basement and the presence of local relict taxa (Raven and Axelrod, 1972; Holloway, 1979; Stevens, 1980; Lowry, 1998). This view prevailed for several decades until recent studies showed both its discordance with geology and the pitfalls of using relicts in biogeography (Murienne et al., 2005; Grandcolas et al., 2008, 2014; Murienne, 2009; Swenson et al., 2014). In this way, several reviews showed that molecular phylogenies dated New Caledonian clades (Grandcolas et al., 2008; Cruaud et al., 2012; Pilon, 2012) to after the re-emergence of the island, i.e. probably 373 Ma according to geology (Paris, 1981; Aitchison et al., 1995; Cluzel et al., 2001; Cluzel et al., 2012; Crawford et al., 2003; Pelletier, 2007). Science is, however, not consensus and several papers have recently

objected to the apparent congruence between systematics and geology by arguing for permanence of New Caledonian biota with ad hoc scenarios of short-distance dispersal (SDD) among nearby islands (Ladiges and Cantrill, 2007; Heads, 2008a, 2010). All these studies showed that New Caledonia is an interesting place for biogeography, and should allow us to disentangle the respective roles of vicariance and dispersal and open a very wide time window to test varied evolutionary scenarios. Some geological or biological inferences or theories already well established should be carefully specified for the debate could focus on the real controversial questions. Here, I review ten points that are frequently misunderstood and that I feel important to clarify for enhancing the quality of future research on New Caledonian biogeography.

Its geological history cannot be understood from the basement only

The deepest geological basement of New Caledonia has a very old continental origin (Paris, 1981; Pelletier, 2007; Maurizot and Vendé-Leclerc, 2009; Cluzel et al., 2012). However, many different layers and rock types have been overlaid on this basement in the context of subsequent and complex tectonic events. It is therefore confusing to describe New Caledonia simply as a piece of Gondwana (Raven and Axelrod, 1972; Holloway, 1979; Stevens, 1980; Lowry, 1998) and not to take into account the consequences of more recent geological events. First, as emphasized by Murienne et al. (2005) and Grandcolas et al. (2008), a recent and important submergence episode is documented by Palaeocene rock layers indicating deep marine sedimentation (thousands of metres) (Paris, 1981). This is the main evidence for submergence of the island: it does incorporate a few indirect assumptions, but merely strong stratigraphic and petrographic evidence interpreted in the framework of the general regional tectonic model. Second, the ophiolitic nappe of Eocene lithospheric origin is also of particular significance. This geological structure has been known for a long time in relation to the discovery of nickel-rich soils and to the development of mining activities (Paris, 1981). Although it was considered as metamorphic or intrusive until the 1970s (Avias, 1953; Routhier, 1953), the presence of the ophiolitic nappe had already made it clear that important environmental changes had occurred in the past in New Caledonia. Before the development of plate tectonics theory, this nappe was supposed to have been overlaid gently on marine and then on terrestrial biota. It was then assumed that local groups adapted progressively to ophiolitic rocks and to the subsequent nickel-rich and unbalanced soils (Morat et al., 1986). Since the 1990s, tectonics has developed integrative views based on several sources of data, from traditional historical geology and analyses of metamorphism to the study of boreholes. It was thus inferred that the ophiolitic nappe was overlaid by obduction of marine lithosphere (sea bottom) onto the island basement during a strong tectonic event, along with deep submergence of New Caledonia (Paris, 1981; Aitchison et al., 1995; Cluzel et al., 2001; Cluzel et al., 2012; Crawford et al., 2003; Pelletier, 2007). Geologically, New Caledonia is actually a piece of Gondwana, but it has existed as a terrestrial island only since 37 Ma and it does not support any strong biogeographical hypothesis of a Gondwanan refuge. Speculating on the intensity and on the extent of the effect of the Eocene obduction

on the New Caledonian landscape (Ladiges and Cantrill, 2007), that is complex to understand in details (Crawford et al. 2003; Pelletier, 2007; Cluzel et al., 2012) will not save the Gondwanan refuge hypothesis, given the previous submergence episode that occurred already long after the separation from the remainder of Gondwana.

Submergence was not like sea-level variation

The paradigm of island submergence is sometimes seen as a minor geographical event that can be conceived by the mind of man, just like strong sea-level variation. In that line, some have assumed that Eocene mountain tops or parts of the island could have escaped submergence (Morat et al., 1984), as noticed by Murienne (2009). Although the mountain chains of New Caledonia are quite ancient (in contrast to those of New Zealand), the magnitude of the long tectonic events during the Palaeocene and Eocene was inferred to be so important that a large part of the basement was deep beneath the sea surface and partly beneath bottom-sea lithosphere. New Caledonia is a long and narrow island whose longest dimension is parallel to the borders of the tectonic plates. It was then strongly submitted to tectonic events. The island is remarkably well studied from a geological point of view and it is clear that it was deeply submerged during major tectonic events, the intensity of which needs to be properly understood by biologists (Paris, 1981; Aitchison et al., 1995; Cluzel et al., 2001; Cluzel et al. 2012; Crawford et al., 2003; Pelletier, 2007).

Zealandia/Tasmantis: not a lost continent

The name 'Zealandia' is increasingly used in the literature to characterize a large area of diverse continental rocks that notably includes the basement of New Zealand and New Caledonia (Luyendyk, 1995; Mortimer, 2004; Trewick et al., 2007). The continental nature of these rocks was known since long ago (Paris, 1981), and until recently the area was known under the name 'Tasmantis' employed both as regards geology (Avias, 1955; Lillie and Brothers, 1970) and biogeography (Smith et al., 2007). However, naming such a geological diverse entity may be confusing for some biogeographers and lead them to assume that it could have behaved as a lost continent (i.e. a large terrestrial land mass some parts of which were flooded while others remained emerged), determining to shared distributions between terrestrial groups (e.g. Wannan et al., 2011). The lost continent paradigm can be traced back to the biblical story of the Deluge, employed in the earliest evolutionary scenarios from the Middle Ages to explain the occurrence of fossils: a large area of terrestrial land is supposed to be almost entirely flooded, determining a strong pattern of relationships between the remaining emerged parts. This scenario implies naive assumptions predating tectonics: the area is supposed to be affected as a whole by a process combining relative terrestrial land stability and sea-level variation, implying flooding after a rise in the sea level or the collapse of the continent. In contradiction, tectonics showed from the mid-twentieth century that the landscape can be shaped by very strong events in a much more

complex manner, including not only sea-level variation but also land subduction, uplift, orogenesis and subsidence occurring very locally and possibly in close opposition. The lost continent story recalls the long-standing myth of 'Pacifica' (Gregory, 1930), briefly resurrected by some biogeographers (Melville, 1966; Nur and Benavraham, 1977; Nelson and Platnick, 1981). Pacifica has been discounted (Nunn, 2009) but unfortunately Zealandia/Tasmantis remains fascinating, because New Zealand and New Caledonia are traditionally considered as continental by many. Zealandia or Tasmantis is not a name for a past terrestrial geographical unit but for a complex series of rock layers that implies diverse emergent and submergent lands at different periods and after different events of subduction, uplift or sea-level variation, and ending today with a large ocean surface where more or less ephemeral islands are scattered.

SDD is not equivalent to local permanence

In the same line of reasoning, assumptions of SDD are often used to rescue vicariance scenarios. Following the confrontation between modern regional studies of biogeography and geology (Murienne et al., 2005; Grandcolas et al., 2008), some authors realized that strict in situ permanence of biota has become an untenable hypothesis for New Caledonia. They then argued that hopping among ephemeral islands on the Norfolk Ridge could explain the permanence of old groups in New Caledonia (Ladiges and Cantrill, 2007; Heads, 2008a). This scenario was envisaged by many studies as one among many possible others (Morat et al., 1986; Swenson et al., 2001; Grandcolas et al., 2008) and it has been made testable by investigating whether the oldest inclusive insular Pacific clade is older than the oldest island, i.e. New Caledonia (Nattier et al., 2011; Swenson et al., 2014). The congruence of this scenario with geology remains to be studied; vanished islands certainly existed but were not suspected to be at the right place or the right time by geologists (Murienne et al., 2005; Grandcolas et al., 2008; Murienne, 2009). Regardless, it should be made clear that SDD is not equivalent to local permanence and cannot be taken as an argument to preserve the assumption of an anterior vicariance event between New Caledonia and adjacent so-called Gondwanan territories. Series of combined SDD events are mostly ad hoc hypotheses, the accumulation of which constitutes 'a house of cards' (Crispet al., 2011). They typically represent a heritage of the literature of the early ages of biogeography (Wallace, 1881; Zimmerman, 1942; Gressitt, 1956; Carlquist, 1965; Axelrod, 1972), and now need to be placed in a testable framework.

Dispersal (as opposed to vicariance) is either long or short distance

There are not two sorts of dispersal, the "bad" one (LDD), speculative and incompatible with biogeographic hypotheses, and the "good" one (SDD), that can be assumed without too many risks. All assumptions of dispersal need to be treated as such and to be submitted to attempts of refutation. In this respect, Ladiges and Cantrill (2007) or Heads (2008a) misrepresented the situation as if LDD was

opposed to SDD and vicariance for explaining the origin of the New Caledonian biota. In fact, the antagonist assumptions are any kind of dispersal (SDD or LDD) against vicariance and extinction. We have emphasized that assuming vicariance between New Caledonia and, say, Australia implied assuming a permanence of terrestrial biota in New Caledonia (Grandcolas et al., 2008). To employ the specific terminology of Heads (2012), SDD was transmogrified into biotic permanence. Ad hoc dispersal assumptions have been extirpated from historical biogeography (Nelson and Platnick, 1981) and they should not now be reintroduced. Instead, it is better to refer to sister-group relationships, rather than misleadingly to permanence, SDD and vicariance.

Relicts do not prove the permanence of biota

Relicts are often taken as a conundrum (how do they still exist?) or even as a strong indication that biota remain permanent (e.g. Ladiges and Cantrill, 2007; Heads, 2008a). They are also often mistaken for odd concepts such as a living ancestor, primitive taxon or missing link (O'Hara, 1992; Crisp and Cook, 2005; Crisp et al., 2011). The reasoning given at length in several recent reviews needs not be repeated here in detail: it clearly states that relicts remain from old groups depleted by extinctions and are not necessarily old species; they need to be studied in a documented phylogenetic framework with the possible help of the fossil record (Grandcolas et al., 2014; Grandcolas and Trewick, 2016). The presence of *Amborella trichopoda* in New Caledonia, a unique species considered by many as the sister-group of all other flowering plants (Qiu et al., 1999), is one of the most emblematical examples of New Caledonian relicts. Unfortunately, although very impressive, this case remains inconclusive, as discussed in detail by Grandcolas et al. (2014): there is no informative fossil record for the monotypic genus *Amborella* that could allow us to disentangle the history of the very old stem-group from the history of the genus. *Amborella trichopoda* cannot be precisely dated; it may be very young as suggested by its recent local genetic differentiation (Poncet et al., 2013) or much older as allowed by its very deep stem-group. Recently, another case study of supposed relict, the group of *Beauprea* plants (Proteaceae), confused the dating of the crown-group and of the stem-group and misleadingly argued for permanence of the lineage in New Caledonia (He et al., 2016). Actually, relicts do not allow us to draw conclusions regarding phenotypic or geographical permanence; rather, they allow detecting large extinction events. In addition, assumptions of relicts and refuges are often twisted in a circular reasoning of mutual justification that needs to be broken (Waters and Craw, 2006).

Who has seen the fault?

It is difficult to refute the occurrence of something that has not been clearly observed nor explicitly described in detail. The case of supposed New Caledonia major fault given by Heads (2008b) is strange. Heads (2008b) referred to geological studies that did not explicitly mention the fault or did not figure it. Most of the studies cited by

Heads (2008b) are outdated regional syntheses and mentioned the fault under different concepts or names (sillon, furrow, line of weakness, fracture zone, geosuture, etc.), and often just in passing. Heads (2008b) himself recognized that local and recent field studies did not recognize it as a major feature along the entirety of New Caledonia (Cluzel et al., 2001; Chardon and Chevillotte, 2006). The geological maps of Paris (1981), the recently published Atlas of New Caledonia (Bonvallot et al., 2012) and the recent geological map of New Caledonia available online (Maurizot and Vendé-Leclerc, 2009) did not show any major fault. The assumed distributional disjunctions (Heads, 2008b) along the unobserved fault represent small-scale distributional patterns that are often poorly documented and that can be interpreted within the framework of phylogenetic studies along with recent environmental change (Murienne, 2009; Nattier et al., 2012, 2013; Anso et al., 2016).

Terranes are not rafts

Another popular word in some recent biogeographical studies is “terrane”. And as with “Zealandia” and “dispersal”, it has gained particular significance, apparently much further than justified by the actual evidence. Undoubtedly, present-day New Caledonia is an accumulation of rocks of different origins onto a continental basement (Paris, 1981; Maurizot and Vendé-Leclerc, 2009). However, the reasoning that different lineages were brought by different terranes (Heads, 2008a, 2010) can be easily refuted (Murienne, 2010). From a biological point of view, tree topology or dating did not fit the theory of diverse origins by means of different terranes: the vast majority of local clades are more recent than 37 Ma and the so-called terranes. From a geological point of view, the terranes were emplaced during tectonic events the reconstruction of which implies most often non-biotic terrestrial conditions (see for example the ophiolitic nappe discussed in section “Its geological history cannot be understood from the basement only”). How could living things travel with lithosphere obducted onto the basement in the Eocene sea bottom? This appears to be a revival of the old demons of bio-geography; after the emphasis placed on the role of SDD, now comes the role of rafts.

Forest climatic refuges = centres of endemism = centres of diversity?

Along with the idea of relicts and escape from submergence often comes the concept of climatic forest refuges (Pintaud et al., 2001; Poncet et al., 2013; Pouteau et al., 2015). The core idea conflating relicts and refuges is that some areas may be especially stable and hospitable and then shelter the remaining old lineages, an idea that is quite widespread in the literature (Parsons, 2005; Grandcolas et al., 2014; Jordan et al., 2015; Proches et al., 2015). In this view, New Caledonia would be a kind of multi-million-year arch based on the combination of assumptions of a Gondwanan refuge and climatic stability in an oceanic insular context (for a similar view on New Zealand, see Gibbs, 2006). The first part of the reasoning is flawed as the island was submerged repeatedly and the second part lacks continuity with the first part.

Positing areas of suitable climatic during the changes of the latest Quaternary may be possible and could elegantly explain some present-day distributions (Pouteau et al., 2015). It does not mean, however, that such areas remain at the same place or of the same nature over millions of years, given that New Caledonia moved from subtropical to tropical latitudes and that the regional climate has changed dramatically since the Eocene (Reusch, 2011). For example, Nattier et al. (2012) showed that the distribution area of microendemic species increased considerably with time, placing the oldest endemics in secondary sympatry. In this context, some Quaternary forest climatic refuges could be centres of endemism for some groups at the least, but they do not necessarily equate to centres of diversity or even centres of origin where a significant amount of deep time evolution is conserved (Pellens et al., 2016). As an example, the most emblematical relict in New Caledonia, *Amborella trichopoda*, considered by many as the sister-group of flowering plants, has a quite wide distribution on the island and is not restricted to particular areas of long-term stability (Poncet et al., 2013; Pouteau et al., 2015).

Islands: sinks or sources, or both?

Oceanic islands were often considered as sinks where a few continental lineages established by dispersal (e.g. MacArthur and Wilson, 1967). Continental islands were seen as refuges where old lineages remained, as emphasized by Gillespie and Roderick (2002). Both paradigms do not fundamentally envisage that islands can be sources for continents or other islands, but more or less ancient sinks. New Caledonia has been considered according to both these classical paradigms and therefore, until recently, never as a source. However, this situation changed as dispersal from islands back to continents recently became an attractive idea (Bellemain and Ricklefs, 2008) and a recent and elegant analysis revealed that New Caledonia and New Zealand have been both sinks and sources in the case of coniferous plants (Condamine et al., 2016). The change of paradigm is not fundamentally innovative as the most basic difference between a source and a sink is a scale effect: being larger and older, an area is expected to shelter more lineages with lower rates of extinction, and whose significantly higher ratio will be able to colonize other areas and to act as a source. The model behind the sink and source paradigm could take into account many other parameters, such as geographical pathways (not just dispersal), climatic equitability/stability and empty niches, that can differ significantly for islands. For New Caledonia, such a paradigmatic change is especially important as it helps in considering the island as otherwise than a Gondwanan refuge/sink. It also echoes the previous consideration that New Caledonia is not a museum but rather a cradle of diversity given the local diversification rates in several groups (Espeland and Murienne, 2011).

Conclusions: what has to be done for New Caledonia?

Listing these ten misleading ideas allows us to draw some general lines of research for the future. First, old ad-hoc assumptions in biogeography such as SDD and rafts must be made carefully testable; such assumptions have appeared recurrently in the literature

and some recent views have repeated with few changes what can be found in Wallace (1881) without giving the appropriate credit. Clearly, the problem is not that such assumptions are formulated (to the contrary) but rather that they have rarely been properly tested. Second, to perform decisive tests, we need to carefully consider a relevant and accurate taxonomic or geographical sample (e.g. Nattier et al., 2011; Swenson et al., 2014; Anso et al., 2016; Skipwith et al., 2016). Sampling accuracy often needs to be improved by long field and taxonomic studies (Najt and Matile, 1997; Najt and Grandcolas, 2002; Grandcolas, 2008, 2009; Guilbert et al., 2014). Third, geological knowledge needs to be confronted with biological analyses and not directly integrated within them to avoid circular reasoning (Waters and Craw, 2006). This geological knowledge must be evaluated carefully with respect to the magnitude or the environmental significance of past events. Ideally, future studies should explore the whole regional time frame of evolution from the breakup of Gondwana (>80 Ma) to the emergence of New Caledonia (37 Ma). This means focusing on old clades, but not necessarily on relict ones that are so depleted that they do not provide a sample of correct taxonomic diversity in space and time, except in the rare case of an accurate fossil record (Grandcolas et al., 2014). The fossil record itself should not be considered as a backbone that is seldom available from the literature but rather should be actively improved upon to get direct information on the early distribution and characteristics of taxa. A rich local Quaternary record has already been studied in New Caledonia (Balouet and Olson, 1989; Anderson et al., 2010; Worthy et al., 2016) and an older and probably even richer record is available from the Cretaceous–Miocene (Genise et al., 2012; R. Garrouste, A. Nel, P. Grandcolas, unpubl. data). It is only under these conditions that New Caledonia will become a natural laboratory comparable to other island systems.

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