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COMMENT

HOW OLD ARE ISLAND ENDEMIC?

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Running title: How old are island endemics?

Abstract

Islands are well-known for their unique biodiversity, i.e. endemic species. Researchers have often assumed that island endemics are as old as the islands they occur on for calibrating molecular dating analyses. A “*reductio ad absurdum*” approach based on phylogenetic topologies is applied to New Caledonian biota in order to demonstrate that the age of an island does not necessarily correspond to the time of divergence of its endemic taxa. Our demonstration does not rely on any molecular clock inference and is therefore free of any flaws related to this method. We argue for further care when assuming that species and the biota they are restricted to (e.g. island, mountain, climatic region) have the same age. Finally, we review evidence on the age of islands and their biota radiations as well as discuss the effect of extinction on island biogeography/biota.

ADDITIONAL KEYWORDS: *Amborella* – biogeography – endemic species –Hawaii – island – molecular clock – New Caledonia.

INTRODUCTION

Islands can be considered laboratories of evolution (Carlquist, 1965) and represent as many scenes where the tape of life has been replayed (*sensu* Gould, 1989). They are home to a significant portion of Earth's biodiversity, including island endemics, which are species only occurring on these isolated pieces of land. Islands therefore represent interesting replicated systems for the study of evolution. Independently whether an island emerged from the ocean ('Darwinian island' *sensu* Gillespie & Roderick, 2002) or was separated from a continent, the particular time of its formation is a valuable information. The age of islands and their endemic species can be used to investigate a wide range of evolutionary questions. How much time was necessary for a pigeon to become a dodo (Shapiro *et al.*, 2002)? How much time was necessary for a tarweed to evolve into vines, shrubs and silverswords (Baldwin, 1997)? How fast is speciation on island (Knape *et al.*, 2012)? How much time is required for an island biota to reach equilibrium (Gillespie & Baldwin, 2010)?

ISLAND AGE AND DIVERGENCE OF ISLAND ENDEMICIS

The age of emergence of volcanic islands can be estimated with relative accuracy with isotopes (McDougall, 1964). Such value was sometimes associated with the divergence time of lineages endemic to island and thus used to calibrate molecular clock (Fleischer, McIntosh, & Tarr, 1998). In the case of volcanic archipelago like Hawaii where islands are recurrently formed over a short time lapse in the vicinity of each other (conveyor belt model), Fleischer *et al.* (1998, p. 536) considered reasonable to assume that "the K-Ar age of the young island represents an approximate date for a split between 'offspring' population on the

younger island and the 'parental' population of the older island". However in most cases where islands are more distant, colonisation may occur much later than the formation of an island. Using the Comoros as another conveyor belt system, Warren *et al.* (2003, p. 72) assumed more conservatively that the "age of the younger island represents an approximate estimate for the maximum age of the split between the 'offspring' population on the younger island and the 'parental' population on the older island" to calibrate a molecular clock. In this context, researchers assumed that the age of an island could thus be used as a maximum age bound to calibrate the divergence of an island endemic lineage (Ho & Phillips, 2009).

Conversely, another reasoning on the topic is also found in the literature when the occurrence of an ancient lineage on an island is considered as an evidence for an ancient age of this island. In the debate regarding whether or not all of New Zealand biodiversity was drown during an Oligocene submersion (Pole, 1994), some authors advocate that the ancient (Eocene) divergence of the New Zealand kauri tree (*Agathis australis*) from its closest extant relatives elsewhere implies the continuous emergence of the New Zealand landmass throughout the Tertiary (Stöckler, Daniel, & Lockhart, 2002; Knapp *et al.*, 2007). There are however more and more examples of island endemic lineages that have stem ages much older than the islands on which they presently occur according to molecular dating analyses (Fleischer, James, & Olson, 2008; Renner *et al.*, 2010; Heads, 2011; Hembry & Balukjian, 2016; Soares *et al.*, 2016).

Geological events such as island formation have been used as calibration points in c. 15 % of molecular dating studies (Hipsley & Müller, 2014), although such approach has been criticized (Renner, 2005; Forest, 2009; Ho *et al.*, 2015).

There is increasing awareness of mismatch between island ages and origin of island endemics, but most lines of evidence come from molecular dating studies. These latter studies can also suffer from serious flaws, particularly regarding calibration protocols using fossils: misidentification, misplacement on cladogram of extant species, inaccurate fossil age (Renner, 2005; Forest, 2009) or the use of secondary calibration points without error margins (Graur & Martin, 2004). We therefore propose here an independent approach using phylogenetic tree topologies from New Caledonian endemic plants to demonstrate that the age of an island and those of its endemic species – generally approximated as their stem age – are not equal.

THE AGE OF NEW CALEDONIAN ENDEMIC: *REDUCTIO AD ABSURDUM*

New Caledonia is located in the South West Pacific and it has been considered as a biodiversity hotspot because of its rich, unique, and endangered flora (Morat *et al.*, 2012). The island has a complex geological history. Originally a fragment of the Gondwanian supercontinent, it separated from Australia ca. 80 Ma ago and was later submerged until its final emersion 37 Ma ago (Cluzel, Chiron, & Courme, 1998; Pelletier, 2006). New Caledonia has a sparse plant fossil record, which has not been recently reviewed (Guillaumin, 1919) and most animal fossils date back from the Quaternary (e.g. Balouet & Olson, 1989). There are two common and conflicting views on the origin of New Caledonian biodiversity: a Mesozoic Gondwanian (vicariance hypothesis) origin (ca. 80 My ago; Ladiges & Cantrill, 2007) or a Cenozoic origin (ca. 37 My ago) through long distance dispersal (Darwinian island, Grandcolas *et al.*, 2008). However most lineages for which a temporal framework is available better fit the second

hypothesis (Grandcolas *et al.*, 2008; Cruaud *et al.*, 2012; Pillon, 2012) including groups previously considered as ancient lineages (e.g. *Araucaria*, Kranitz *et al.*, 2014).

Amborella, the sister group to all other extant angiosperms, is endemic to New Caledonia and the sole survivor of a Late Jurassic lineage (ca. 160 Ma; Amborella Genome Project, 2013). Phylogenetic positions of several other endemic lineages were also recently inferred (Buerki *et al.*, 2012; Hopkins, Rozefelds, & Pillon, 2013; Bayly *et al.*, 2013; Barrabé *et al.*, 2014) and are summarized in figure 1. In each case, the endemic lineages A, B and C can be distinguished and might have evolved according to three contrasting scenarios. In a first scenario, we assume that the lineage A is the same age as New Caledonia. If the separation of New Caledonia from Gondwana (vicariance) triggered the divergence of an endemic lineage A from its continental sister group, then the endemic lineages B and C, that are older than A, differentiated before New Caledonia became an island. In the alternative (dispersal) hypothesis, the ancestor of A colonised New Caledonia over water when it emerged and long distance dispersal triggered the differentiation of the endemic lineage A from its ancestor independently of its spatial origin. The endemic lineages B and C being older than A, their divergence predated the emergence of New Caledonia. If we now assume in a second scenario that lineage B diverged when New Caledonia separated from the continent or when it emerged, then A differentiated after either event, and C differentiated before either event. Lastly, if we assume in a third scenario that lineage C diverged when New Caledonia separated from the continent or when it emerged, lineages A and B differentiated both later.

In any scenario some endemic lineages diverged at a time that does not match with the formation of New Caledonia as an island, whether we assume a continental or a “Darwinian” origin. Our demonstration does not rely on molecular clock and is therefore free of any flaws associated with such approach. In brief, it should not be assumed that the age of an island is the age of divergence of its endemic taxa and we therefore stress researchers not to calibrate phylogenetic trees accordingly. The age of an island endemic, as approximated as the age of the divergence from its closest extant relatives, does not necessarily reflect the time when this lineage became endemic to the island because of the complex and often intractable play of extinction and dispersal (Grandcolas, Nattier, & Trewick, 2014). In the present case, it may not even be possible to determine in which order taxa A, B and C became endemic to New Caledonia as a result of either vicariance, dispersal or extinction processes.

ISLAND AGE AND AGE OF ISLAND RADIATIONS: A BRIEF REVIEW

Island endemics might be used to calibrate molecular dating analyses to the condition that they diversified on the island/archipelago (Renner, 2005). For example, the ages of the Hawaiian islands and the Marquesas have been used as a maximum age to calibrate the first split (crown age) of radiations endemic to those islands (Clark *et al.*, 2008). This approach assumes that “a lineage that has diversified within an area and is endemic to that area most probably post-dates the origin of that area” (Clark *et al.*, 2008, p. 687). In turn, in the case of the debated complete submergence of New Zealand during the Tertiary, Crisp, Trewick & Cook (2011) argued that “the drowning hypothesis would be falsified by the existence in New Zealand of an endemic radiation with a crown age

reliably dated back to the Oligocene (23–34 mya) or older”. When reviewing a large number of radiations endemic to the main Hawaiian islands, Price & Clague (2002) found indeed that most of them had a most recent common ancestor postdating the formation of those islands, with two remarkable exceptions: fruitflies (Russo, Takezaki, & Nei, 1995) and lobeliads (Givnish *et al.*, 2009). The latter may have first colonised one of the outer Hawaiian islands, which are part of the same island chain and still emerged, but do not offer appropriate habitat for those organisms anymore (Givnish *et al.*, 2009). Another example has also been reported recently in the Mascarene islands with a radiation of *Dombeya* endemic to Mauritius and Réunion that has a crown age older than either islands (Le Péchon *et al.*, 2015). This pattern may be explained, again, by the prior colonisation of a putative nearby island that would now be submerged.

Alternative explanation would require multiple colonisations from nearby landmass(es) (e.g. Madagascar), with extinction pruning the closest relatives on this(ese) landmass(es) to render the island lineages monophyletic (e.g. Buerki *et al.*, 2013 for a discussion on Madagascar and neighboring islands).

Examples of radiations with crown ages older than the islands they are endemic to are still few and known for only two island systems that were formed over volcanic hotspots (namely Hawaiian islands and the Mascarenes). The evidence presented here relies only on molecular dating analyses and would therefore have to be confirmed by additional independent data.

EXTINCTION AND ISLAND BIOGEOGRAPHY

Extinction is an overlooked process and the inference of biogeographical scenarios based solely on extant taxa can potentially be very misleading (Keppel,

Lowe, & Possingham, 2009). The debate on the persistence of the New Zealand flora throughout the Tertiary and the biogeography of the genus *Agathis*, which nowadays ranges from Sumatra to New Zealand seems now outdated with the recent discovery of fossils in South America (Wilf *et al.*, 2014). Several genera that are strictly endemic to New Caledonia have a fossil record elsewhere, e.g. *Amphorogyne*, *Paracryphia* and *Phelline* in New Zealand (Pole, 2010), *Codia* in Australia (Barnes & Hill, 1999), *Beauprea* in New Zealand and Australia (Pocknall & Crosbie, 1988). *Amborella* diverged more than 160 millions years ago while the modern populations coalesce to about 0.9-2 millions years (Amborella Genome Project, 2013). There is therefore a long timeframe during which it is difficult to infer what happened to this lineage and where it occurred. This is especially the case for this lineage since the region it inhabits underwent a very complex palaeogeographical history from the Cretaceous onwards, with a peak of tectonic activity at the Eocene/Oligocene boundary (corresponding to the collision of the Australian and Eurasian plates; Buerki, Forest, & Alvarez, 2014 for more details). Such active tectonic activity over million years could easily have “buried” the fossil evidence of *Amborella* and its currently extinct relatives therefore blurring the spatio-temporal history of this lineage (Buerki *et al.*, 2014). Extinction removes nodes and shrink species distribution so that stem ages of narrow endemics is likely to be an overestimation of the length of their unique history. It is only in recent system like the Hawaiian islands that extinction may have a limited impact and make assumption associated with a calibration of a molecular clock reasonable (Fleischer *et al.*, 1998).

CONCLUSIONS

The divergence of island endemics does not necessarily match the age of an island and some evidence suggests that endemic radiation may in some cases predate the formation of the islands they are now restricted to. As more and more molecular dating studies become available, future meta-analyses should allow characterizing the distribution of stem ages and crown ages of island endemic lineages in relation to the age of the island. Then it will be possible to infer whether island ages can be used to calibrate molecular clocks. For now, this type of calibration should be done with the greatest caution if not abandoned. The importance of extinction in biogeography is still insufficiently accounted for and it should not be assumed that a lineage now restricted to an island has always occurred there and only there (Crisp & Cook, 2005; Buerki *et al.*, 2013; Grandcolas *et al.*, 2014). This is also very important because without including extinct lineages and their distributions into biogeographical inferences, we will never be able to accurately infer the spatio-temporal histories of these groups (e.g. Meseguer *et al.*, 2015).

Our conclusions can extend to other systems, and the age of some ecosystems and of their endemic lineages may not always be the same, e.g. the Cape Floristic Province (Linder, 2005; Warren & Hawkins, 2006), the biota of Mount Kinabalu (Merckx *et al.*, 2015) or hydrothermal vents (Little & Vrijenhoek, 2003), as well as the closure of the isthmus of Panama (Bacon *et al.*, 2015). The reason for the mismatch between island age and island endemics is an interesting field to explore. Why did New Caledonia or New Zealand retain so many ancient lineages such as *Amborella* or the tuatara? Novel methodological approaches are required and integrated ecological studies comparing extinct and current forest communities (Kooyman *et al.*, 2014), or linking climatic

preference with the anatomy of extant ‘relicts’ (Pouteau *et al.*, 2015) are promising avenues. While in the Galapagos, Darwin (1845, p. 378) stated that “both in space and time, we seem to be brought somewhat near to that great fact – that mystery of mysteries – the first appearance of new beings on this earth”. Today there are still many mysteries to unravel about island biology.

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Figure 1. Phylogenetic relationships of some selected New Caledonia endemic lineages (in bold), here labelled as A, B and C. Some nodes and branches, not occurring in New Caledonia, where omitted from the portion of the tree and represented by dotted lines.

