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The origin of island biota: Several things in one

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Abstract. Islands can be continental or oceanic. The latter ones, well known as test tubes or natural laboratories, are only colonized by dispersal and their biota are new assemblages of species with subsequent and potentially interesting evolutionary events. Their study however requires considering sophisticated hypotheses of colonization, keeping geological knowledge independent and sampling widely the island regional context.

Islands have always been fascinating to people and even the most "terrestrial" persons repeatedly heard about them. Scientists coming to study them were already fed since their childhood with some famous and spirited literature describing islands as refuges for sailors and tramps, territories for social utopia or hidden places for treasures and fights (Stevenson, Defoe, Nordhoff & Hall, Wells, Huxley, Merle, etc.) This social background strongly shaped our way of thinking island biological evolution. Scientists then see islands as remarkable microcosmos and most theories depicting their evolution treat them as systems isolated from other biota with specific processes involving refuges, novel interactions, extinctions or relicts. These recurrent topics or views produced since more than one century and a half of dedicated scientific literature would gain to be disentangled and critically re-analyzed. We must rediscover how many different kinds of islands exist, we must test common and unquestioned postulates about the evolution of their biota, and finally drawn the main critical issues which are in need of study with an appropriate sampling strategy. We could also ask finally whether islands significantly differ from continental biota or are they just workable simple systems? To answer these questions, we have chosen to focus on a few issues that seem to us more important to consider and more amenable to scientific tests.

1. Islands: How many kinds and the test tube metaphor

First of all, a common opinion features an island as a piece of land surrounded by water. Unfortunately, this definition is not operationally decisive: Given the earth structure, all terrestrial lands could be said islands, from very large continents to tiny islets. Which land size is small enough for being called an island?

To be honest and more accurate, scholars early defined continental versus oceanic islands [1–3]. Continental islands are pieces of land that were always emerged and therefore geologically not

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lithospheric, i.e. small continents, an arbitrary size measurement which usually points to Madagascar, New Zealand, etc. Once again, not different from but smaller than other continents (e.g. Australia).

In contrast, oceanic islands are lands that emerged from the water, whatever their size. This category is less ambiguous and characterizes islands as new-born and therefore populated by dispersal. Most of the theoretical works of the last decades actually deal with oceanic islands. The metaphor of the island as a test tube or a natural laboratory of evolution also pertains to oceanic islands because their biota are like an experiment where special species combinations are set up from nothing at a zero point and can be then followed along the time [5]. This metaphor has been especially developed with the theory of equilibrium formulated by McArthur & Wilson [4] which considered the biota of oceanic islands as resulting from the balance between immigration (driven by distance from continent) and extinction (driven by land size).

Conversely, the biota of continental islands can be partly inherited from their past continental connection. In such a system, the island size has not primarily determined the biota since they are inherited from a larger territory. Such "islands" are more a place to understand the becoming of relicts, the occurrence of extinction events and the confrontation between paleo-endemics (inherited from the continent) and neo-endemics (arrived by dispersal).

From this short overview, this should be clear that the term "island" should never be employed alone since it mixed two different kinds of lands. In addition, among the oceanic islands themselves, different kinds could be defined according to their geological origin. Islands can be generated by geological hotspots, forming archipelagoes with the succession of lands emerging and then subsiding with magma production through a mantle plume; they can be also generated by lithosphere flexure during tectonic events; etc. Such different origins may have important consequences for biota evolution. For example, hotspots generate long-lived archipelagoes with rapid turnover of emerged islands while lithosphere flexures produced islands with more dicrete and isolated emergence histories. This should be considered in the future.

2. The island geological background: A fixed context or a testable assumption?

In evolutionary studies, earth sciences have often been misleadingly understood as bringing proofs and certainties. For still many people, fossils would prove evolution by their sole existence and stratigraphy would be a scale upon which the succession of ages can be read directly. Geologists and paleontologists know very well that their findings include as much theories and assumptions as other sciences, which actually makes them testable and scientific! Fossils need to be included in phylogenetic analyses together with extant species to interpret their evolutionary significance and stratigraphy can only be understood with respect to sedimentary and tectonic models.

For island biogeographical studies, the geological background needs then to be considered as a specific group of assumptions that must be considered independently and confronted to the results of biological studies and their inferred timescale [6–8]. Mutual use of information between both domains of knowledge must be carefully controlled to prevent any dependent or even circulary reasoning. For example, molecular phylogenies that permit to study the rates and tempo of evolution can be dated with statistical methods that require a fossil calibration. However, the datings obtained cannot be confronted to geological scenarios that would use the same fossils as stratigraphic markers.

Coming back to the study of the origin of island biota, it means that the geological age of insular territories is not necessarily given as an absolute date coming from some isotopic measurement. For tectonic reasons, an island could have basement rocks which date back to a certain period but be submitted to complex cycles of submergence or emersion, some of which could even be not decisive or difficult to evaluate for terrestrial biota. In addition, we need to establish biological evidence independently so that both scenarios could possibly confirm each other. Ages must be estimated on each side, geologically and biologically. One should avoid saying that a geologically old island dates the local insular clade as equally old and vice versa. Calibration of molecular phylogenies to date an insular clade can be carried out by using the geological age of some other auxiliary and external territories. These external territories can be other and unrelated islands (i.e. that do not share a common process of origin such as islands produced by the same hotspot, for example) or continents as far as they harbor relatives of the insular clade.

3. Better to test original and sophisticated assumptions – more than just continental drift versus dispersal

In the past, ad hoc explanations in biogeography commonly referred to hypothetical evidence for continental bridges and dispersal events. Presently referring to such naive scenarios is not anymore conceivable because our knowledge of the earth history has increased a lot since a few decades (continental drift, physical dating, etc.) and because our methodology in phylogenetic reconstruction and molecular dating precludes to imagine past hypothetical evolutionary events without any clear justification.

Ad hoc statements are now made in another way, especially in the context of the change of geological paradigm. Instead of imagining dispersal events among lands seen as motionless, biogeographical studies tried to link phylogenetic relationships with simplified large-scale geological scenarios. For continental biota, drift is the main geological event that is generally invoked. For oceanic islands, physical dating of the island is most often considered as a maximum limit for the origin of clades by dispersal. If a vicariance explanation remains however preferred, alternative scenarios are made with respect to local drift-like scenarios (e.g., hotspot origin or lost continent hypothesis).

We must understand that referring to such simplified geological scenarios even when they are geologically correctly assessed are ad hoc choices among many possible others. For example, rather than referring to continental drift, one could consider Pangean bioclimatic zones, past land assessed connections after the start of the drift (e.g., north atlantic land bridge), etc. For islands, such a practice has generated untested and dogmatic views such as the Gondwanan old New Caledonia or the recent Galapagos volcanic islands. Both are now on the way to be abandoned: it appears that New Caledonia even though its basement is continental has been submerged during Paleocene and Eocene and the hotspot of Galapagos Islands includes some very old islands drowned off the presently oldest island of the archipelago [9, 10]. For these two archipelagoes, the traditional views are now untenable: New Caledonia has necessarily been populated by dispersal around 37 My ago and Galapagos lineages may be much more ancient that the few millions years of the present-day emerged islands.

Such misconceptions also extend to the study of sea level changes and islands in the context of global change. Once again, gross physical environmental patterns are seen as given and uniformly immutable: the sea level increase – predicted by all climatic models as agreed by a vast majority of scientists – is often seen as an elevation number that could simply be applied to any place according to mapped topographic data [11], when it is actually very complex and with diverse and mostly deleterious effects that remain to be carefully studied [12].

4. Opening the window: Islands studied with reference to other lands

Speaking of calibration of datings, we already argue that we need to consider not only the islands but also the other lands around them. This is actually a very general requirement. As in any phylogenetic or more widely comparative study, we need to consider outgroups, i.e. items outside the study focus that will serve as a reference to root the comparisons [13]. In the case of islands, referring to external references, other emerged lands (neighbouring but unrelated islands, continents), allows to understand from where and when come from the species living on islands. More unexpectedly, it could also allow to infer that some island species were able to disperse back to continents and that islands are not only sinks but can also be sources [14].

Such a wide geographical sampling also allows building a better set of testable hypotheses about the geological context of island diversifications. Instead of focusing only on one geological scenario with a specific time scale, widening the sampling allows to consider many scenarios, some of them possibly speculative. Dealing with the example of Pacific islands, if we consider only one single island or archipelago, we could only try to relate its biota with the geological age of the island (high or low estimate or both). If we look wider at the Pacific scale, we will consider other islands, some of which often viewed as continental and anyway much more ancient (New Caledonia, New Zealand, Fiji). We can also consider then islands in local systems generating emerged lands whose age can be old as well (either hotspots or flexures caused by plate extension or contraction). We can even try to falsify some weird geological models such as the lost continent hypothesis [15] whose last avatar can be found in some recent writings of biogeographers [6]. A small-scale study would unavoidably brings a weak conclusion in terms of recent dispersal to explain the origin of the island biota. A large-scale study will allow testing various hypotheses, making the results much stronger. It will also probably show that recent dispersals are the last layer of a series of events involving present islands and past emerged lands. In a more general way, such a widened perspective is simply a way to make better science by testing more sophisticated assumptions whose refutation is not so easy [16].

5. A plea for an adequate taxonomic sampling

Testing such large scale evolutionary assumptions requires that the sampling is adequate not only from a geographical point of view but also from a taxonomic point of view. This statement could seem quite trivial but looking at some recent points of view or studies shows that it is not always carefully considered. Actually, the statement is obvious for the sampling of the present taxonomic diversity but many studies do not realize that even a nice taxonomic present day sampling can neglect the bulk of the diversity that has ever existed, given the occurrence of large past extinction events. The situation is even worst when such extinctions occurred very unevenly, affecting more some parts of larger clades than others and possibly biasing phylogenetic analyses. This is especially the case of relict species which are often used as flag species in evolutionary reasoning but however specifically belong to mostly extinct groups [9, 17]. Relicts are misleadingly considered as old taxa that would allow stating that an island is old [18]. We already see that directly equating the age of the taxa with the age of the island is quite speculative but doing so with the extremely biased sampling that characterized relicts is actually hopeless.

6. Conclusion

Oceanic islands as lands recently emerged from oceans are interesting places with biota built-up de novo and whose origin can be generally traced back easierly. These biota can show new and original specific combinations with subsequent evolution and adaptation [19, 20]. All islands must be studied with external references both to relatives of insular taxa and to other terrestrial territories, islands and continents. Such a widened context, still often neglected or not built as a sampling programme, is the key for understanding the origin and evolution of insular biota. Among many benefits, wide-scale approaches are worthwhile for avoiding biases caused by poor taxonomic samples or extinction events. Logical independence should be preserved by avoiding referring only to local geological history to infer local biological history and vice versa.

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