The origin of diversity in Insects: speciation, adaptation and the Earth dynamics

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The diversity of Insects is often explained as a product of major radiations, trigerred by remarkable adaptations that allowed them to exploit different environments and to accompany the rise of flowering plants. A significant part of Insect diversity results however from allopatric speciation with niche conservatism that exposed species to different conditions and stimulated adaptive divergence. We demonstrated that for several groups of Insects (cockroaches, crickets and grasshoppers) in the island New Caledonia.

Since Darwin and Wallace, islands are considered as laboratories of evolution, being closed systems of manageable size. New Caledonia is especially interesting in this respect, according to unique characteristics. Being the oldest oceanic island in the world and quite isolated from continents, biological evolution occurred there in situ during long periods. As a tropical and medium-sized island harbouring a very rich biodiversity, it also offered facilities to study many different evolutionary questions. New Caledonia (hereafter NC) has thus the best characteristics as a model system, allowing testing very diverse evolutionary assumptions with limited efforts and infrastructures. Unfortunately, these amazing geographical characteristics have also constrained the scientific study of NC until now, especially because of its isolation from large academic centers.

Establishing NC as a modern oceanic model system resulted however from our work, later than the 90ies. Before, NC had the reputation of an amazingly old Gondwanan place and was intuitively considered as a continental fragment. If so, its usefulness as a model system to study evolution would have been limited since the biota of continental islands (e.g. Madagascar or New Zealand) are a complicated mix of organisms dating back to the separation with neighbouring continental territories or having colonized the island by dispersal. In most of these cases, it happened difficult to distinguish between both these different components and to examine evolutionary assumptions that require a reference dating point. The reasons why NC was traditionnally considered a continental territory were the age of its deep geological basement and the local occurrence of relict species. In agreement with this common assumption, the NC geological deep basement is ancient and predates gondwanan breakup. But this basement has been submited to important environmental disturbances because of the island location at the limit between two tectonic plates. Actually, the island has been submerged twice for a long time at Paleocene and Eocene epochs and only emerged around 37±3 Ma.

This geological background was in need of independent testing with biological studies. We thus built multiple molecular phylogenetic trees of different groups of organisms, dated with probabilistic methods and external calibration points. A first review (Grandcolas et al., 2008) and a more recent meta-analysis (Nattier et al., 2017) of these studies showed that most groups colonized NC and diversified just after 37 My, confirming the geological scenario of recent terrestrial emergence. However a few local species belong to groups were dated much older than 37 My, representing true relicts, i.e. recent species that remained from old clades (Grandcolas et al., 2014). These old clades can only be assumed to have been ancestrally present in the region, colonizing NC after its emergence and going extinct in other territories, either drowned islands or mutated continental ecosystems.

These different results strongly indicated that NC is an oceanic island, even if very old – actually the oldest one in the world – and that its local biota dated back to island emergence. Relicts are fascinating species, unfortunately too sparsely known after the major extinction of their relatives to support any robust biogeographic scenario. Fossil data are absolutely needed to assess the evolutionary history of these taxa without speculation.

Setting up this biogeographic scenery has allowed to properly conduct speciation studies by inferring the age and the ancestral phenotypic characters of local lineages. We did that in several groups of insects, cockroaches, crickets and grasshoppers and we showed that speciation occurred mainly in relation to orography, in allopatry and with niche conservatism. Closely related species occurred as narrow endemics in the same habitats of neighbouring areas, mainly on adjacent small mountains. Sympatry, when observed, was inferred to be secondarily caused by the increase of distribution area of older species. Even if most speciation events seemed to have occurred without any important evolutionary change, some adaptive shifts have been detected in several cases, from different food plants on metalliferous soils to different habitats in the forest understory. The major conclusion that can be drawn from high speciation rate and narrow endemicity in New Caledonia is that speciation went before, not always together with adaptive divergence. Here we offer both a new and powerful natural laboratory of evolution, calibrated in space and time, and a model of speciation where niche conservatism is the engine for adaptive divergence.

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