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 1990s. 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 neighboring 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 traditionally 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 submitted 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 [1] and a more recent meta-analysis [2] 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 that were dated much older than 37 My, representing true relicts, i.e. recent species that remained from old clades [3]. 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 one 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 neighboring 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.

Disclosure of interest The author declares that he has no competing interest.

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A glance at the deep past history of insects

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With more than 1,100,000 described species, the insects are the most diverse clade of extant animals, far before all other groups. Nevertheless, they undergo a drastic decrease of their populations, due to the sixth extinction of human origin. Thus it is important to define when and how they became so diverse and if they were impacted by the major crises of biodiversity in the deep past to estimate the importance of the current one. Insects are generally among the best preserved terrestrial fossil organisms, much more complete than the vertebrates. They are also much more frequent. Thousands can be found in Konservat-Lagerstätten since the Carboniferous. They are preserved either in lacustrine sediments as compression fossils, or embedded in amber (fossil resins) (Fig. 1).

The Hexapoda (or six-legged arthropods, viz., wingless Collembola, Diplura, Protura ; wingless and winged Insecta) are among the oldest known terrestrial organisms, with first records dated from the Middle Devonian of Rhynie in Scotland. Recent molecular phylogenetic dating suggests that they appeared during the Silurian or even the Ordovician, with the first terrestrial plants. The Devonian hexapodan record is very scarce and disappointing, with less than six described fossils, all wingless [1].

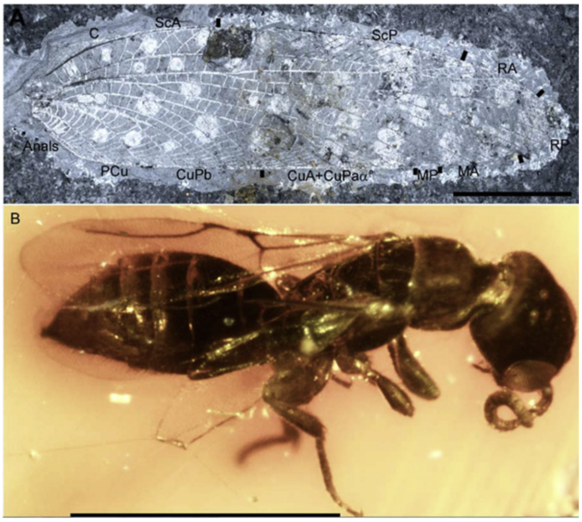

Fig. 1 A. Compression fossil, Orthoptera, Middle Permian (China). B. Amber inclusion, Hymenoptera Bethylidae, earliest Eocene (France). Scale bars: 10 mm (A), 1 mm (B).

A. Fossile en compression, Orthoptera, Permien moyen (Chine). B. Fossile dans de l'ambre, Hymenoptera Bethylidae, Éocène basal (France). Échelles: 10 mm (A), 1 mm (B).

The early Carboniferous one is even worse, without any fossil insects. But at the very end of this period and during the late Carboniferous, the insect diversity exploded, with a 'sudden appearance' of winged insects with very diverse feeding resources, e.g., carnivorous, plant suckers, leaf eaters, detritivorous, gall-makers, etc. The wingless clades remained a minority and the high diversification of the Carboniferous Hexapoda clearly concerned the winged forms. Wings and flight were probably the first crucial structures and function that allowed the first burst of diversification of the insects. Flight allows them to escape predators, find new resources, sexual partners, and travel to new environments. The most popular fossil insects are the Paleozoic 'giant' dragonflies Meganeuridae. These flying insects with very large wingspans (ca. 70 cm wide) had large bodies but comparable to those of some extant beetles. In fact, the unique really giant Carboniferous terrestrial arthropod was *Arthropleura*, a myriapod that was more than 1 m long. It is supposed that the great increase of oxygen proportion in the air during the Late Carboniferous favored the gigantism among the terrestrial arthropods, due to their breathing via trachea. The question is in fact more complex, because the winged insects knew a unique situation during the late Paleozoic, as they had no flying vertebrates as predators. As they were the only flying animals, they probably knew a phenomenon of parallel increases of sizes of predators (the Meganeuridae) and preys, the Palaeodictyoptera that also became larger and larger [2]. At the end of the middle Permian, both clades are very diverse, with still very large taxa, while the oxygen proportion began to decrease. The first gliding 'lizard-like' vertebrates are also recorded at the same time, and certainly began to predate these giant insects, which became rarer during the late Permian and no longer existed in the Triassic. The late Carboniferous was also the time of the oldest known holometabolous insects, with complete metamorphosis (wasps, beetles, scorpionflies), and of the oldest bugs (Hemiptera). These were discovered very recently because they were very small insects [3]. They are now the most diverse animal clades, with the 'big five' (Hemiptera, Hymenoptera, Diptera, Lepidoptera, and Coleoptera). But during all the Paleozoic, these insects were clearly very few. Holometaboly in itself was not 'sufficient' to cause their diversification and each of these orders 'separately' diversified during the last 220 Ma. The exact impact on the insects of the most important Permian–Triassic crisis of diversity remains difficult to estimate because there are very few latest Permian and earliest Triassic outcrops with insects. Thus if we know that the Triassic entomofaunas are very different from the Permian ones, we cannot establish that the great changes that occurred between the two periods happened during this crisis or before, during the late Permian or even at the end of the middle Permian. Nevertheless, the Palaeodictyoptera and the Meganisoptera are no longer present in the Triassic, while all the Triassic entomofaunas are clearly 'dominated' by the beetles and other Holometabola. Beetles were still minority during all the Permian in the fossil record. The 'true' flies (Diptera) and crown group of Hymenoptera are also dated from the Middle Triassic. At the end of this period, all the extant orders were present, except, maybe the parasite groups such as fleas (Siphonaptera), whose oldest fossils are middle Jurassic. The 'modern' entomofauna is thus much older than the extant mammal orders. During the Jurassic, the insects continued their diversification, with the first parasitoid wasps (there is no record of parasitoid insects before). The Cretaceous was the second crucial period for the insect (especially the Holometabola) diversification, with the oldest eusocial taxa (termites, wasps, bees, ants). The Albian–Cenomanian (ca. 100 Ma.) was the time of replacement of the gymnosperms by the angiosperms in all the terrestrial biotas, and the time of appearance of nearly all the extant insect families (even some extant genera have this age). It is also an important time of extinctions of several older Jurassic clades, replaced by extant taxa. Only the insects that adapted to the new environments related to flowering plants could diversify. The modern insect–plant relationships were established during the late Cretaceous. The recent new studies of the extraordinarily rich and diverse entomofauna of the 'mid' Cretaceous Burmese amber allowed one to discover that the Cretaceous insect world was as complex, rich and diverse as the extant one. The Cretaceous–Cenozoic (K–T) crisis had clearly a very weak impact on insect diversity, at least at the family level [4]. In fact, there were more extinctions and appearances of new families during the Paleocene–early Eocene than during the K–T crisis. These were periods of global warming followed by global cooling. The entomofaunas suffered the successive periods of cooling of the Oligocene, Miocene, and the Pliocene–Pleistocene glaciations, causing the extinctions of numerous widespread families that survived in small areas (the Australian mastotermitid termites or the Tasmanian hairy cicadid Tettigarctidae are the most spectacular examples).

The deep past history of insects is unique, with bursts of diversification ca. 330 Ma, 220 Ma, and 100 Ma ago. The causes of the first one remain poorly known, those of the second one are probably linked to the renewal of the ecosystems during the early Triassic, and the third one to the great floristic change. At least the K–T crisis did not affect much insect diversity. Thus the current crisis of biodiversity that begins to greatly affect the insect biomass, is extremely alarming. It may be more important than the K–T one.

Disclosure of interest The author declares that he has no competing interest.

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The metamorphosis of insects and their regulation

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Metamorphosis was a key innovation in insect evolution, wherein the individual acquires characteristic adult features and stops molting during postembryonic development. The ancestral metamorphosis mode was hemimetaboly, in which the embryogenesis gives rise to a first instar nymph with the essential adult body structure. The nymphs grow gradually and the final molt to the adult stage completes the formation of functional genitalia and wings. The metamorphosis mode known as holometaboly emerged from hemimetaboly, which is characterized by embryogenesis that produces a larva with a body form that may be substantially different from that of the adult. The larva grows through various stages until molting to the pupal stage, which bridges the gap between the morphologically divergent larva and that of the winged and reproductively competent adult. In the hemimetabolan and holometabolan modes, metamorphosis is regulated by two hormones: the juvenile hormone (JH) and the ecdysone, plus its biologically active derivative, 20-hydroxyecdysone (20E). 20E is a steroid, and its main role is to promote the successive molts, including the metamorphic one, whereas JH is a terpenoid, whose function is to repress metamorphosis [1]. The action of these hormones is underpinned by the mechanisms that transduce the hormonal signal through a pathway of gene activation. The 20E signaling pathway was first described in the 1990s [2], whereas the most important details of the JH pathway were unveiled recently. Important components of the JH signaling pathway are the JH receptor, which is the basic