COMMENTARY

Are there many different routes to becoming a global biodiversity hotspot?

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A major question in evolution and ecology is why biodiversity is so unevenly distributed across the planet. The most obvious and salient diversity pattern is the order-of-magnitude greater species richness in the tropics compared with the temperate zones. Superimposed on this latitudinal diversity gradient is a much more complex and intricate pattern of regional and more local biodiversity hotspots (1, 2). These are places with unusually high concentrations of species and especially endemic species. Documenting these patterns is of great significance, most obviously for conservation, with ever more sophisticated and higher-resolution biodiversity hotspot maps becoming available as the world's biota are mapped in greater detail (3). More fundamentally, we need to document hotspots to understand the underlying macroevolutionary and ecological processes shaping the distribution of diversity across the Earth. Most globally significant biodiversity hotspots lie firmly within the tropics or in the Mediterranean climate zones of the world, such as California and the Cape Floristic Region of South Africa. Several coincide with major mountain ranges, including most notably the tropical Andes and the temperate Hengduan Mountains, two of the world's hottest hotspots (2, 4). It is this Hengduan Mountain hotspot that is the focus of Xing and Ree's study in PNAS (5), which provides the first integrated analysis of the evolutionary origins and biotic assembly of Hengduan plant diversity.

Although formal quantification of biodiversity hotspots really only started 30 y ago (1), the outstanding plant species richness of the Hengduan Mountains has been known for more than 150 y, having been first revealed by the intrepid 19th century plant collectors—Joseph Hooker, Ernest Wilson, George Forrest, Frank Kingdon-Ward, and others. These explorers penetrated into the deeply dissected and remote mountains and river gorges of Yunnan, Sichuan, Sikkim, and eastern Tibet in search of botanical novelties and especially garden plants, and discovered a veritable treasure house of rhododendrons, primulas, lilies, Himalayan blue poppies, and many other plants that make up the spectacular plant species diversity of the Hengduan hotspot (6) (Fig. 1).

Fig. 1. Shrubby *Rhododendron traillianum* and *Picea likiangensis* var. *balfouriana* forest at 4,300-m elevation, close to the tree line at Shangri-La Great Snow Pass, in the Hengduan Mountain biodiversity hotspot, Yunnan, China. The genus *Rhododendron* is one of the 19 plant lineages analyzed by Xing and Ree (5), and includes two species-rich subclades dominated by species from the Hengduan Mountains, which show elevated rates of species diversification dating from the Late Miocene coinciding with the rapid uplift of the Hengduan Mountains. Photo courtesy of Jian Huang (Xishuangbanna Tropical Botanical Garden, Yunnan, China).

Although the species richness and endemism of the Hengduan hotspot is well established, the evolutionary origins of its unique biota remain poorly understood. Biotic assembly is the product of colonization from outside areas, local recruitment via *circa situm* adaptation, in situ speciation, and extinction. While extinction remains extremely challenging to measure, time-calibrated molecular phylogenies can provide insights into the origins of taxa that make up the biota of a particular area, allowing inferences about geographical origins, colonization, and in situ species diversification, and the timing and tempo of these processes. For the Hengduan region, two problems have hindered such analyses up to now. First, previous studies have relied on single-taxon phylogenies, which can provide only limited insights. Second, the complex relationships and distinct uplift histories of the Qinghai–Tibetan Plateau, the main Himalayan range, and the Hengduan Mountains have been confounded and widely misinterpreted (7). The

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study by Xing and Ree (5) addresses both these issues by adopting a multitaxon approach based on biogeographic and evolutionary rates analyses of 19 unrelated plant lineages, and by carefully defining and disentangling the timing and rates of colonization and in situ diversification for each of these three adjacent montane regions. By doing this, Xing and Ree demonstrate that biotic assembly in the Hengduan shows a younger diversification more heavily dominated since the Late Miocene by in situ speciation than the closely interconnected Qinghai-Tibetan Plateau and Himalaya, in line with the later timing of Hengduan uplift.

Previous studies of biotic assembly using similar multitaxon phylogenetic approaches have gained insights into the relative contributions of colonization and in situ diversification in the assembly of several plant hotspots (8–13), but none has summed these parameters cumulatively through time as elegantly as Xing and Ree (5). One of the novel aspects of Xing and Ree's study is that they detect an intriguing inflection point in the assembly of Hengduan species diversity, which coincides with a period of rapid Hengduan mountain uplift around 8 Ma when cumulative in situ species diversification overtakes immigration as the main contributor of additional species diversity.

The significance of Xing and Ree's study goes well beyond the confines of the Hengduan, providing insights into questions about the biotic assembly of hotspots in general. With Xing and Ree's data at hand, we can compare the trajectories underlying the assembly of Hengduan plant diversity with those of other hotspots. Two other mountain hotspots provide interesting immediate comparisons. First, a study of the endemic biota of the small and geographically isolated Mount Kinabalu in Sabah, Malaysia (11), showed that this hotspot was assembled predominantly via colonization and local recruitment, with little or no in situ diversification of species. Indeed, on Kinabalu, there were apparently several instances of multiple independent congeneric colonizations that gave rise to endemic Kinabalu species, illustrating just how strongly colonization has been favored over in situ diversification on this mountain (11). In stark contrast are the apparent trajectories of diversification in the high-elevation Andean grassland (Páramo) hotspot, which show a dominant role for rapid and recent in situ species diversification derived from relatively infrequent colonization events (13). Although there is no detailed quantification of the relative contributions of colonization and in situ diversification through time for the Andes as achieved for the Hengduan by Xing and Ree (5), the many examples of Páramo radiations, that is, species-rich clades that current phylogenies suggest were derived from single colonization events, contrast sharply with the placements of Hengduan endemic species in multiple clades intermixed with species from other areas (5). Of course, mountains are very much like islands (12), and these differences between the Hengduan, Kinabalu, and the Andes make much sense in relation to theoretical predilections of island biogeography. Greater isolation of the Andes compared with the more closely connected Hengduan limits dispersal and favors in situ diversification over colonization, whereas the small (island) size of Mount Kinabalu limits opportunities for in situ speciation.

One feature that stands out for both the tropical Andes and the temperate Hengduan, is their extreme physiographic heterogeneity. These regions encompass some of the steepest and most extended environmental gradients and dissected topographies on the planet, resulting in the intimate juxtaposition of contrasting habitats over very short geographic distances (Fig. 1). Physiographic heterogeneity is a key environmental predictor of species

richness (14, 15), and it is in mountains like the Andes and Hengduan that such heterogeneity is highest. A notable outcome of this heterogeneity in the Andes is that geographically adjacent biomes at different elevations show contrasting trajectories of plant diversification in terms of timing, rates, and species richness (16, 17). It will be interesting to see, once sufficient Hengduan plant clades have been partitioned into elevation zones, or forest vs. alpine habitats, rather than lumping them together as in Xing and Ree's study, whether such biome-dependent trajectories of diversification are also apparent in the Hengduan Mountains.

Moving beyond these immediate montane hotspot comparisons, the wider picture also reveals many apparent differences in the timing, tempo, and processes underlying the biotic assembly of biodiversity hotspots more generally. In the Cerrado biome of

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South America, evidence suggests a dominant role for local recruitment via recent in situ adaptation to fire, and subsequent in situ species diversification rather than long-distance colonization (8). The Cape Floristic hotspot of South Africa is dominated by a small number of exceptionally species-rich plant clades that have diversified largely in situ over an extended period at relatively slow and constant rates (9). In California, high species richness has also been attributed to in situ diversification dynamics rather than accumulation of diversity from elsewhere, albeit with much variation among individual lineages in speciation and extinction rates (10, 18). These are all preliminary snapshots of individually large, complex, and very incompletely understood systems, but they do suggest striking differences in the balance between colonization and in situ diversification and especially in the timing and rates of these parameters. This suggests that there may be many routes to becoming a global biodiversity hotspot, with differences dictated by the idiosyncrasies of geohistorical circumstances. Alternatively, we may be observing similar pathways but at different stages of hotspot ontogeny, analogous to Whittaker's dynamic theory of island evolution (19).

Although multitaxon studies encompassing disparate evolutionary lineages can provide insights into the biotic assembly of biodiversity hotspots, such approaches also have limitations in terms of modeling the dynamics of biota assembly. More sophisticated methods for estimating rates of biotic assembly of entire communities have recently been developed (20), but these are computationally intensive and require phylogenies of major lineages with complete sampling of all species in a community and all their nearest relatives. Although this has been achieved for some groups on islands with modest species richness, such as Galapagos birds (20), it has not yet been done for more species-rich clades that contribute substantial diversity to the major global biodiversity hotspots. Only through such studies will we be able to really compare trajectories of biodiversity hotspot assembly across the planet.

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