

## **The Monsoon Tropics—Gateway or Refugium?**

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Ever since Joseph Hooker (1860) first set out to explain the evolutionary and geographic origins of the Australian flora, two theories on the significance of the tropical north have competed for dominance: whether it is (i) a gateway or bridge through which biota have entered from the north, or (ii) a region where climate has changed little from that of millions of years past, harbouring relicts of an ancestral, indigenous biota. But these theories do not necessarily conflict; in fact, recent workers have tended to accept a role for both, and attention has been focused on their relative contribution. After plate tectonic theory was accepted, the gateway hypothesis gained impetus and shifted emphasis—towards whether and to what extent tropical biota invaded after the Miocene collision between the Australian plate and the Sunda Plate (Truswell *et al.* 1987). The hypothesis of an indigenous biota has focused almost exclusively on the wet tropics, with the assumption that rainforests are the most likely relicts of Gondwanan flora and fauna (Christophel and Greenwood 1988; Schodde 1989). This is surprising given that today the wet tropics are confined to a tiny corner of the north-east, whilst the vast majority of northern Australia is dominated by communities experiencing a monsoonal climate. Nevertheless, nearly all the recent symposia and multi-authored books on the biogeography of northern Australia and the adjacent Malesian region (Whitmore 1981; Whitmore 1987; Kitching 1988; Knight and Holloway 1990; Walker 1992) have emphasised the wet tropics whilst almost ignoring monsoonal areas. So, the Australian Systematic Botany Society's meeting on 'Origin and Evolution of the Flora of the Monsoon Tropics' at Kuranda, north Queensland, in July 1994 was a welcome change of emphasis.

This issue of Australian Systematic Botany contains a number of papers from the Kuranda symposium. Not all the papers are closely connected with the main theme and not all the papers that were presented appear here. This introduction concentrates on the theme, citing contributions that are published both here and elsewhere.

Clearly it is necessary to define at the outset what is meant by 'monsoon tropics'. The monsoonal climate is well researched and its causes well understood. Trivially, it is a warm seasonally wet–dry climate in which the 'wet' is driven by complex interaction between air rising over a hot dry hinterland and moist air evaporated from a suitably warm pool offshore. In Australia, the monsoon occurs during the southern hemisphere summer. Truly monsoonal climate (as experienced by south-eastern India) is fairly restricted in Australia to wetter regions such as the Arnhem Land environs, but nearly all of the tropics are considered 'monsoonal' in a looser sense, albeit tending towards aridity. The intensity and duration of the monsoonal 'wet' is controlled by the southern oscillation (or El Niño) cycle in a way that is still not fully understood. At the symposium, J. Luly reviewed this research but his paper does not appear here.

Whilst the mechanics of present-day monsoonal climate are well-researched, suprisingly little is known about its history. It seems that there is only indirect evidence, reconstructed from fossil flora assemblages, using the principle of uniformitarianism—i.e. it is assumed that the physiognomy (size and shape) of leaves in a flora bore the same kind of relationship to climate in the past as it does today. Greenwood reports here a physiognomic analysis of three central Australian floras from the Eocene and concludes that the vegetation of that period and place were varied, being partly 'monsoonal' in character, but perhaps only

marginally seasonal. He suggests that rainforest may have formed galleries rather than being continuous. From the very northern edge of the continent, on Melville Island, Pole and Bowman report here a fascinating new deposit of Tertiary plant fossils with very unusual character and suggestive of a strongly monsoonal climate. Unfortunately, the precise age of this assemblage is undetermined. Conventional wisdom suggests that Australia experienced a uniformly mild, aseasonal and wet climate supporting rainforest until the Miocene, albeit with drier pockets (Truswell 1990). These recent analyses of macrofossils suggest that seasonal if not monsoonal climate may have established much earlier, more extensively and farther south than previously thought.

Undoubtedly, the advent of plate tectonic theory in the 1960s provided a fresh approach to biogeography in general (Raven and Axelrod 1974; Briggs 1987) and the study of northern Australia and Malesia in particular (Whitmore 1981; Truswell *et al.* 1987; Whitmore 1987). Whilst controversies remain to be resolved (Audley-Charles *et al.* 1988; Burrett *et al.* 1991; Michaux 1991), these now focus more on small scale (terrane) events than on the major continental movements. The present symposium did not consider geological hypotheses. Moreover, the study of biogeography does not need geological hypotheses *a priori*. Biotic distribution patterns themselves can and should be the basis for hypotheses about earth processes that can be tested *a posteriori* using geological evidence (Ball 1976; Rosen 1978). In recent years, biogeographic methods have been radically changed by the marriage of phylogenetic methods with Croizat's vicariance theory (Nelson and Platnick 1981; Humphries and Parenti 1986). The traditional approach has been descriptive, usually constructing scenarios for individual taxa—where they originated and where they dispersed to—supplemented in recent years with explanation derived from plate tectonics. The new approach is analytical: it identifies repeating distributional patterns in many taxa, and postulates common causes, often also (but not necessarily) derived from plate tectonics. The power of the new approach is that it hypothesises general explanations which can be corroborated (or falsified) by new evidence. A hypothesis for a single lineage, even if based on a 'good' phylogeny, is very difficult to test: witness the raging controversy about human origins.

Several papers on cladistic biogeography were presented at the symposium. Those appearing herein are treatments of *Spatholobus* (Fabaceae) by Ridder-Numann and several genera of Sapindaceae by Turner. Both propose a combination of vicariance and dispersal to explain the distributional patterns. Hill presented analyses of *Cycas* (Cycadaceae) and the bloodwood eucalypts (Myrtaceae), the latter now treated as *Corymbia* (Hill and Johnson 1995), but he has not submitted these for publication. This is unfortunate because both genera are large and well-represented in the monsoonal and adjacent arid areas, from which few plant phylogenies are available. Other cladistic biogeographic papers presented but not appearing here include analyses of Anacardiaceae by Wannan, and *Boronia* sect. *Valvatae* (Rutaceae) by Duretto. One paper published elsewhere (Crisp *et al.* 1995) uses phylogenies of several plant taxa to reconstruct general area patterns in Australia and New Guinea. Wet tropical and monsoonal areas were treated separately and appeared to have long, independent histories, even though they are geographically proximate. Interestingly this result seems consistent with the suggestions by Greenwood, Pole and Bowman (above) that monsoonal climate has a long history in Australia.

Broad-scale analyses of area patterns using phenetics were presented by Whiffin *et al.* for the Lauraceae (not published here) and Jacobs and Wilson for aquatic plants (herein). Among the deficiencies of this approach is that it will unite areas based on shared absences, which are biogeographically meaningless. Some papers in this issue present a descriptive approach to the biogeography of individual taxa: one on Bryoideae of north-east Queensland by Spence and Ramsay, and another on Palawan mosses by Tan.

Ecological approaches investigate biogeography on a different time-scale, and look to different kinds of explanations. These usually deal with the last million years or so, emphasising events that sift existing species, causing their ranges to expand and contract, rather than events such as speciation and extinction (Myers and Giller 1988). Several papers in the symposium dealt with ecological issues in biogeography. A fascinating analysis of woodland plants along the moisture gradient from the 'top end' to central Australia by Egan

and Williams (herein) supports two existing hypotheses: that life form is related to climate, as assumed by palaeoecologists (above); and that there is a major ecological boundary at 16–17°S. Their most interesting finding is counter intuitive: that plants with root-storage are favoured not by arid environments, but are limited to the more humid areas north of 14°. But the authors wisely suggest that historical (phylogenetic) factors should also be considered in explaining this pattern—for instance, the root storage plants may belong to certain taxa which may have always been limited to northern areas. Crowley presents a most interesting reconstruction of coastlines and their mangrove forests along the tropical Australian coastline during the last few thousand years. A very important symposium paper that does not appear here uses fossil charcoal to show that the tropical rainforests virtually ‘disappeared’ from the historical record during the recent glaciation, apparently replaced by eucalypt forest (Hopkins *et al.* 1993). We know that the rainforest did not literally disappear, because it is present in renowned diversity today. This should sound a warning to all who interpret absences in the fossil record literally. A comprehensive survey of the monsoonal rainforests of the ‘top end’, also published elsewhere (Liddle *et al.* 1994), led the authors to analyse the geographic affinities of the species in this community. Surprisingly, and by contrast to the ancient endemism shown by taxa in rainforest and sclerophyll communities, most species extend overseas (e.g. to Malesia) and many extend as far as Africa and America. This suggests that monsoonal rainforest communities are highly dynamic and comprised of pantropical taxa that are much more dispersible than most of the Australian flora. Biogeographic comparison of these with the endemic tropical taxa (Crisp *et al.* 1995) would make an interesting study.

Other symposium papers in this issue cover topics such as phylogeny and co-evolution (Fay on fruit-piercing moths and Menispermaceae), ant–plant relationships (Mackay and Whalen on euphorbs), familial relationships (Conran on Byblidaceae) and anatomy (Bhat on Bombacaceae). Last but certainly not least, K. D. Hyde presents an unashamed and eloquent plea for serious study of some neglected but ecologically very important organisms: fungi. He argues convincingly that if we are serious about biodiversity and its conservation, then research on this grossly underestimated group is essential and overdue.

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