

## Review Article

### FOREST ECOLOGY RESEARCH IN BORNEO: 2003-2008

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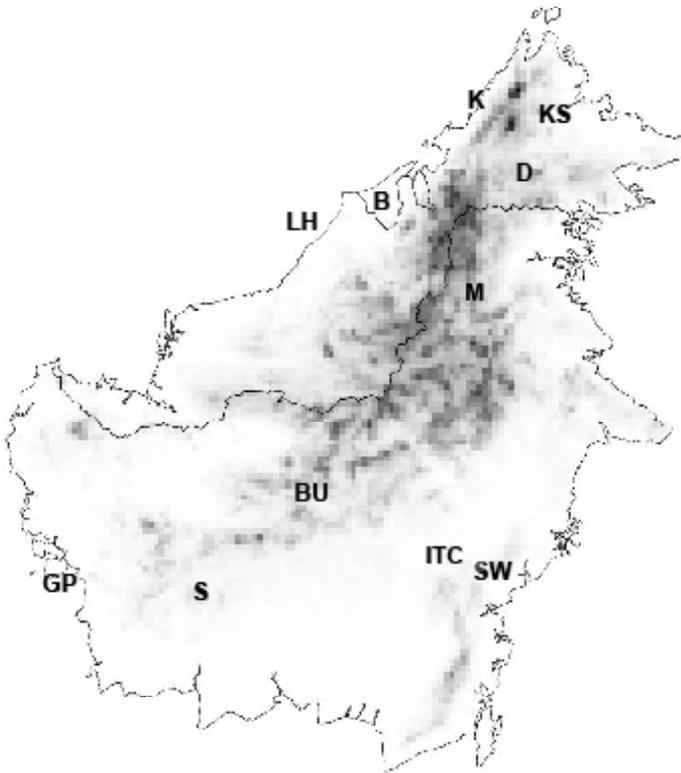
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Borneo is the second largest tropical island in the world (after New Guinea). It has one of the most diverse floras, with around 14,400 plant species (Roos *et al.* 2004), of which around 3,000 are trees (MacKinnon *et al.* 1996). Around 30 % of all plant species are found nowhere else (Roos *et al.* 2004). In addition, Borneo is the center of diversity of the important timber tree family, the Dipterocarpaceae, where at least 267 species are found (Ashton 1982). Lambir Hills in northwestern Sarawak has the highest density of tree species in the world, with 1,173 tree species (in 286 genera and 81 families) in only a 0.52 km<sup>2</sup> area of forest (Lee *et al.* 2002) and in the environs of Mount Kinabalu in Sabah there are over 5000 plant species (Beaman 2005). In terms of conservation priorities, Borneo falls within the Sundaland biodiversity hotspot, one of the five hottest hotspots (Myers *et al.* 2000), is split between two of the world's seventeen megadiverse countries (Mittermeier *et al.* 1997), and harbors four of the "Global 200" priority regions for conservation (Olson & Dinerstein 2002). By any measure, Borneo is exceptionally biodiverse.

My aim in this review is to present ecological work that has been carried out on Borneo in the period 2003 to 2008 with a particular focus on forest ecology. "Forest ecology" covers a number of topics and I will consider here mostly terrestrial plant ecology in a broad sense (I will not examine animal ecology in any detail). The topics which I feel are most worthy of my attention, and which I have knowledge to comment upon, are focused upon here under the following groupings: (i) floristics, *i.e.* descriptions of plant communities with a view to examining larger-scale patterns of species diversity on the island, (ii) new plant species that have been discovered and described, (iii) community ecology, with a focus on habitat specialization of tree species. I will then look at (iv) rates, patterns and drivers of deforestation with some thoughts on forest conservation and (v) the effects of disturbance on the forest and patterns of recovery. I will finish with a (vi) section on biogeochemistry and carbon (C) storage in Borneo's forested ecosystems and how C storage might be affected by some of the geographical variations and disturbances noted previously. My focus will be on studies conducted in the forests of Borneo but will include those which have a wider ecological significance. Figure 1 shows the location of the sites mentioned in the text. It is notable, and of some concern, that the majority of the studies reported here have the main authors primarily



**Figure 1:** The island of Borneo with the location of study sites mentioned in the text. Barito Ulu (BU), Belalong (B), Danau Valley (D), Guntung Falung (GP), ITCI logging concession (ITC), Kabili-Sepilek (KS), Lambir Hills (LH), Malinau (M), Mount Kinabalu (K), Sungai Wain (SW) and Wasmiset Sungai (S). Darker shading indicates increasing elevation.

based in Europe, America, or Japan; where local authors are included they are often as research counterparts rather than primary authors. In terms of capacity building, it would be great to see local authors publishing their work in the higher-impact international journals (although there is the other side of the coin, these journals are often too expensive to subscribe to in the region).

### 1) Floristics

New descriptions of tree communities (from permanent plots where trees over a certain diameter are marked and identified) have been published from Barito Ulu

and Wanariset Sangai in Central Kalimantan (Brearley *et al.* 2004; Wilkie *et al.* 2004), Belalong in Brunei (Small *et al.* 2004); Sungai Wain in South Kalimantan (Eichhorn & Slik 2006); and CIFOR's Malinau Research Forest in East Kalimantan (Kartawinata *et al.* 2006). When considered together in combination with other plot descriptions, these studies form a larger body of work and their value is increased considerably as species distributions and large-scale patterns of variation in tree communities can be ascertained. For example, Slik *et al.* (2003) collated data on tree species abundance from 28 locations across Borneo and showed that tree diversity was highest in southeast Kalimantan and central Sarawak. Furthermore, the forests of Borneo could be divided into five floristic groups using statistical clustering methods and those groups which were north of the central mountain range were clearly different from those to the south, suggesting that the mountains effectively prevent large-scale dispersal of many tree species (Slik *et al.* 2003). The Borneo-wide network of permanent plots is expanding but there are areas which need more coverage, notably parts of West and Central Kalimantan and some of the Sarawak/Kalimantan border regions. Expanding the number of plots will allow ecologists to examine patterns of diversity in more detail and make strong inferences on the environmental factors affecting island-wide tree diversity.

A database of over 28,000 plant collections from Mount Kinabalu has been described by Beaman (2005) and this allowed Grytnes & Beaman (2006) to document elevational patterns of species richness in this incredibly diverse mountain landscape. They found that the elevation with maximum species richness was generally 900 to 1200 m. with a moderate decline in species richness at lower elevations and a steeper decline towards the higher alpine zone. This pattern varied somewhat by floristic group, with a steady decline in species richness with elevation for trees, but the mid-elevation pattern of highest species richness, as mentioned above, being more notable for ferns and epiphytes.

## 2) New species and species descriptions

The density of collection of herbarium specimens needed to describe new species fully, was 35 specimens per 100 km<sup>2</sup> on Borneo, which is the lowest in the Sundaland region (Johns 1995). However, this is further split highly unevenly with Sabah having 126 collections per 100 km<sup>2</sup> and Kalimantan (comprising about ¾ of the land area) having an order of magnitude less, with 12 collections per 100 km<sup>2</sup>. Nevertheless, there have been numerous new species described during the period of this review and I note here some which have caught my eye (this is by no means an exhaustive list): *Nepenthes chaniana* (Nepenthaceae; Clarke *et al.* 2004), *Nepenthes glandulifera* (Lee 2004), *Dissochaeta atrobrunnea* (Melastomaceae; Kadereit 2004), *Beilschmiedia oligantha* (Lauraceae; Nishida 2005), *Etilingera palangensis* (Zingiberaceae; Takano & Nagamasu 2006), *Musa barioensis* (Musaceae; Häkkinen 2006) and *Ficus lumutana* (Moraceae; Berg 2008). Between 2003 and 2008, two more volumes of the *Tree Flora of Sabah and Sarawak* (Soepadmo *et al.* 2004, 2007), with descriptions of the families Apocynaceae, Cunoniaceae, Dipterocarpaceae, Herndandiaceae, Meliaceae, Polygalaceae, Symplocaceae and Thymelaeaceae, were published, bringing the total number of volumes to six. The final volume of the *Flora of Mount Kinabalu* was also

produced (Beaman & Anderson 2004). Plant collections in parts of Kalimantan should be increased as this area is very under-collected and we will undoubtedly see many new species continue to be described in the near future.

### 3) Community ecology

#### 3.1) Habitat specialization

A key research theme in this period has been the determination of habitat specialization by trees in the forests of Borneo, and there have been a number of papers showing the degree of habitat specialization from a number of sites across the island. Northern Borneo has been a particular focus for this work as it has forests on a range of soil types, from relatively more nutrient-rich clay soils to more nutrient-poor soils with more sand in them. As a general pattern across sites, the dominant families in lowland forests usually remain consistent (*e.g.* Dipterocarpaceae and Euphorbiaceae; Slik *et al.* 2003) but the dominant species differ by both habitat and by geographical location. This suggests some degree of limited large-scale seed dispersal and independent evolution in different sites (Cannon & Leighton 2004). For example, Cannon & Leighton (2004) examined 69 small plots at Gunung Palung in West Kalimantan and found that, among common species, 67 % were significantly associated with a single one of the five habitats studied (alluvium, peat, freshwater swamp, granite and sandstone) with only 16 % of species found as habitat generalists. Similar patterns were seen in a montane forest on Mount Kinabalu where 20 out of 42 common species in a 2.75 ha. plot showed specialization in relation to topography (Aiba *et al.* 2004). Among the Dipterocarpaceae, Paoli *et al.* (2006) showed that 18 out of 22 species were positively or negatively associated with a habitat type at Gunung Palung, and that diversity of this important tree family was highest on the nutrient-poor granite-derived soils. Comprehensive tests of associations with topography and habitat have been carried out at Lambir Hills, which has varied topography and a range of contrasting soil types where around 350,000 trees have been mapped in a 52 hectare (0.52 km<sup>2</sup>) plot. At this site, Davies *et al.* (2005) showed that 87 % of the tree species (with more than 50 individuals) had distributions significantly biased with respect to the habitat gradient in the plot and Yamada *et al.* (2006) also found eight out of ten members of the Sterculiaceae to show significant associations with habitat. Similarly, from Kabili-Sepilok in Sabah, DeWalt *et al.* (2006) determined soil-related specialization for lianas where 30 out of 42 species studied showed significant habitat associations and the rankings of liana biomass and diversity matched that of soil fertility.

The physiological basis of this habitat specialization is the natural extension of this work and is currently under study. For example, Palmiotto *et al.* (2004) found that, at the seedling stage, the growth of four out of five species was significantly greater on their preferred soil type at Lambir Hills (although for the species from the more nutrient-rich soils this was only realized under higher light conditions) and there was no difference in growth between the two soil types for the soil generalist species. At Kabili-Sepilok, Baltzer *et al.* (2005) showed how species specialized to nutrient-poor sandstone soils were more water-use efficient when compared to species from the nutrient-rich alluvial soil but that this was traded-off against higher metabolic rates and

reduced nutrient-use efficiency. Edaphic (soil-related) specialists were not capable of physiological acclimation when grown on their non-native soil type: species from the nutrient-rich alluvial habitat could not gain the high water-use efficiencies when grown on the sandstone soil and species from the sandstone soil had increased metabolic costs when grown on the alluvial soils. Interestingly, Russo *et al.* (2005) showed that soil specialists did not always have a home soil advantage in terms of growth rates but that, with increasing size, species were lost from their non-preferred soils more rapidly than from their preferred soils, leading to clear patterns of species distributions. Most studies have been conducted on a small fraction of the species present in the forests, often with a focus on the Dipterocarpaceae. It would be valuable to extend the taxonomic breadth of such studies and also to consider the importance of biotic interactions, such as pathogenic or mutualistic fungi, or insect or vertebrate herbivory, in structuring plant communities.

In an Amazonian forest, differing rates of herbivory of species on different soil types also appeared important in leading to habitat partitioning (Fine *et al.* 2004) and there is some evidence that this was the case where it has been studied at Kabili-Sepilok (Eichhorn *et al.* 2006). Dipterocarp seedlings native to more nutrient-rich soil suffered greater rates of herbivory on mature leaves when planted in the nutrient-poor site; in contrast, species native to the nutrient-poor soil suffered mature leaf herbivory equally on both soil types. In contrast, for new leaves, herbivory rates were greatest on each seedling species' native soil type (Eichhorn *et al.* 2006). In a similar vein, the number of Lepidoptera species feeding on the dipterocarp seedlings was lower when the seedlings were in their non-preferred soil type, although this was not seen for Coleoptera or Orthoptera (Eichhorn *et al.* 2008).

### 3.2) Density- and distance-dependent mortality

Studies have looked at the role of the Janzen-Connell effect in maintaining species richness (*i.e.* are seedlings prevented from recruiting in the immediate vicinity of parent trees because of high specialist pathogen and/or herbivore pressure?) and Blundell & Peart (2004) showed that density-dependent mortality of seedlings was occurring in *Shorea quadrinervis* (Dipterocarpaceae) at their study site in Gunung Palung. Furthermore, it was found that survival of seedlings in the same forest was related to the phylogenetic diversity of surrounding seedlings (*i.e.* how closely each seedling is related to each other), with seedling survival enhanced when it was in the vicinity of a group of species more unrelated to it (Webb *et al.* 2006). Stoll and Newbery (2005) extended this work to later life stages to show that adult dipterocarp trees at Danum Valley in Sabah grew faster (twice the diameter growth rate over ten years) in the absence of neighbors of the same species when compared with those with a higher density of neighboring same species.

### 3.3) Phenological patterns

Two long-term studies of phenological patterns and their relationships with climate have been published by Sakai *et al.* (2006) from Lambir Hills, and by myself and colleagues from Barito Ulu (Brearley *et al.* 2007). Both studies have presented evidence that droughts appear to promote reproductive activity on a large-scale – the phenomenon

known as mast fruiting (Sakai *et al.* 2006; Brearley *et al.* 2007). We have also identified low intensity masting events, during which fewer trees reproduce and seedling survival is poor. The low reproductive success during these low intensity events appears to be due both to a high level of flower loss, perhaps due to low numbers of pollinators, and high seed predation as predators are not swamped with resources as they would be during a mast year (Maycock *et al.* 2005). Shorter term droughts also appear to cause leaf shedding and flushing (Ichie *et al.* 2004). In addition, Cannon *et al.* (2007) showed that reproductive activity during mast-fruiting events at Gunung Palung was much lower in montane ecosystems and freshwater peat swamp ecosystems (probably due to the lesser importance of dipterocarps in these ecosystems). These phenological studies should be continued to include an increased number of El Niño events. It would also be useful if a standardized protocol could be used by phenology researchers to allow more meaningful comparison between sites, with the inclusion of large-scale meteorological data.

#### 4) Deforestation: rates and causes

Around half of Borneo still remains forested (Langner *et al.* 2007), with rates of deforestation within the region some of the highest globally and appearing to be increasing, at least in Indonesia (Koh 2007). Fuller *et al.* (2004) showed the deforestation rate to be around 2 % per year in Kalimantan with a higher rate in East Kalimantan where forests were more likely to be burned. However, this is not evenly spread among habitat types, with lowland forest having the highest deforestation rate, most probably due to higher population pressure, ease of access, and greater timber stocks. A more recent study by Langner *et al.* (2007) showed the average deforestation rate between 2002 and 2005 was 1.7 % per year, but this was higher (2.2 %) in peat swamp forests.

Deforestation has also been occurring within protected areas in Indonesia. For example, Curran *et al.* (2004) reported on exceptionally worrying rates of deforestation of more than 2 % per year *within a national park!* Rates of deforestation in the 10 km. buffer around the park were double this. Overall, from 1985 to 2001, forest loss in protected areas in Kalimantan was over 56 % (Curran *et al.* 2004).

The major causes of deforestation are commercial logging (including illegal logging) which also includes clearance to create oil palm plantations (Koh & Wilcove 2008) as Indonesia and Malaysia are currently the largest global producers of palm oil (<http://faostat.fao.org>). Around 55-60 % of oil palm expansion between 1990 and 2005 has come at the expense of forested land (Koh & Wilcove 2008). Fires, especially during El Niño years, are also an important driver of forest degradation (van der Werf *et al.* 2008) and an increasing threat is that of open-cast coal mining (Brearley 2007) with Indonesia appearing to be one of the fastest growing producers in the world, with the center of production in Kalimantan (Anon. 2004). Expansion of oil palm is arguably the biggest of these threats and future research should focus on how this expansion is affecting ecological communities and how they might recover if plantations are abandoned.

In terms of conservation, it is often considered that planning without local people's needs in mind can lead to failure of the conservation scheme or even conflict. Work by Sheil *et al.* (2006) has examined local people's priorities for conservation in the Malinau region in East Kalimantan with many people considering unlogged forest to be

the most valuable land-use type – this gives hope for conservation schemes promoted by “outsiders” if they also involve local stakeholders as a “pragmatic and ethical means to foster a new constituency and to achieve conservation across a wider landscape” (Sheil *et al.* 2006). Follow-up work suggested that many local people support some form of forest conservation, but also consider local views to be important in planning this (Padmanaba & Sheil 2007). Ali & Jabobs (2007) have outlined how forest conservation can be linked to healthcare, especially in upriver parts of the island, and discuss strategies for linking these two essential activities through “conservation agreements.”

## 5) Disturbance and recovery

### 5.1) Droughts and fires

Numerous studies examining the effects of the 1997/1998 El Niño drought and fires have been published – this was the most severe drought event observed directly in the region. One of the most important is that of Potts (2003) who showed that tree mortality rates at Lambir Hills were about three times higher during the drought period than prior to it. Interestingly, the mortality rate of large common trees was greater than that of large rare trees, suggesting a compensatory mechanism whereby rare species could be maintained in the landscape. Slik (2004) showed that tree mortality rates during the drought period in the ITCI logging concession in East Kalimantan were, again, about three-and-a-half times higher in undisturbed forest compared to eight-and-a-half times higher in logged forest, much of this was due to the fact that pioneer trees, such as various *Macaranga* species, were more common in the logged forest and over half of these pioneer trees died during the drought. Delissio & Primack (2003) found that seedling mortality was also elevated during the drought and Bebber *et al.* (2004) showed that mortality during the drought was greater for seedlings which had higher levels of insect herbivory (*e.g.* mortality of seedlings with more than 50 % defoliation was twice as great as those with less than 10 % defoliation), although heavily defoliated seedlings were fairly rare in the forest. Some forests were subjected to drought and then, due to the drier conditions, were more susceptible to fires. Van Nieuwstadt and Sheil (2005) found that, in the forests of Sungai Wain in East Kalimantan subjected to drought and fires, about three quarters of all trees died around two years after the event compared to about one quarter dying in the forests subjected to drought only. It is also worth noting that drought had a greater negative effect on larger trees whereas fires had a greater negative effect on smaller trees, leading the authors to argue that, due to more rapid replacement of smaller trees, the impact of the drought was more severe than that of the fires (van Nieuwstadt & Sheil 2005). Furthermore, trees on ridges and hilltop positions were more affected than those in lower topographical positions (Slik & Eichhorn 2003), meaning that repeated fires may well have greater effects on species that do not reach larger sizes and those with a habitat preference for ridges, potentially leading to changes in species composition over time. Slik & Eichhorn (2003) showed how forest which had been burned twice (1982-3 and 1997-8) had a higher number of pioneer trees and a lower number of climax trees when compared to an unburned forest. Numbers of pioneer trees in forests burned once (1997-8) were intermediate whereas numbers of climax trees were similar to the twice-burned forest. Seven years after the fire, forests were still strongly

affected, with recovery being very slow (Slik *et al.* 2008). We need to continue data collection from these sites to determine how forests will recover over the longer term and also to consider the effects of these disturbances on below-ground ecosystems.

### 5.2) *Shifting cultivation*

A series of studies has been carried out on the effects of shifting cultivation on tree species diversity in the vicinity of Gunung Palung National Park (Lawrence 2004, 2005, Lawrence *et al.* 2005). She showed how tree species diversity declined and there was increasing dominance by certain species after an increasing number of cycles of shifting cultivation, and how this decline in diversity was more noticeable for the smaller (< 10 cm diameter) trees (Lawrence 2004). Species diversity in these secondary forests also decreased with increasing distance from primary forest (Lawrence 2004). Follow-up work discussed how the change in species composition was only partly mediated by changes in soil nutrient status and discussed the importance of seed dispersal in determining species composition (Lawrence *et al.* 2005). Colleagues and I have shown how, even after 55 years of succession, despite the forest structure of recovering secondary forest being somewhat similar to that of primary forest (82 % recovery for basal area, 88 % recovery for tree height and 74 % recovery for biomass), the floristic composition is still very different, with a coefficient of similarity of only 24 % (Brearley *et al.* 2004). With secondary forests playing an increasingly important role we need to consider how these forests may provide ecosystem services in the future (*e.g.* carbon sequestration and storage) and how this compares with primary forests.

### 5.3) *Logging disturbances*

Other anthropogenic disturbances were studied by Berry *et al.* (2008) who examined plots in the Danum Valley area to determine differences in tree species composition between unlogged plots and those logged 18 years previously. They found no difference in species richness on a plot basis, but the variation among logged plots was greater and, at the landscape scale, logged forest supported more species of small trees. This should not, however, be taken as a lack of an effect of logging on the forest, as the species composition in the two forest types was still very different nearly 20 years post logging.

There are indications that reduced impact logging is a promising and sustainable way forward both from an ecological as well as an economic perspective (van Gardingen *et al.* 2003). As obvious as it may seem, this is essentially a logging operation which is planned in advance, maps are made of the area and the trees to be extracted, and the trees are felled in a way to avoid damage to other trees, skid trails are minimized to avoid soil damage and climbers are often cut to prevent falling trees pulling down other trees which may be entwined by these climbers. Sist *et al.* (2003) showed how reduced-impact logging might be of ecological benefit at a site in East Kalimantan where, at lower cutting intensities, this technique reduced the number of trees damaged during timber extraction by around 40 % and also reduced soil damage by skidding logs, although benefits were less clear under higher logging intensities. However, effects need to be considered on a site-by-site basis as Forshed *et al.* (2008) found that, during

supervised logging operations in Sabah, directional felling was of minimal benefit but that climber cutting had a much greater positive effect on subsequent tree growth. It is heartening that timber produced under conditions certified as “sustainable” can be sold for a higher price, at least under some circumstances (Kollert & Lagan 2007). Sadly, more sustainable methods of logging have not been adopted widely and it would be of great benefit to examine why this is and continue to promote the ecological and economic benefits of such methods.

## 6) Biogeochemistry and carbon storage

It is noteworthy that the forests of Borneo store more carbon (C) above ground on a per area basis than do their Amazonian counterparts (Paoli *et al.* 2008). Paoli *et al.* (2008) showed that the effects of soil fertility on above-ground biomass (and hence C storage) was not particularly marked, but the most fertile of the soil types examined at Gunung Palung did have a higher density of the largest trees (which make up a particularly large proportion of the forest biomass). This suggests, when compared with the work of Cannon & Leighton (2004), that forest structure may be less strongly dependent upon soil variation than is community composition. However, Paoli & Curran (2007) further showed that above-ground production was strongly related to soil nutrient status across three forest types, specifically to extractable soil phosphorus, indicating a soil fertility effect on C cycling.

Dent *et al.* (2006) detailed the differences in soil nutrients, litterfall, and litter decomposition rates among different forest types at Kabili-Sepilok and Takyu *et al.* (2003) showed how above-ground biomass, net primary production (NPP) and decomposition rates were lower in ridge-top than lower slope positions on three soil types on Mount Kinabalu. This followed from the earlier work of Kitayama & Aiba (2002) who showed how these parameters all decreased with altitude on Mount Kinabalu.

It would be very useful if forest biomass could be determined successfully by remote sensing as this would save a large amount of money over time- and labor-intensive field surveys. Phua & Saito (2003) attempted this for the forests in Kinabalu Park and found that remote sensing could only be used to show very broad differences in forest structure. In contrast, more recent work by Tangki & Chappell (2008) found that the technique was a useful tool to determine tree biomass in a series of logged and unlogged forest sites. How remote sensing will fare in mapping landscape variation in biomass in undisturbed forest remains to be determined for the forests of Borneo, although there are promising results from Amazonia (Saatchi *et al.* 2007).

## Conclusions

Borneo is a highly diverse island and we are still describing the species found there, how they are distributed across the island, and what the important physiological factors and biogeographical determinants that affect species distributions are. Sadly, rates of deforestation remain high but we do know that, under favorable conditions, forests can recover from various forms of disturbance to provide a valuable repository of both carbon and biodiversity.

**Acknowledgements:** Jon Binnie and Douglas Sheil are thanked for their comments and Ferry Slik is thanked for the use of his map of Borneo.

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