Diversity, size composition and spatial aggregation among trees on a 1-ha rain forest plot at La Réunion

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Because lowland rain forests of oceanic islands have almost always been destroyed soon after human colonization, there exist few quantitative descriptions of tree species composition and diversity in such forests. For this reason, the diversity and structure of a lowland tropical rain forest were studied on a 1-ha permanent plot on the oceanic island of La Réunion. A total of 1270 individuals of gbh ≥ 25 cm (girth at breast height), including at least 43 species, were mapped, measured and identified. Several species were represented only by large individuals. Ten species among the 23 common enough to test are randomly distributed over the hectare, while 13 show aggregated spatial distributions. The tree species diversity, size structure and spatial distribution observed in this island plot are discussed in light of patterns occurring in continental lowland tropical rain forests. In the study area, the high density of trees and the tendency of conspecific individuals to be clumped may be linked to several factors: hurricane disturbance, lack of seed dispersers and patchy seed rain.

Keywords: tree diversity; forest structure; lowland tropical rain forest; hurricane effects; La Réunion; Mascarene Islands

Introduction

In tropical rain forests, patterns of species richness, size and spatial structure of tree populations are expected to differ between volcanic oceanic islands and continental areas. Island environments are characterized by geographic isolation and small area effects which strongly limit colonization and species diversity (MacArthur and Wilson, 1967; Carlquist, 1974). Moreover, tropical island rain forests, especially on volcanic islands, are much younger than most continental forests (Mueller-Dombois et al., 1981). In the Hawaiian Archipelago, the indigenous tropical rain forests are dominated by only two species, *Metrosideros polymorpha* Gaud. (Myrtaceae) and *Acacia koa* A. Gray (Mimosaceae) (Mueller-Dombois and Loope, 1990; Wagner et al., 1990; Drake and Mueller-Dombois, 1993). The humid forest zone at middle elevations (500 m) on Isla Santa Cruz of the Galapagos Islands is composed of monospecific stands of *Scalesia pedunculata* (Asteraceae) in which forest dynamics are very similar to those in *Metrosideros* forests in Hawaii (Itow and Mueller-Dombois, 1988). Depauperate insular tree diversity has also been recorded on the Solomon Islands, where the number of tree species on small plots is no higher than in some temperate forests (Whitmore, 1989).

Insular forest communities have escaped for a long time from common continental selective forces like herbivory and trampling by mammals (Janzen, 1971; Mueller-Dombois and Loope, 1990), but on the other hand they can be subjected to strong regional
disturbances like hurricanes. Almost every year, La Réunion is threatened by several tropical depressions circulating in the southwest Indian Ocean area at various intensities and distances from the island. Firinga in 1989 was the last intense tropical cyclone with wind speed surpassing 200 km h\(^{-1}\) that directly affected La Réunion. Both frequent tropical depressions and more occasional intense cyclones influence Mascarene Islands forest communities and may act at the tree population level as described for stunted windblown cloud forests (Lawton and Putz, 1988).

Until now there have been very few quantitative ecological studies of insular tropical rain forests, the best documented being on the Hawaiian islands (Mueller-Dombois, 1987; Vitousek, 1992; Drake and Mueller-Dombois, 1993). In the southwest Indian Ocean area, no study of tree diversity in permanent plots is available except the work of Vaughan and Wiehe (1941) in Mauritius upland forest.

In this study I present results on species diversity, composition and spatial distribution of trees, measured on a 1-ha permanent plot of lowland rain forest from the oceanic island of La Réunion, which emerged roughly 2 million years ago as the result of volcanic activity.

Four questions are addressed: (i) How many individuals and how many species coexist in the low altitude tropical rain forest on La Réunion Island? (ii) What is the relative frequency of the different species? (iii) What is their size distribution? (iv) What are their spatial distribution and their scales of spatial structure?

As in the majority of tropical oceanic islands such as Hawaii (Stone and Scott, 1985; Vitousek, 1988) or St-Helena (Cronk, 1989), the original low altitude habitats of the Mascarene Archipelago were destroyed or greatly reduced by the combination of human activities (agriculture, urbanization) and invasion by introduced species (Cadet, 1977; Cheke, 1987; Macdonald et al., 1991). At La Réunion, only 1–2% of the original area of low altitude rain forests still remains (Strasberg and Thébaud, unpublished data). The loss of genuine diversity linked to these rapid changes is considerable in such habitats, even if fragmented areas persist.

In the southeastern part of La Réunion, one of the last remnants of low altitude rain forest survives. In these fragments of forest several presence-absence surveys were performed by Cadet (1977) over areas of 200–1000 m\(^2\), but no data were taken on spatial distribution patterns of species and regeneration dynamics were not investigated.

**Materials and methods**

*Study site*

La Réunion, the largest of the volcanic islands of the Mascarene Archipelago, is situated 800 km east of Madagascar and rises to an altitude of 3069 m (Fig. 1). The study area is situated at 21°20'S latitude, 55°15'E longitude. It is located in the Natural Reserve of Marelounge, in the southeastern part of the island on the slopes of the active volcano, Le Piton de La Fournaise (2361 m). Mean annual rainfall is 4 m and the minimum monthly rainfall (August–September) is between 150 and 200 mm (Cadet and Figier, unpublished data). The mean annual temperature is about 23°C; the minimum monthly mean (20°C) occurs in August and the maximum (26°C) in January or February (Cadet, 1977). The average diurnal temperature range is about 6°C. The prevailing wind throughout the year (>200 days per year) is the south-east trade-wind with 40 km h\(^{-1}\) average speed. In the summer wet season frequent hurricanes blow with variable intensities in the Mascarene area (e.g. 15 censused by Météo France between November 1993 and April 1994 with one