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Reproduction and Evolution in Some Genera of Neotropical Melastomataceae

by

SUSANNE S. RENNER

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Abstract

RENNER, S. S. (Botanical Institute, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark). Reproduction and evolution in some genera of Neotropical Melastomataceae. *Memoirs of the New York Botanical Garden* 55: 143-152. 1990. The seven species of *Bellucia* are short-lived trees or shrubs occurring in Central and northern South America. They are bee-pollinated and their yellow berries are dispersed by monkeys and other animals. Three species are self-incompatible. The related genus *Loreya* comprises 13 species of medium-sized to large trees, most of them in subandean forests at the southwestern periphery of the Amazon basin. *Loreya* species are bee-pollinated and their red/blue or yellow berries are dispersed by marsupials and birds. The capsular-fruited genera *Macairea*, *Sandemanina*, and *Rhynchanthera* are wind-dispersed. *Macairea* has 22 species, most of them endemic to savannas of Venezuelan Guayana. At least one species reproduces predominantly via agamospermy. *Sandemanina*, a long-lived shrub of Amazonian white sand savannas, is pollinated by small bees and is also capable of agamospermy. The 15 species of *Rhynchanthera* are mostly centered in the savannas of south-central Brazil; they are bee-pollinated and at least one species is self-compatible. The differences in evolutionary modes among these groups seem related to the kind of habitat they occupy and to their dispersal systems, but are otherwise unrelated to phylogenetic distance.

Key Words: *Bellucia*; *Loreya*; *Macairea*; *Rhynchanthera*; *Sandemanina*; distribution; habitat; pollination; fruit dispersal.

Introduction

In the field, one may come to understand the functional role of flowers or fruits as structures adapted for specific pollination and dispersal systems; one certainly develops a feeling for the kind of habitat occupied by the species. During fieldwork on the reproductive biology of Melastomataceae (1980–1982 and 1984/85), mostly in Brazilian Amazonia, I observed several of the members of five genera (*Bellucia*, *Loreya*, *Macaírea*, *Rhynchanthera*, and *Sandemania*) which I have since treated taxonomically (Renner, 1987, 1989a, and in press). The species differed in their breeding systems, tendency to hybridize, dispersal mechanisms, and particularly in their habitat preferences. It is well known that breeding and dispersal systems influence speciation and that speciation in higher plants is also influenced by distribution and levels of instability of habitat (Simpson, 1953; Slatkin, 1987). Here, I contrast the five genera in terms of the mode of evolution most significant in promoting speciation in each group. This is done by relating biological information with morphological and distributional data. There are few published distribution maps of Melastomataceae, and therefore the present mapping of generic distributions may be helpful to others working on neotropical plants occupying similar, and in some cases rare, habitats.

Evolution Mode Most Significant for Speciation

BELLUCIA

Bellucia is a genus of seven species, four medium-sized trees and three shrubs. It ranges from southern Mexico to northern Bolivia and east through the Guianas into Maranhão and Bahía in Brazil (Fig. 1). *Bellucia* species frequently invade newly cleared sites; they are, for example, following man along recently built roads. *Bellucia grossularioides* (L.) Triana has been introduced to the Caribbean and *B. pentamera* Naudin to the Old World, both as potential fruit crops.

Bellucia is characterized by a papillose cuticle on the lower side of the leaves which causes a waxy appearance. On the upper surface, the leathery leaves are dark green and glossy. In bud,

the petals in *Bellucia* are completely covered until the last stages before anthesis, either by a thin calyptra or, in two species, by thick, triangular calyx lobes. The three shrubby species and one of the arborescent ones bear flowers in the axils of leaves; in the remaining species, the inflorescences are borne on the trunk and on the older branches below the leaves. All axillary-flowered species of *Bellucia* have calyptrate buds; the reverse, however, is not the case.

Controlled pollination experiments carried out with two of the arborescent and one of the shrubby species of *Bellucia* have shown that they are self-incompatible (Renner, 1989b). Since these species are incapable of agamospermy they are obligatorily outcrossed. *Bellucia* species all have similar large flowers (six to eight cm across in the trees and three to four cm in the shrubs), which are visited by numerous species of bees in the Anthophoridae, Oxaeidae, and Apidae. Many of these bees are big, strong-flying, and trap-lining (Renner, 1986/1987). I have found no indication of partitioning of pollinators by co-occurring species of *Bellucia*. For the sympatric species *B. dichotoma* Cogniaux and *B. grossularioides* (L.) Triana, I demonstrated the lack of a genetic barrier experimentally. The first has inflorescences on the trunk, the second in the axils of existing leaves. The fruits resulting from the artificial crossings contained viable seeds, and pollen of adult suspected hybrids stained well in lactophenolic cotton blue, an indication that it was viable, too. The chromosome number is $n = 20$ in *Bellucia pentamera*, the single species counted (Solt & Wurdack, 1980), but the hybridizations indicate that at least the arborescent species have similar genomes. I also observed suspected natural hybrids between *B. aequiloba* Pilger and *B. pentamera* Naudin and between *B. grossularioides* and *B. pentamera* (all of them trees) in the field and in herbarium material. Of the last two species, the first has a calyptra, the second triangular calyx lobes. In view of these contemporary hybridization events among the species of *Bellucia*, favorable traits such as the axillary position of the flowers or the calyptrate bud cover may well have spread via hybridization in the past. This would explain why all four different combinations of the states of these two traits are found in the four arborescent species.

Bellucia fruits are globose, greenish-yellow berries about 2–3 cm in size. They contain thou-

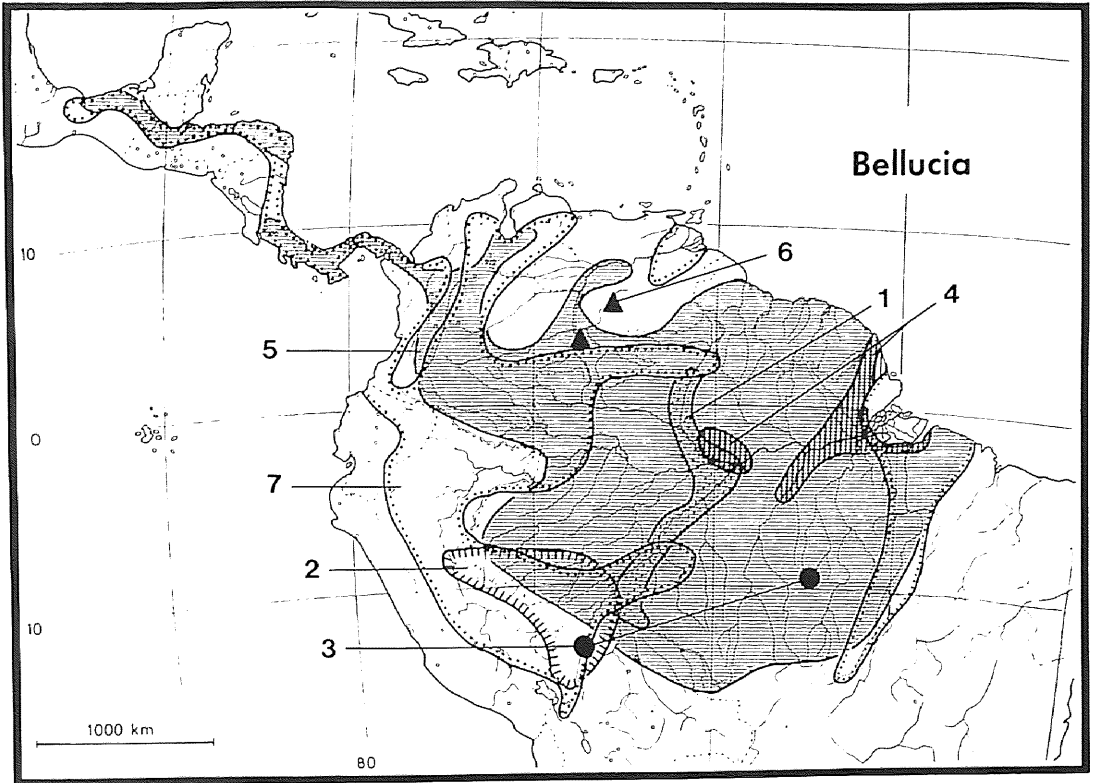


Fig. 1. Distribution of the seven species of *Bellucia*: 1. *B. acutata* Pilger, 2. *B. aequiloba* Pilger, 3. *B. beckii* Renner, 4. *B. dichotoma* Cogniaux, 5. *B. grossularioides* (L.) Triana, 6. *B. huberi* (Wurdack) Renner, 7. *B. pentamera* Naudin.

sands of small, 0.5–1 mm long, seeds and are eaten by a wide range of animals including monkeys (M. van Roosmalen, pers. comm.), bats (S. Marquez, pers. comm.), marsupials (*Caluromys philander*; Atramentowicz, 1982), birds (pers. obs.), tapirs (label data), turtles (M. van Roosmalen and D. Moskowitz, pers. comm.), other reptiles, and ants (both pers. obs.) once they have fallen to the ground. Judging by the considerable size, agreeable odor, and greenish color, it seems that monkeys have been the major selective factor in the evolution of *Bellucia* fruits. In Surinam, the seeds are dispersed by *Ateles paniscus*, the black spider monkey, who swallow the mature fruits whole; perhaps more rarely they are also eaten by *Cebus* monkeys (Roosmalen, pers. comm.).

In general, species of *Bellucia* have many features of typical weeds: they require a considerable amount of light for the establishment of

their seedlings, they flower and fruit continuously for many months to several years and produce large numbers of seeds, they possess efficient means of seed dispersal, they grow rapidly and they become fertile after a few years.

LOREYA

Loreya comprises 13 species and is centered in the southwestern subandean part of the Amazon basin (Fig. 2). All species are trees, some reaching heights of 20 m and more; the majority are shade-loving and are found in lowland rain forests, where the different species are adapted to either well-drained upland clay soils, non-inundated river banks, or periodically inundated areas adjacent to black or white water rivers. One species occurs at the edges of savannas. Most species of *Loreya* seem to be rare and normally to occur at low densities.

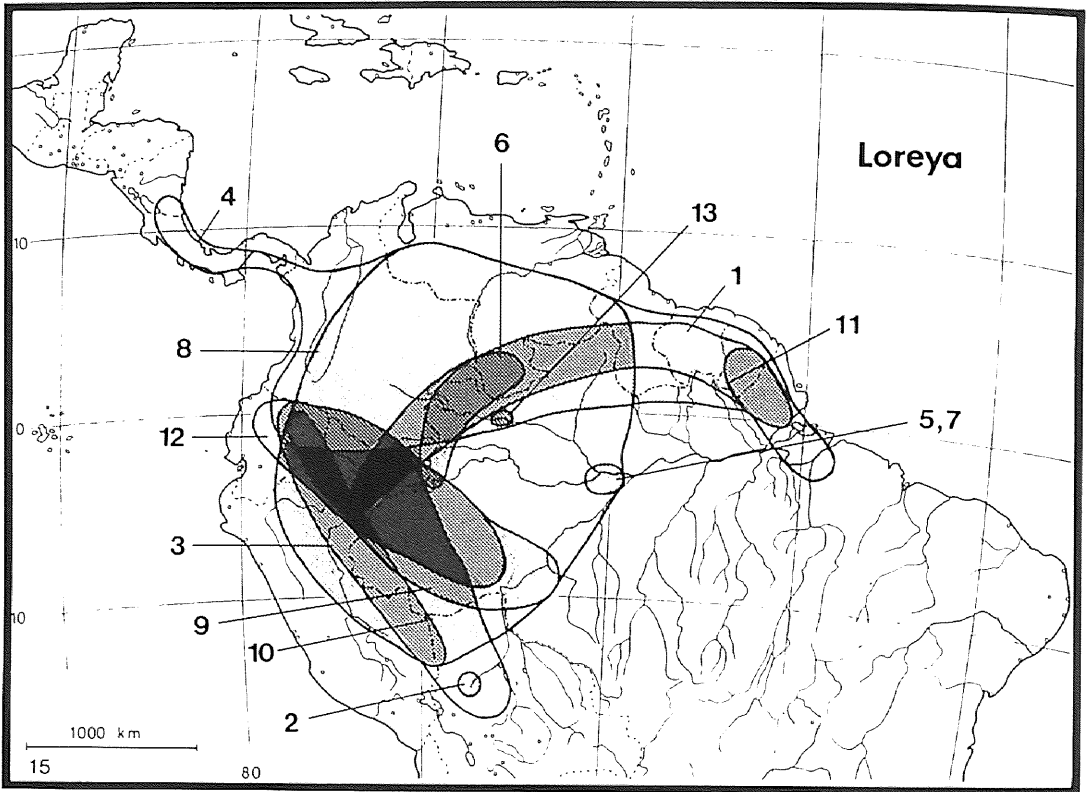


Fig. 2. Distribution of the 13 species of *Loreya*: 1. *L. arborescens* (Aublet) DC., 2. *L. gracilis* Renner, 3. *L. klugii* Renner, 4. *L. mespiloides* Miquel, 5. *L. nigricans* (Hook f.) Triana, 6. *L. ovata* Triana, 7. *L. riparia* Renner, 8. *L. spruceana* Triana, 9. *L. strigosa* Gleason, 10. *L. subandina* Wurdack, 11. *L. subrotundifolia* (Wurdack) Renner, 12. *L. umbellata* (Gleason) Wurdack, 13. *L. wurdackiana* Renner.

Loreya has flowers similar to *Bellucia*, albeit smaller. These flowers are consistently borne on the older branches below the leaves or the trunk. Contrary to *Bellucia*, the petals in the *Loreya* buds outgrow the calyx, which has only vestigial lobes. They are thus exposed at an early stage, instead of being covered until the onset of anthesis as in *Bellucia*. Finally, the leaves of *Loreya* are thin and do not have a papillose lower leaf epidermis. These traits probably make *Loreya* more vulnerable to water loss than *Bellucia*; this would explain why most *Loreya* species occur in subandean forests which have a high rainfall.

Loreya is pollinated by pollen-collecting medium-sized to big euglossine and anthophorid bees (Renner, 1989b). The species flower during distinct periods of about four to eight weeks and fruit for about one to three months. There is no indication of hybridization among them. The diversity in fruit color and size suggests that

adaptive radiation in dispersal relationships has occurred within *Loreya*. Eight species have glabrous, small berries which are purple and turn blue when mature and which are bird-dispersed. The remaining species have larger, more or less hairy, yellow fruits, which are eaten by mammals such as marsupials (Atramentowicz, 1982), tapirs, and wild pigs (herbarium label data). Even though a divergence within the genus into a mammal- and a bird-dispersed group has occurred, some species are associated with both dispersal agents. For example, the purplish-red fruits of *L. mespiloides* are removed diurnally and nocturnally at almost the same rate, being attractive to both birds and marsupials (Charles-Dominique, 1986; Foresta et al., 1984). A further step might be evidenced in the divergence in fruit color and size between the species-pair *L. riparia* Renner and *L. subrotundifolia* (Wurdack) Renner. These are morphologically similar; however,

the first has larger, yellow fruits and the second smaller, purple fruits. The two occur in different habitats and are geographically isolated.

RHYNCHANThERA

Rhynchanthera, in the Microlicieae, is a genus of only slightly woody shrubs comprising 15 species; it ranges from Mexico through the Guianas and Brazil south into Bolivia and Paraguay (Fig. 3). The genus is most diverse on the Brazilian plateau; ten of the fifteen species occur in cerrado vegetation in Goiás, Minas Gerais, and Mato Grosso. There are several impressive disjunctions (shown in Fig. 3). For instance, the southern Brazilian species *R. cordata* and *R. dichotoma* also occur in Peruvian savannas and *R. bracteata*, until recently only known from the Colombian llanos, has now been collected in savannas in Bolivia. *Rhynchanthera* species often grow in moist savannas dominated by grasses where they form large populations; they spread into drier savannas ("cerrado") by means of gallery forests. In Venezuela and central Amazonia, savannas are sometimes burned during the dry season by local people (Wurdack, pers. comm.; pers. obs. near Manaus), but *Rhynchanthera* quickly recolonizes burned areas from seeds. *Rhynchanthera* species flower for long periods; the seeds are about one mm long and are gradually shaken out of the sturdy, upright capsules by the wind.

Rhynchanthera has five fertile stamens, the thecae of which terminate in slender spoon-shaped beaks, and five minute staminodia. In ten of the 15 species, the fertile stamens are dimorphic, one being longer than the other four. It seems unlikely that the stamen dimorphism is of significance in pollination biology because in both monomorphic and dimorphic flowers the pollinating *Xylocopa*, *Centris*, and *Eulaema* bees alight and behave in the same way. They grip and bundle the stamens and then proceed to extract the pollen which is their only reward. Often, bees force their way into half-closed buds, indicating that some floral odor (imperceptible to humans) or pollen odor attracts them. I have observed individual bees collecting pollen from co-occurring species (*R. hispida* Naudin and *R. grandiflora* (Aublet) DC.), one of which has monomorphic, the other dimorphic fertile stamens. As usual in Melastomataceae, the bees

collect pollen from the tubular anthers using thorax vibrations which are transmitted via the legs onto the stamens. The vigorous shaking causes pollen to shoot out of the anther pores. Grains from all five fertile stamens are probably deposited mixed together on the bees' abdomens. In *Rhynchanthera* flowers, the stigmas contact the bees on the ventral or lateral side of the abdomen depending on the size of the bee. The most widespread (Mexico to Bolivia) species, *Rhynchanthera grandiflora*, is self-compatible and incapable of agamospermy (Renner, 1984 and 1989b).

In herbarium material, I have found putative hybrids between several species which co-occur in Minas Gerais, São Paulo, and Mato Grosso. Their phylogenetic relationships are mostly unresolved because few leaf and flower characters co-occur consistently.

There are three chromosome counts for *Rhynchanthera grandiflora*: $n = 10$, $n = 11$, and $n = (9)10$ (Solt & Wurdack, 1980). One other species, *Rhynchanthera serrulata* (L. C. Rich.) DC. has $n = 9$ (Solt & Wurdack, 1980) and the Central American *R. paludicola* has $n = 20$ (Davidse, 1970). However, none of these are involved in the above mentioned hybridizations.

MACAIREA

Macairea, consisting of 22 species of long-lived shrubs and subshrubs, is most diverse in Guayana, with 19 of the 22 species found in this phytogeographic province (Fig. 4). Different species variously occur on soils derived from granitic parent material or from sandstone, in regularly flooded savannas or permanently unflooded ones. More than a third of the species are found exclusively at higher elevations on the sandstone tops of the Guayana highlands. Two more widespread lowland species, from which, on morphological grounds, the mountain species seem derived, are sometimes found at mid-elevations but do not reach the summit areas. Some of the montane species are known from different summits relatively close to each other, which attests to the good dispersability of the 0.5–1.4 mm long, anemochorous seeds. Other species have disjunct distributions between Venezuelan Guayana and savannas many hundreds of kilometers further south (Fig. 4). The most impressive example is *M. multinervia* Benthams, which occurs in the savannas of Humaitá, 1300 km south of

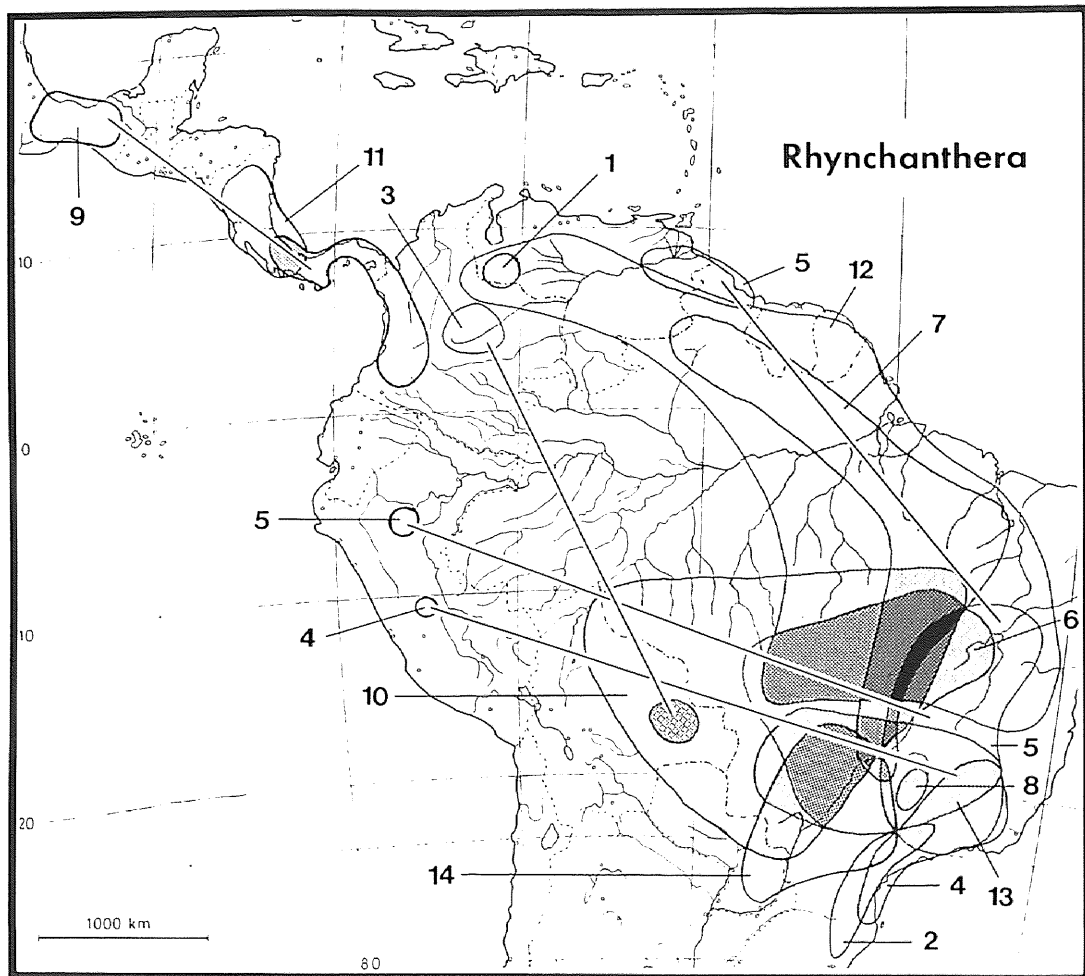


Fig. 3. Distribution of 14 species of *Rhynchanthera*. The range of the most widespread species which extends from southern Mexico through northern South America to the tropic of Capricorn is not shown. 1. *R. apurensis* Wurdack, 2. *R. brachyrhyncha* Chamisso, 3. *R. bracteata* Triana, 4. *R. cordata* DC., 5. *R. dichotoma* (Desr.) DC., 6. *R. gardneri* Naudin, 7. *R. hispida* Naudin, 8. *R. latifolia* Cogniaux, 9. *R. mexicana* DC., 10. *R. novemnervia* DC., 11. *R. paludicola* (Donn. Smith) Gleason, 12. *R. serrulata* (L. C. Richard) DC., 13. *R. ursina* Naudin, 14. *R. verbenoides* Chamisso.

the Gran Sabana in Venezuela from where it was first collected.

In the Gran Sabana, medium-sized euglossine bees have been observed visiting *Macairea parvifolia* Benth. and *M. pachyphylla* Benth. (N. Rodrigues, pers. comm.). However, during many hours of observation spread over two flowering seasons, I have seen no insects visiting any flowers in a large population of *M. theresiae* Cogniaux growing on a white sand savanna near Manaus, Brazil. The anthers contained few pollen grains and the grains did not stain well in lactophenolic

cotton blue. Experiments showed that these plants produced viable seeds apomictically. Agamospermy is known to occur in some 20 neotropical melastome species (Renner, 1984 and 1989b; Sobrevila & Arroyo, 1982) and may be particularly important in understory herbs and savanna species. The striking morphological homogeneity, but also the heterogeneity sometimes observed within *Macairea* populations from single savannas, suggests that they consist of clones. Apomictic seed production would make such species independent of pollinators, while retain-

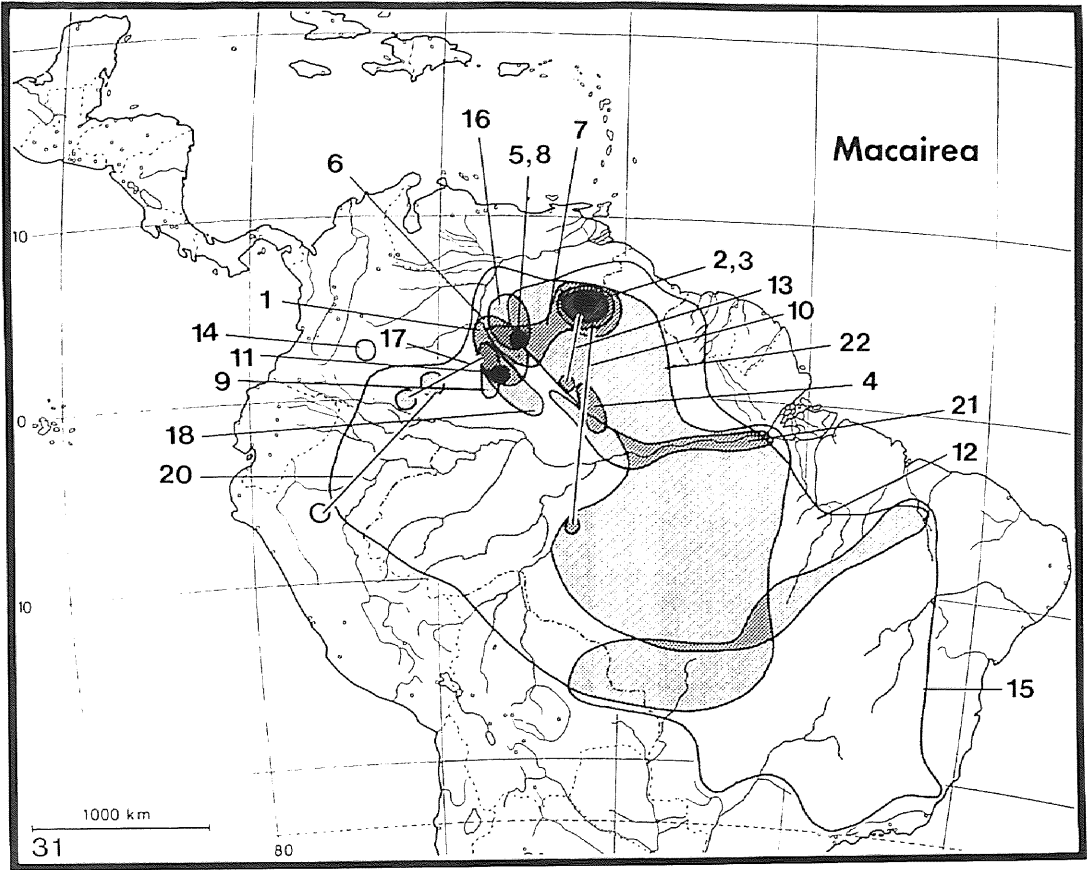


Fig. 4. Distribution of the 22 species of *Macairea*: 1. *M. axilliflora* Wurdack, 2. *M. cardonae* Wurdack, 3. *M. chimantensis* Wurdack, 4. *M. cuieirasii* Renner, 5. *M. duidae* Gleason, 6. *M. lanata* Gleason, 7. *M. lasiophylla* (Benth.) Wurdack, 8. *M. linearis* Gleason, 9. *M. maroana* Wurdack, 10. *M. multinervia* Benth., 11. *M. neblinae* Wurdack, 12. *M. pachyphylla* Benth., 13. *M. parvifolia* Benth., 14. *M. philipsonii* Renner, 15. *M. radula* (Bonpl.) DC., 16. *M. rigida* Benth., 17. *M. rufescens* DC., 18. *M. spruceana* Triana, 19. *M. stylosa* Triana, 20. *M. sulcata* Triana, 21. *M. theresiae* Cogniaux, 22. *M. thyriflora* DC.

ing the advantages of producing seeds, i.e., the potential for dispersal and dormancy. Most notably, it would give them the potential to build-up a new population from a single propagule.

The chromosome number is $n = 12$ in three species of *Macairea* and $n = 11$ in one species (Solt & Wurdack, 1980). In herbarium material, I have found no indication of hybridization within *Macairea*.

SANDEMANIA

Sandemanian hoehnei (Cogniaux) Wurdack (Tibouchineae) is a long-lived shrub endemic to

the sclerophyllous vegetation on Amazonian white sand savannas (Fig. 5) (Renner, 1987). These savannas on extremely nutrient-poor pure sand are hardly ever flooded, except perhaps after particularly heavy rainfalls (see Anderson, 1981; Anderson et al., 1975; Klinge, 1985). Here, shrubs of *Sandemanian* grow surrounded by cushions of lichens, occasional orchids, or bromeliads. Because of the patchy availability of this kind of habitat, *Sandemanian* has a disjunct distribution with some populations apparently separated from each other by several hundred kilometers. Long-range dispersal of the wind-dispersed, 0.8–0.9 mm long seeds is one explanation of how these plants reach their isolated habitats.

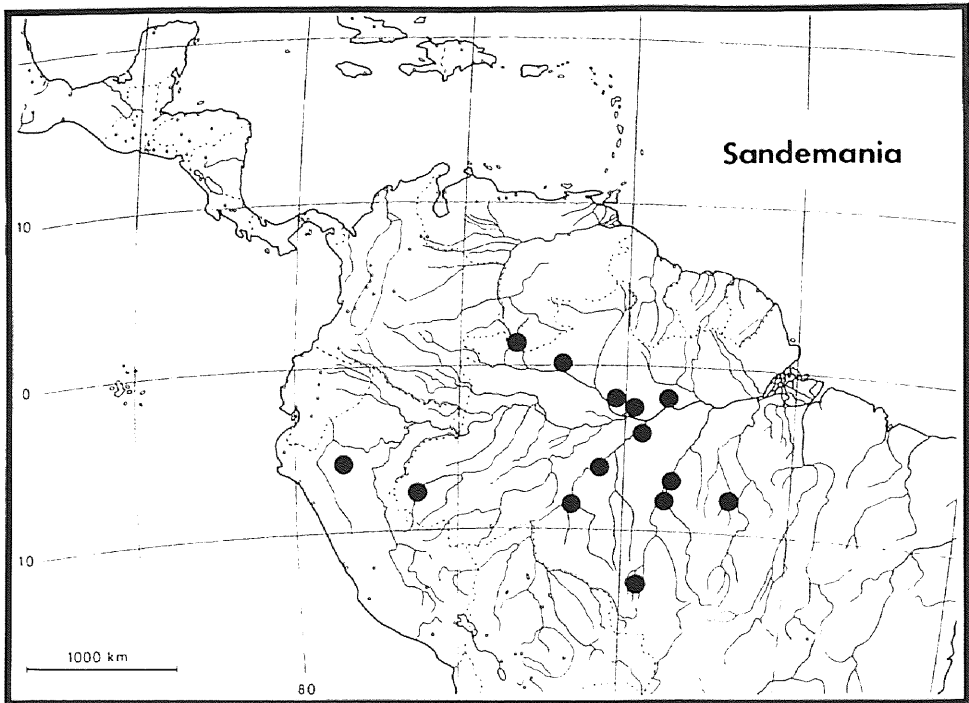


Fig. 5. Distribution of the monotypic *Sandemanian hoehnei*.

An alternative explanation might be some form of casual animal dispersal, not yet noted, that allows for more frequent long range introductions. There is little indication that this type of white sand savanna was once much more widespread.

Sandemanian flowers once a year for about three months and is pollinated by small- to medium-sized, 5–13 mm long, halictid bees. Several plants I experimented on frequently produced agamosperous seeds. In *Sandemanian hoehnei*, gene exchange is expected to be low for three reasons. First, in the restricted patches of habitat, population sizes are small. Secondly, the distances between the populations of different savannas are certainly too large to be covered by the bees pollinating *Sandemanian* or for any but infrequent transport of seeds by wind currents. A third probability is that many members of each population actually form clones. Therefore it is not surprising that, in morphology at least, there is not much variability. The only variation seen is the presence or absence of glandular hairs but this is not correlated with any other characters.

Why does *Sandemanian* not show at least in-

ipient speciation? The explanation may be that the species' habitat, while being stressful in terms of nutrient and water supply, is at the same time stable. Because the white sand savannas, in which *Sandemanian* occurs, are neither subject to fire nor flooding, populations of *Sandemanian* may persist for long periods. Nor are they replaced by plants of later successional stages because they form part of an edaphically determined subclimax. In plants adapted to stressful, stable habitats speciation rate is expected to be low. Extreme specialists are usually out-competed in all but their own habitat and in the absence of drastic changes in their present niche, chances that they will shift into a new one are low.

Conclusions

Any interpretation of the cause of evolution in the five genera discussed here is severely restricted by the almost complete absence of karyological data. Even given information on chromosome numbers, one would still be unable to side-step the difficulty of not knowing to what

extent the genetic processes correlate with the visible results of speciation. Also, one can only account for present numbers of species by using largely theoretical models of how certain (present) factors affect speciation rates. It seems clear that diversification in pollination systems has played a small role in the speciation of these genera. The basic type of Melastomataceae flower, found in all five groups, is probably the result of the early coevolution of melastome ancestors with bees. It restricted the capability of most Melastomataceae to adapt to larger (non-insect) pollinators with different foraging needs.

Both self-compatible species (*Rhynchanthera*, Microlicieae) and self-incompatible ones (*Bellucia*, Miconieae) were found in the genera discussed. In other genera of Melastomataceae (e.g., *Tococa*, Miconieae), the breeding system varies among the congeneric species (Renner, 1984 and 1989b).

Bellucia, *Loreya*, *Rhynchanthera*, *Macairea*, and *Sandemania* belong to three different tribes in the Melastomataceae (*Loreya* and *Bellucia* to the Miconieae, *Rhynchanthera* to the Microlicieae, and *Macairea* and *Sandemania* to the Tibouchineae), defined by their fruit and seed characters. The profound difference in fruit dispersal mechanisms between the capsular- and the berry-fruited groups seems to have influenced the occurrence and frequency of disjunctions. The maps of the generic ranges of *Macairea*, *Rhynchanthera*, and the monotypic *Sandemania* are replete with apparent results of long-distance dispersal (e.g., *M. multinervia*, *R. bracteata*, *R. cordata*, *R. dichotoma*). The distribution maps of *Bellucia* and *Loreya*, the berry-fruited genera, on the other hand, do not show any such disjunctions; and this even though *Loreya* is often rare and poorly collected which might have resulted in "collecting artifacts" (i.e., apparent disjunctions resulting from insufficiently collected areas). Within and among the baccate-fruited groups further adaptive radiation in dispersal strategies has occurred. *Bellucia* consistently has yellow fruits, probably mainly mammal-dispersed; in *Loreya*, yellow- and blue-fruited species are dispersed by different animals.

Considering, for a moment, the species of all five genera, 22 of the 38 wind-dispersed species are local endemics, whereas only four of the 20 animal-dispersed species are. However, the wind-dispersed groups (*Macairea*, *Sandemania*,

Rhynchanthera) all occur in savanna habitats, which are insular in large parts of northern South America, whereas the animal-dispersed genera (*Bellucia* and *Loreya*) occur predominantly in lowland forests which are more continuous. The proportion of narrow endemics is low in *Bellucia* and *Rhynchanthera*, intermediate in *Loreya*, and very high in *Macairea* (where it reaches 86%).

It has been said that any larger genus will consist of a high proportion of endemic species and a smaller number of more widely distributed species (Valentine, 1972). A possible explanation, why small genera, such as the ones dealt with here, differ greatly in level of endemism and number of species is that they are the result of different modes of evolution. For example, the extreme specialist *Sandemania hoehnei*, occurring in a long-undisturbed habitat such as the white sand savannas of Amazonian lowlands, appears to have evolved primarily by what Simpson (1953) termed "phyletic" (that is, lineage) evolution. In *Bellucia*, the complete bud cover and papillose leaf cuticle probably originated in subandean populations as adaptations reducing transpiration during Pleistocene dry-cool times. These initial innovations could have been followed by the evolution, in certain lineages, of traits like the calyptrate calyx and axillary position of the flowers. Subsequently, *Bellucia* spread in the lowland forests and with its shrubby species entered savannas. At present, co-occurring species of *Bellucia* hybridize.

In *Loreya*, diversification seems to have involved mostly the size and color of the fruits and edaphic adaptation. To the extent that the drought-sensitive *Loreya* species failed to adapt to more open, windier, and less humid habitats, many may have died out during drier periods in the past, which would explain why the known species are morphologically so isolated from each other.

Finally, in *Macairea* and *Rhynchanthera*, the concentration of species in Guayana and south-central Brazil respectively, is the result of the relative diversity in topographical and microclimatic conditions encountered in these areas. Perhaps in these two groups, the mode of evolution consisted of a pre-Quaternary diversification in Guayana and the Brazilian shield, followed by more recent splitting. The high incidence of endemism in *Macairea* is correlated with the occurrence of many of the species on the summits

of Guayana table top mountains. In *Rhynchanthera*, on the other hand, there is more opportunity for hybridization, because more species are sympatric in the vast savanna areas of the Brazilian planalto.

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