

## **ENDEMISM AND NON-ENDEMISM IN THE FLORA OF SOUTH-WEST MADAGASCAR**

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**ABSTRACT.-** The flora of the South-Western Domain of Madagascar is known for its diversity of bizarre xerophytes and high levels of species endemism, both characteristics being due, at least in part, to the harshness of the climate. However, new discoveries and taxonomic revisionary work over the past 60 years have caused much of the published information about species diversity and endemism in Madagascar to become out-of-date. While information on the endemic components of the flora and their distribution may be of considerable value to conservation and intrinsic fascination to biologists, the non-endemic components provide an important insight into the origins and evolution of the flora. This paper reviews species endemism and diversity in the domain, and examines in detail the non-endemic component of the flora, in an attempt to provide a better understanding of the origins and relationships of the flora.

**KEY-WORDS.-** Seed dispersal, Africa, Xerophytes, Biogeography, Deciduous thicket

**RESUME.-** La flore du domaine sud-ouest de Madagascar est connue pour sa diversité de xérophytes bizarres et par son taux élevé d'espèces endémiques, ces deux caractéristiques étant la conséquence, au moins en partie, des conditions extrêmes du climat. Cependant, de nouvelles découvertes associées aux travaux de révision réalisés dans les derniers 60 ans, ont démontré que la plupart des informations publiées sur la diversité spécifique et l'endémisme à Madagascar étaient périmées. Si les informations sur les composants endémiques de la flore et leur distribution peuvent être d'une valeur considérable pour la conservation et pour la fascination intrinsèque des biologistes, les composants non-endémiques apportent un important aperçu sur les origines et l'évolution de la flore. Dans la présente note, sont révisés l'endémisme spécifique et la diversité dans le domaine, et examinés en détail les composants non-endémiques de la flore, dans le but d'apporter une meilleure compréhension sur les origines et les relations de la flore.

**MOTS-CLES.-** Dispersion des semis, Africa, Xérophytes, Biogéographie, Fourré caduque

### **INTRODUCTION**

The flora of the South-Western Domain of Madagascar is known for the diversity of bizarre xerophytes that characterise the deciduous thicket of the area. Any visitor to the area cannot fail to have been impressed by the plants: the famous cactus-like Didiereaceae, the only family endemic to the south-west of Madagascar; the other succulents, many of which flower dramatically during the driest months while most of the vegetation is dormant; the swollen trunks of the Baobabs (*Adansonia* spp.) and the other « bottle-trees » such as species of *Delonix*; or the sudden flush of flowering that takes

place locally after rains, that almost overnight converts bushes that appeared dead into a display of flowers and young leaves.

South-west Madagascar is also well-known for its high number of endemic species, which include taxa that are relatively widespread within the area as well as local endemics known from only a few small populations. Species endemism in south-west Madagascar has often been misquoted in the literature at around 90%. This figure is based on that of PERRIER DE LA BATHIE (1936), but it actually represents the number of species found in the south-west that are endemic to Madagascar, not the number of species strictly endemic to the area. As such it is impossible to relate the level of endemism in the south-west, or indeed in any floristic domain of Madagascar for which only this type of data is available, to levels of endemism of other floras elsewhere in the world.

Since PERRIER DE LA BATHIE'S work the level of endemism of the known flora of the region have been influenced by three factors. Firstly, many new species have been described, secondly many species have been lost in synonymy under more widespread species and thirdly several species have been found to occur in south-west Madagascar that also occur elsewhere. HUMBERT (1959) accepted PERRIER DE LA BATHIE'S estimation of levels of endemism, however now, about 60 years later, it is timely to review this in the light of recent discoveries and taxonomic changes.

It is clear that endemism in south-west Madagascar is not equally distributed between different vegetation types. The low level of species diversity and endemism in the wooded grasslands (savannah ecosystems as they are often called) has been thoroughly documented by MORAT (1973), and information for the mangrove vegetation is readily available (KOECHLIN *et al.*, 1974; RABESANDRATANA, 1984). However comparable data is not available for the deciduous thicket which makes up the bulk of the primary vegetation of the region, nor for the riverine gallery forests.

The basic reasons why Madagascar as a whole is rich in endemic species are well documented (see other contributions in this volume). Details of the tectonic history and palaeoclimate forming the basis of current our understanding of the biogeography of Madagascar, and are believed to be the main causes of the high endemism in Madagascar. However the aridity of the south-west serves to biologically isolate the area, at least partially, from the rest of the island. Despite the powerful forces that have caused and maintained a high level of species endemism in the area, the fact remains that a percentage of its species are not endemic and are shared with other regions of Madagascar and elsewhere. The question « why do certain plant species occur in south-west Madagascar and elsewhere? » has to be asked.

There are 4 possible answers to this question.

1. Species may have been present in Gondwanaland before the separation of the continents - however given our understanding of geological history this is unlikely, at least in the case of flowering plants.

2. Species may have been dispersed gradually across relatively short distances via continuous land bridges, or « island hopped » across « stepping stones ».

3. Species may have been dispersed long distances by chance dispersal by migratory flying animals (primarily birds), or by wind or ocean currents.

4. By human introductions, intentional or accidental.

In each of cases 2 to 4 above, the mechanism of seed (or spore) dispersal of an individual species is obviously of considerable importance in understanding how it may have been dispersed to its present distribution range. Seed dispersal mechanisms are therefore an important aspect of the study of the causes of plant species endemism, although this is an area of study that has been explored very little, at least in relation to the flora of south-west Madagascar.

The present study has the following aims.

1. To review the actual level of plant species endemism in south-west Madagascar.
2. To determine the relative endemism in the major vegetation types in south-west Madagascar.
3. To investigate the relationship of seed dispersal mechanisms to patterns of endemism.

The delimitation of the study area follows that of earlier authors (VIGUIER, 1914; PERRIER DE LA BATHIE, 1921, 1936; HUMBERT, 1955) (see Fig. 1).

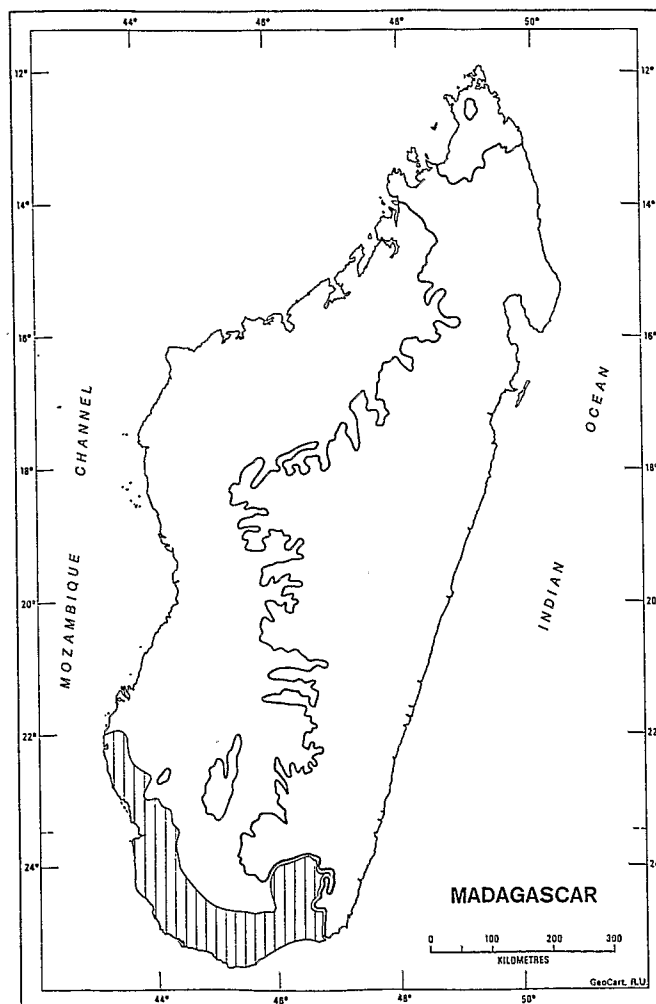


Fig. 1. Map of Madagascar showing the south-western region (shaded).

## METHODS

While it would be desirable to undertake an analysis of all species in the region, this is impractical for several reasons. Firstly because the taxonomy of many groups is inadequate. Secondly because accurate up-to-date information on the distribution of many species is not available in the literature and would be extremely time consuming to compile from herbarium records. Therefore only a sample of the flora of south-west Madagascar has been included in the study. Thus certain Rubiaceae, Fabaceae, Euphorbiaceae and the genus *Grewia*, among others, have been excluded, and the study has been limited to tree and shrub species only. The sample consists of 448 species that are considered to be adequately known and for which reliable information is readily available. Data has been obtained from flora accounts and other literature, from the TROPICOS database, and from personal collection records, including detailed surveys in riverine forest in the Special Reserve of Beza-Mahafaly and in Berenty Private Nature Reserve. As such the sample represents over 50% of the entire tree and shrub flora of the region.

Each species was classified according to the following broad biogeographic categories.

1. Endemic to south-west Madagascar. A rather broad circumscription was taken, species that have their main distribution range within the south-west, but which extend along the coast to Morondava or Fort Dauphin, or which occur on rocky outcrops in the southern interior such as around Ihosy have included.

2. Endemic to Madagascar (including the Comoro islands), but not confined to the south-west. These have been subdivided into:

i) those that are widespread throughout Madagascar, occurring in both the Eastern and Western Regions;

ii) those that also occur elsewhere in the Western Region;

iii) those that also occur in the Eastern Region;

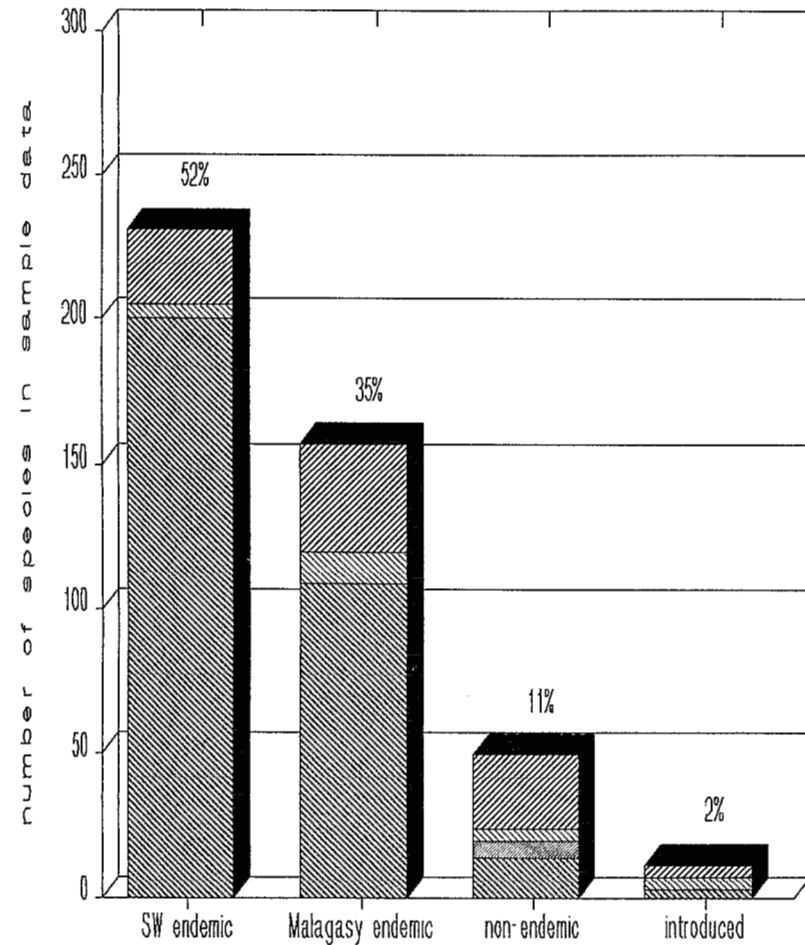
3. Not endemic to Madagascar.

Seed dispersal mechanisms for each species has been recorded based on whether the plant possesses fleshy fruits known to be or likely to be dispersed by migratory birds, and whether the plant is known to be dispersed by ocean currents. Species with neither adaptation are referred to as « short-distance dispersers ».

## RESULTS

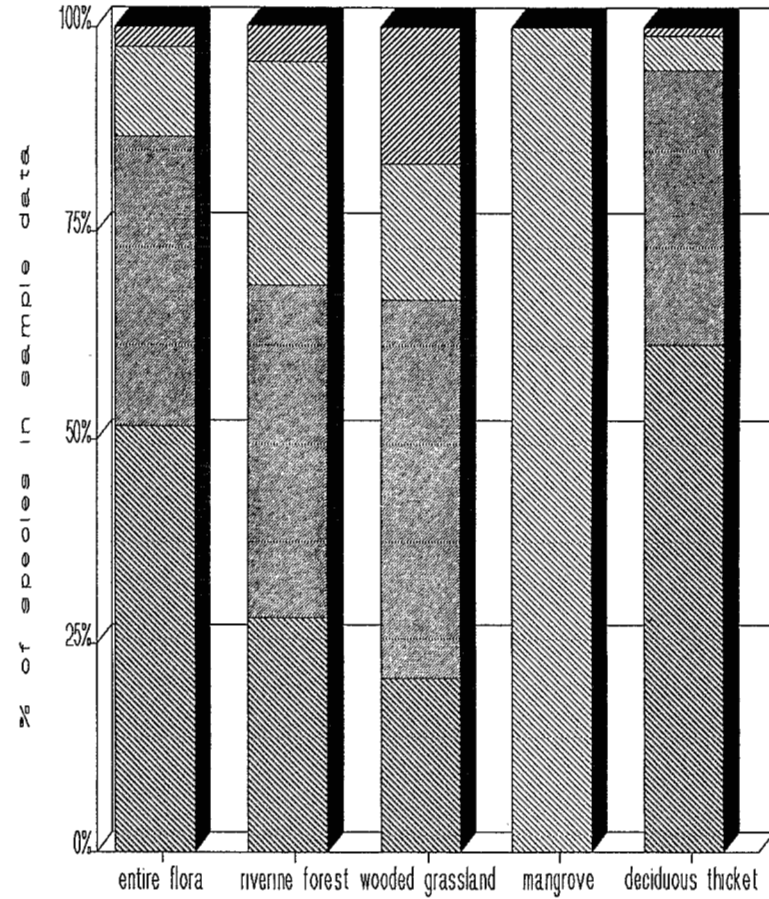
### 1. OVERALL ENDEMISM AND RELATIVE DIVERSITY

Of the sample of 448 species, 231 (51.56%) are endemic to south-west Madagascar, and a further 157 (35.04%) are endemic to Madagascar. Eliminating the 11 species that are known or believed to have been introduced by humans, we obtain a



2

riverine forest    wooded grassland    mangrove    deciduous thicket



3

introduced    non-endemic    Malagasy endemic    SW endemic

Fig. 2. Breakdown of species in each biogeographic category according to vegetation type.  
 Fig. 3. Percentage breakdown of species in each vegetation type according to biogeographic category.

figure of 52.86% for species endemism, and an additional 35.93% other Malagasy endemics not restricted to the south-west. Many more species occur in deciduous thicket (72.77%) than other vegetation types. The non-endemic and introduced components of the flora, comprise of 49 (10.94%) and 11 (2.46%) species respectively. More than half (51.02%) of the non-endemic, but (presumed) native species occur in riverine forest. A detailed breakdown of numbers of species in each biogeographic class according to vegetation type is given in figure 2.

## 2. ENDEMISM IN EACH VEGETATION TYPE

The deciduous thicket has by far the largest proportion of endemic species (61.35%). The riverine forest and wooded grassland floras consist of only 28.26% and 20.83% endemic species respectively. The wooded grassland contains the highest percentage of introduced species, although at 16.67% this is surprisingly low. The mangrove vegetation comprises entirely of non-endemic species. A detailed breakdown of the percentage of species in each vegetation type according to biogeographic class is given in figure 3.

On its own, the flora of the deciduous thicket consists of 61.35% endemic species and 33.44% other Malagasy endemics, or put another way a non-Malagasy endemic component of only 5.21% of its species.

## 3. SPECIES SHARED WITH OTHER AREAS OF MADAGASCAR

Of the 157 species that are shared between the south-west and other parts of Madagascar, 74.50% are shared with the west (25.36% of the entire flora), 8.05% with the east, and 17.45% occur in both. The distribution of these among the different vegetation types is similar to that of the entire flora.

## 4. DISTRIBUTION OF SEED DISPERSAL MECHANISMS

Of the entire sample, 171 (38.17%) have fleshy seeds, known or likely to be bird dispersed, 8 (1.79%) are known to be transported long-distances by ocean currents and the remaining 269 (60.04%) of the species are not adapted for dispersal either by migratory birds or ocean currents. This proportion is not equal across the different biogeographic classes or the different vegetation types. Only 70 (30.30%) of the endemic species are bird-dispersed, while considerably higher proportions of bird-dispersed species are found among the other biogeographic classes. This is particularly noticeable in the case of the non-endemic component of the flora, which includes 67.34% bird-dispersed species and 16.33% ocean-dispersed. A detailed breakdown of the numbers of species in each biogeographic class according to dispersal mechanism is given in figure 4.

Of particular interest are the eight species which are not Malagasy endemics but which have no obvious adaptations for bird or ocean current dispersal. Two of these are weedy species, which may have been introduced by humans although there is no direct evidence for this. One of the species, *Pisonia aculeata*, is of little consequence, being

relatively uncommon and confined to ruderal habitats, however the other, *Hyphaene coriacea*, is an important component of wooded grasslands. The distribution patterns of the remaining six species are more enigmatic, these are given in Table I, and are discussed in greater detail below.

## 5. RELATION OF DISPERSAL MECHANISMS TO VEGETATION TYPES

Riverine forest has a higher proportion of bird dispersed species, with 47.83%, rather than less than 40% in all the other categories. Details of the ocean-dispersed species are given in Table II, they include all six mangrove species, and two species of disturbed habitats which occur primarily in south-west Madagascar on riverine forest margins. A detailed breakdown of percentages of species in each vegetation type according to dispersal mechanisms is given in figure 5.

## 6. SYNTHESIS OF DISPERSAL MECHANISM, VEGETATION TYPE AND BIOGEOGRAPHIC CLASS

In riverine forest more bird-dispersed taxa are non-Malagasy endemics (36.36%) than short-distance dispersers (15.22%). The difference is accounted for by a corresponding increase in south-west endemics (18.18% versus 39.13%). Wooded grassland has a very low level of non-Malagasy endemic short-distance dispersers (6.25%) and many bird-dispersers (37.50%), none of its bird-dispersers are south-west endemics. The deciduous thicket completely lacks non-Malagasy short-distance dispersers, its non-Malagasy component consists entirely of bird dispersers.

## DISCUSSION

The results confirm the south-west of Madagascar as an area with extremely high species endemism. Endemism is markedly higher in the deciduous thicket than the other vegetation types in the south-west. Endemism is low in the wooded grassland supporting the hypothesis that this is not a primary vegetation type in the region. The non-endemic components of the flora, consist predominantly of species that are at least endemic to Madagascar, especially, although not uniquely, the rest of the western region, with which it shares 25/23% of its species (excluding introduced species). The south-west does, however, contain some eastern elements.

The present analysis suggests that the flora of the south-west consists of an assemblage of species that is well differentiated from that of other parts of Madagascar. As such, and in contrast to the opinion of most earlier authors, the area may deserve phytochorological recognition at a higher level than as a domain within a widely circumscribed western region. With an estimated level of endemism of over 50%, and a total endemic flora exceeding 1000 species, south-west Madagascar qualifies as a regional centre of endemism according to WHITE's (1983) criteria

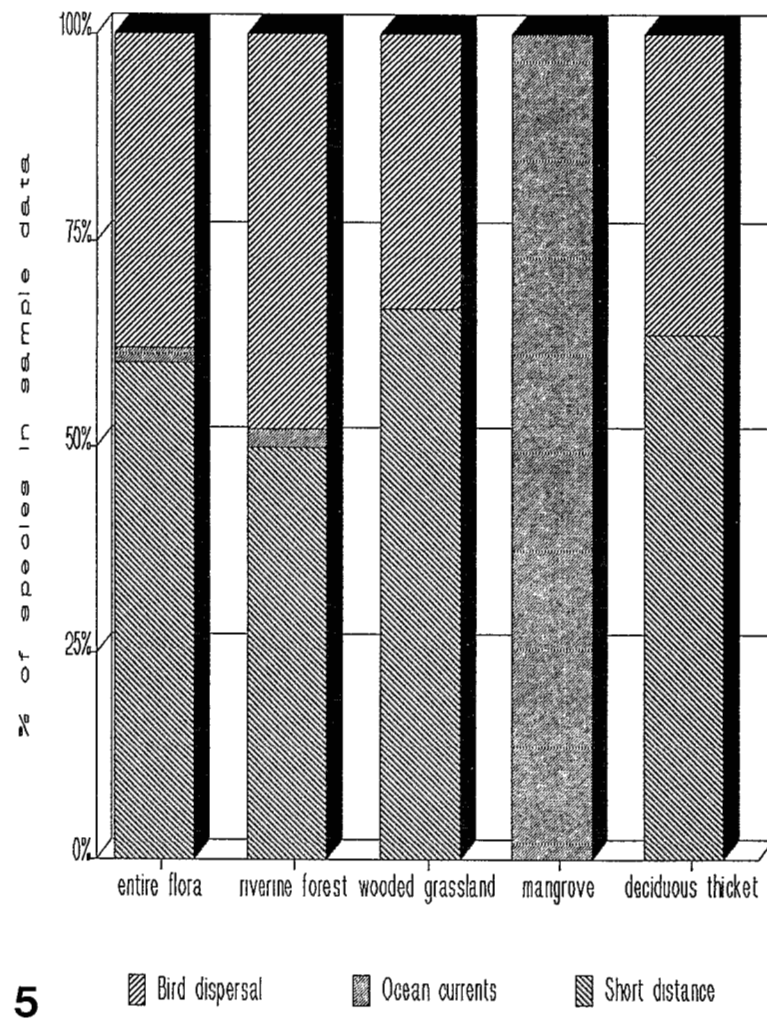
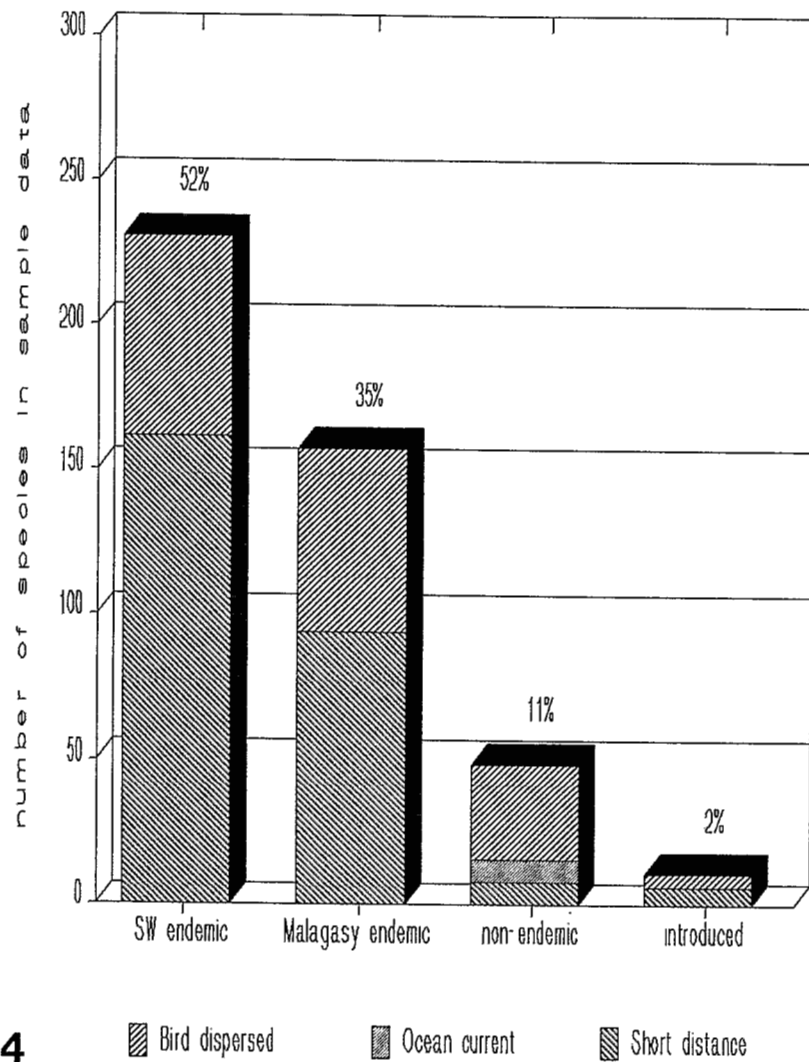


Fig. 4. Breakdown of species in each biogeographic category according to dispersal type.

Fig. 5. Percentage breakdown of species in each vegetation type according to dispersal type.



In general most bird-dispersed species belong to genera which are relatively poorly represented in both south-west Madagascar and the island as a whole, this applies to both endemic and non-endemic genera. Many of these genera are better represented outside Madagascar, and many of the species have their closest relatives in Africa, for example *Elaeodendron humbertii*. It seems likely that these represent taxa which have been introduced comparatively recently, and which have diversified relatively little or not at all. There are, however, some important exceptions, e.g. *Clerodendrum*.

On the other hand, the short-distance dispersed species mostly belong to genera that are well diversified in Madagascar, often throughout the island, and which are more diversified in Madagascar than elsewhere. For example, very diverse large genera such as *Croton* and *Dombeya*, and smaller genera such as *Adansonia* and *Delonix*. The short-distance dispersers that belong to small genera, are frequently taxonomically isolated, such as *Lemuropisum edule*, *Androya decaryi*, although their nearest relatives may also occur in Madagascar. It is suggested that these taxa are in general a more ancient component of the Malagasy flora which have been isolated from other land masses for a much longer period in comparison with the bird or ocean dispersed taxa.

The occurrence of six non-Malagasy endemic short-distance dispersers in south-west Madagascar within the sample of species studied deserves further comment. One of these *Gyrocarpus americanus* is widespread in both new and old world dry tropics including parts of eastern and southern Africa in apparently natural habitats. In Madagascar it is a common constituent of deciduous thicket. It possesses remarkable winged fruits which may be capable of being dispersed long-distances by wind currents, and this may account for its dispersal to Madagascar.

The remaining five species are all common constituents of riverine forest to which they are essentially confined in south-west Madagascar. The taxonomic status of one of these, *Euphorbia tirucalli*, is uncertain, the Malagasy plants have been regarded as distinct (*Euphorbia laro*) from those occurring elsewhere. *Tamarindus indica* is an extremely widespread tropical species, which has a modern distribution that has undoubtedly been influenced by humans, due to its diverse uses and traditional signification in many cultures. In contrast the other three species are African species, *Acacia royumae* is confined to certain river valleys in coastal areas of eastern Africa, *Bivinia jalberti* also has a restricted distribution in eastern and southern Africa, while *Breonadia salicina* is a more widespread, extending to west Africa. All of these species are somewhat taxonomically isolated in Madagascar. It is suggested that they may have been dispersed to Madagascar from Africa by rafting of fallen trees bearing fruits. If this means of dispersal is a viable means of dispersal and colonisation, it is not surprising that species that have been able to exploit it are riverine species. Not only would they be more likely to fall into rivers which would transport them to the sea, but they would also be more likely to be deposited in a suitable habitat (*i.e.* the banks of an estuary) than non-riverine species.

Migration along land-bridges or short-distance island hopping may have been an important factor in the initial colonisation of Madagascar, and the dispersal of plant species from Madagascar. However there is no evidence from the present study that this is an explanation of the current distribution of individual plant species, since the non-endemic components of the flora can be explained more satisfactorily by other means.

A summary of the results and conclusions presented in this paper are given in Table III. The study takes into account only a sample of the trees and shrubs of the south-west of Madagascar. It would be interesting to extend the study to herbs, sub-shrubs and

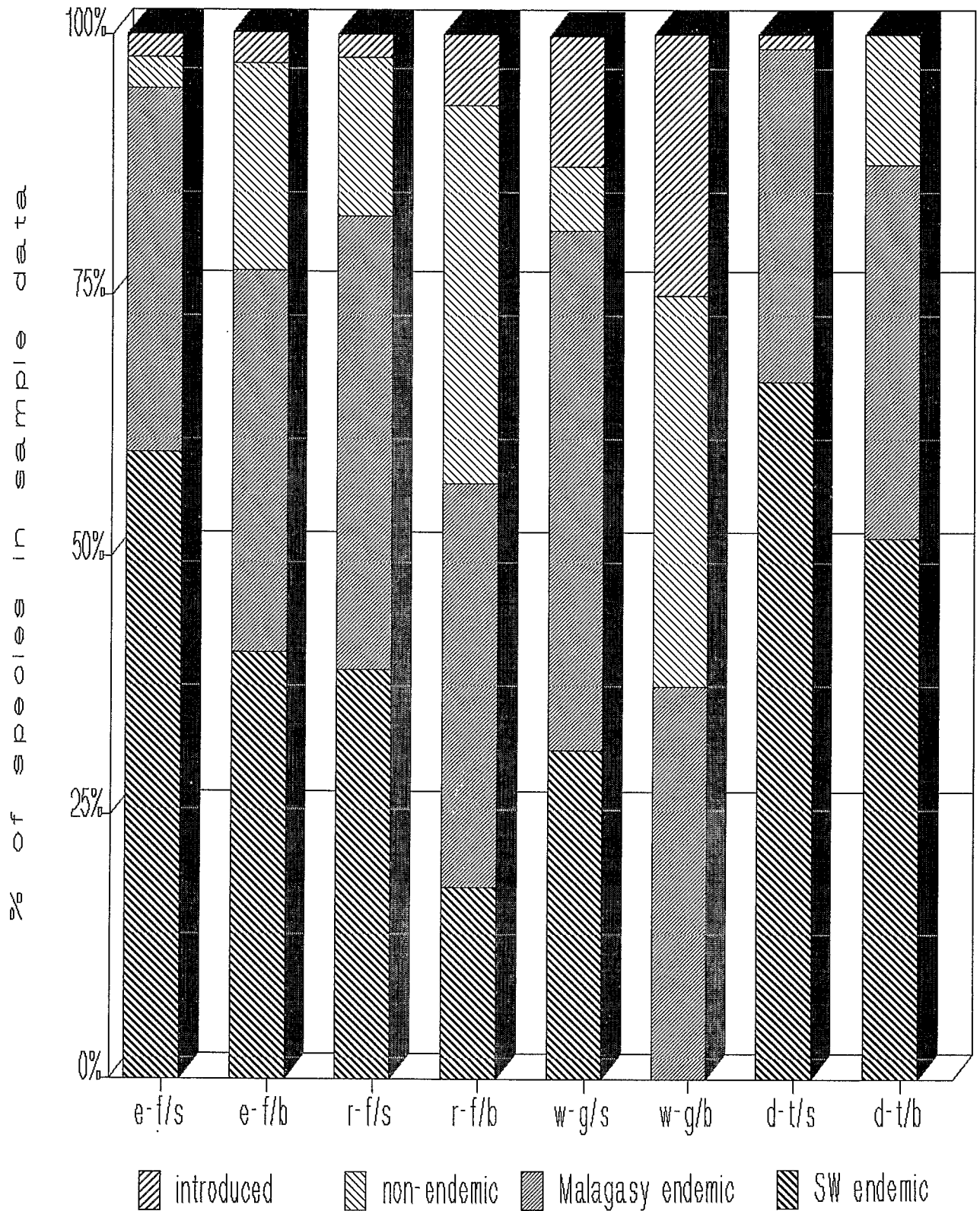


Fig. 6. Percentage breakdown of species in each vegetation type (excluding mangrove) with dispersal type according to biogeographic category (e-f = entire flora; r-f = riverine forest; w-g = wooded grassland; d-t = deciduous thicket; /s = short-distance dispersal; /b = bird dispersal).

lianas, however many of these are very poorly known taxonomically. Among these other life-forms bird dispersal is rare, and the possibility of other means of long-distance dispersal even more limited, except for human dispersed weeds. Among these plants one might therefore expect to find an even higher level of endemism than among the trees and shrubs.

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**Table I.** Generalised distribution and usual habitats of species which are not Malagasy endemics but which occur in SW Madagascar and which are not weedy.

\*Malagasy plants may not be conspecific.

Species	Distribution outside Madagascar	Usual habitat
<i>Acacia royumae</i> Oliv.	Local in E Africa.	Riverine.
<i>Bivinia jalberti</i> Tul.	Local in SE Africa.	Riverine.
<i>Breonadia salicina</i> (Vahl)	Widespread in SE & E Africa.	Riverine.
<i>Euphorbia tirucalli</i> L.*	Widespread Old-world.	Riverine.
<i>Gyrocarpus americanus</i> Jacq.	Widely dispersed Old/New world dry tropics.	Not riverine
<i>Tamarindus indica</i> L.	Widespread Old/New-world.	Essentially riverine.

**Table II.** Habitats of non-endemic species dispersed long distances by ocean currents.

Species	Habitat
<i>Avicennia marina</i> (Forsk.) Vierh.	Mangrove
<i>Bruguiera gymnorhiza</i> (L.) Lam.	Mangrove
<i>Caesalpinia bonduc</i> (L.) Roxb.	Disturbed, especially river margins
<i>Ceriops tagal</i> (Perrottet) C. Robinson	Mangrove
<i>Entada africana</i> Guillaumet	Disturbed
<i>Lumnitzera racemosa</i> Willd.	Mangrove
<i>Rhizophora mucronata</i> Lam.	Mangrove
<i>Sonneratia alba</i> Sm.	Mangrove

**Table III.** Summary of main results and conclusions.**The flora of the SW of Madagascar comprises:**

1.	endemic species (231 species)	52%
2.	Malagasy endemics, not confined to SW (157 species)	35%
3.	non-endemics dispersed by ocean currents (8 species)	2%
4.	non-endemics dispersed by wind (1 species: <i>Gyrocarpus americanus</i> )	<1%
5.	non-endemics dispersed by birds (33 species)	7%
6.	species with no apparent means of long-distance dispersal, occurring in riverine forest (5 species)	1%
7.	species introduced intentionally or accidentally by humans (11 species)	2%