PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A Comparison of the Efficacy of Higher Taxa and Species Numbers in the Assessment of Biodiversity in the Neotropics

Ghillean T. Prance

Phil. Trans. R. Soc. Lond. B 1994 **345**, 89-99
doi: 10.1098/rstb.1994.0090

A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics

GHILLEAN T. PRANCE

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.

CONTENTS

SUMMARY

The neotropical region as a whole is much more species diverse than the palaeotropics but no more diverse at the family and only slightly at the generic level. Only 6.4% of neotropical species belong to plant families that are confined to the region and there is a greater generic diversity in Africa than in the neotropics indicating that species are much better indicators of total diversity. The striking difference in species make up between the northern Andean region and Amazonia is important to recognize in conservation planning. In the northern Andean region, herbs and shrubs with Andean-centred distributions predominate whereas in Amazonia, trees and shrubs with Amazonian-centred distributions predominate. The analysis of species distributions show both centres of endemism and centres of diversity which are not apparent when only higher taxa are considered. The local demography of species varies considerably within the lowland rainforest regions and this is discussed using data from quantitative inventories. It is concluded that accurate assessment of the taxon component of biodiversity of the neotropics must be based at the species level rather than at that of higher taxa, and that species data are a valuable tool for conservation planning.

1. INTRODUCTION

This contribution deals with the taxon, especially the species, component of biodiversity rather than habitat and genetic diversity which are equally important. The neotropical region is a good one to choose to discuss the quantification of organismal biodiversity from the taxon point of view because for many groups of organisms it is the most species-rich area in the world. This is certainly true for higher plants where it is estimated that there are about 90 000 species (Raven 1976; Prance; 1978*a*; Gentry 1982*a*). This compares with between 40 000 and 45 000 for Africa (Beentje *et al.* 1994) and between 42 000 and 50 000 for the area covered by Flora Malesiana (Johns 1992). The latter figure is considerably more than the 25 000–30 000 cited by Jacobs (1974). On the other hand, as a result of its greater diversity, the neotropical region is more poorly known floristically than any other part of the tropics. This introduces many uncertainties into calculations estimating biodiversity based on species numbers. New species are still being discovered daily in the neotropics from many different regions and in the different vegetation types. There is still a new species in each batch of 100 collections of Chrysobalanaceae sent to me for identification and there is a new species per every hundred numbers of plants collected in Amazonia (Prance & Campbell 1988), and this continues (for example, Prance 1992). It would, therefore, be useful if higher taxa indicated the same pattens of diversity as species to make more rapid assessments.

Although the species diversity of the neotropics is much greater than in the other tropical areas the family diversity is no more (table 1), and the generic diversity only slightly higher, and so it is not surprising that most discussions of neotropical biodiversity have been confined to the species level.

Phil. Trans. R. Soc. Lond. B (1994) **345,** 89–99
Printed in Great Britain

Table 1. *Comparison of plant taxic diversity of three major tropical regions*

	Africa	Malesia	neotropics
families	271	310	292
genera	3750	3250	4200
species	40 000–45 000	42 000	90 000

Table 2. *Predominantly or exclusively neotropical families with their habitat preference*

(Data from Prance 1978*b*; Gentry 1982.)

tropical forest families	
Bromeliaceae	46 genera/2128 species (one African); largely epiphytes
Caricaceae	3/29 (plus two African sp.)
Caryocaraceae	2/25
Cyclanthaceae	11/178
Dialypetalanthaceae	1/1
Duckeodendraceae	1/1
Humiriaceae	8/46 (plus one African sp.)
Lacistemaceae	2/14
Quiinaceae	4/53
Rapateaceae	15/79 (plus one African sp.)
Rhabdodendraceae	1/3
Vochysiaceae	7/182 (plus 2 African sp.)
Trigoniaceae	1/24 (plus one Madagascar and one Asian sp.)
Lecythidaceae sensu strictu (subfamily Lecythidoideae)	9/210
families of dry and/or Andean South America (a few reach N. America)	
Brunelliaceae	1/51
Calyceraceae	4/46
Columelliaceae	1/4
Gomortegaceae	1/1
Malesherbiaceae	1/27
Myzodendraceae	1/11
Nolanaceae	1/18
Tovariaceae	1/2
Tropaeolaceae	2/92
families of dry parts of tropical North America	
Crossosomataceae	1/4
Fouqueriaceae	2/8
Garryaceae	1/18
Lennoaceae	3/8
Theophrastaceae	5/110 (also in S. America)
families of dry tropics of North and South America	
Cactaceae	62/2000
Julianaceae	2/5
Koeberliniaceae	1/1
Krameriaceae	1/15
Loasaceae	12/266 (plus one African sp.)
Martyniaceae	3/13
families of Guayana highland	
Saccifoliaceae	1/1
Tepuianthaceae	1/6
Thurniaceae	1/3
Sarraceniaceae	3/17 (one genus of 6 sp. in Guayana, others N. American)
miscellaneous families[a]	
Cannaceae	1/55
Cyrillaceae	3/13
Mayacaceae	1/9 (one in Africa); aquatic
total: 5777 species	

[a] Note this does not include a few groups that have been split off as families by a few authors, but not generally accepted (e.g. Euphroniaceae and Mendonciaceae).

2. NEOTROPICAL PLANT FAMILIES

Of the 292 neotropical plant families (Maas & Westra 1993) approximately 40 are exclusively or almost exclusively neotropical (see table 2), and surprisingly they account for only 5777 of the 90 000 species (i.e. only 6.4%) of the total species diversity. Over 4000 of the species are in just two families that have shown explosive radiation into special niches, the Bromeliaceae as epiphytes and the Cactaceae as specialists in arid regions. Table 2 also shows that most of these families are habitat specialists and that their species occur predominantly in one particular habitat. This is in marked contrast to many of the pantropical families that contain the other 93.6% of the species. These data would indicate that the family level is not the best way to access the total biodiversity of the neotropics because of two factors: (i) there are fewer families in the neotropics than in Malesia; and (ii) the small number of species accounted for by the endemic families. However, family diversity is important to include in the assessment of evolutionary diversity of the region. The taxic diversity indicated by the divergence into a separate neotropical family is vital information for conservation planning. Some of the neotropical families contain only one or a few rare species. In evolutionary terms these are of particular interest and every effort should be made to conserve these groups which are either more recent off-shoots of the evolutionary process or important relic groups. As plant family relationships are more confidently represented in modern phylogenetic systems, especially with data from molecular systematics (e.g. Chase *et al.* 1993), it will be easier to evaluate the importance of each family endemic to the neotropics.

3. GENERIC DIVERSITY

In many of the large pantropical families that occur in the neotropics, the generic diversity is no larger than in other continents, as for example in the Chrysobalanaceae (table 3) which is typical of many other groups. In Chrysobalanaceae there is one more genus in Africa than in the neotropics. However, as would be expected with double the number of species in the neotropics, when all flowering plant families are considered there are about 500 more genera in the neotropics than in Africa.

Although some neotropical genera are endemic to a certain region or habitat, many extend over a wide range and therefore, like families, the genera are most important in biodiversity assessment for their taxic diversity. In many large genera the reason for this species diversity is that they have adapted into many different available habitats. Table 4 shows how the species of *Caryocar* are divided between different habitats. There are more species in lowland rainforest, but there are also separate species in cerrado, caatinga, Amazonian white sand, mountain slopes

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 3. *Continental distribution of genera of Chrysobalanaceae, endemic genera in italics*

neotropics	Africa	Malesia
Acioa	*Bafodeya*	*Atuna*
Chrysobalanus	Chrysobalanus	*Hunga* (+New Caledonia)
Couepia	*Dactyladenia*	*Kostermanthus*
Exellodendron	Hirtella	Licania
Hirtella	Licania	Maranthes
Licania	*Magnistipula*	*Parastemon*
Maranthes	Maranthes	Parinari
Parinari	*Neocarya*	
	Parinari	
total 8	9	7

Table 4. *The distribution of species of* Caryocar *in different habitats*

habitat	range
terra firme forest	
Caryocar glabrum	widespread Amazonian
C. nuciferum	Guianas, Panama, Chocó
C. pallidum	Central Amazonian
C. villosum	widespread Amazonia
C. costaricensis	Central America
C. edule	Atlantic coastal forest
C. amygdaliferum	Colombia: Magdalena river valley
C. dentatum	southwest Amazonia
C. amygdaliforme	Peru
savanna (Cerrado)	
C. brasiliensis	
C. cuneatum	
submontane forest	
C. montanum	
cattinga nordeste	
C. coriaceum	
upper Amazon white sand caatinga	
C. gracile	
Várzea and Igapó	
C. microcarpum	

and flood plain forest. Diversification has taken place by moving into a range of different habitats. The species of *Caryocar* in terra firme rain forest are rather separated geographically (table 4).

There is a reasonably accurate recent catalogue of the flora of Peru (Brako & Zarucchi 1993). This list of flowering plants and gymnosperms contains 17143 species in 224 families and 2458 genera. Only 51 of these genera are endemic to Peru (2.07%) whereas 5354 species (31.23%) are endemic which again indicates the value of species as indicators of biodiversity. The total number of genera in the neotropics has been estimated as 4200 (Gentry 1982*a*). Species are unevenly divided among these genera, a few genera having a large number of species (e.g. *Psychotria* in Rubiaceae) and many genera containing few species.

4. SPECIES DIVERSITY

(*a*) *The two major centres of neotropical species*

The enormous species diversity of the neotropics has already been mentioned and is what makes the region so important in terms of conservation. Gentry (1987) pointed out that most neotropical species fall into one of two categories: (i) species that are predominantly canopy trees and lianes and have an Amazonian centre of diversity; and (ii) species that are predominantly epiphytes, shrubs or palmetto type herbs that have largely extra-Amazonian centres of diversity. The second category is a cause of the enormous species diversity of certain groups in the Andean region and southern Central America, which accounts, to a large extent, for the extraordinary species diversity of Costa Rica, Panama, Colombia and Ecuador in comparison to their area (see table 5). This analysis shows where a large number of species could be conserved in a relatively small area.

The high species diversity of epiphytes and understorey shrubs, herbs and palmettos of the northern Andes accounts for a large amount of the larger number of species in the neotropics compared with other regions. Conservation action in the neotropics has largely focused on Amazonia yet it is the northern Andes that is more under threat and harbour much of the total species diversity. The neglect of this region was well pointed out by Henderson *et al.* (1991).

The epiphytic groups which contribute to Andean diversity include Araceae, Bromeliaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Guttiferae, Piperaceae (*Peperomia*) and Orchidaceae. The understorey families which have diversified in the Andean region are especially Acanthaceae, Melastomataceae, Monimiaceae, Myrsinaceae, Piperaceae (*Piper*), Rubiaceae and Solanaceae, and also the palmettos in Marantaceae, Musaceae and Zingiberaceae. There seems to have been an evolutionary explosion of species in some genera of the above families in response to the varied ecosystems available in the moist lower slopes of the Andes and because of the relatively recent uplift of these mountains. There has been a large amount of co-evolutionary interactions with nectarivorous bats and humming birds in this region. The families listed above are not nearly so species diverse in Amazonia where the understorey has fewer, more widely dispersed species in a less dense

Table 5. *Estimate of species numbers compared with area of selected neotropical countries*

	area / km^2	vascular plant species	species per km^2
Bolivia	1098581	18000	0.016
Brazil	8511965	55000	0.006
Colombia	1138914	35000	0.031
Costa Rica	50900	12000	0.236
Ecuador	283561	20000	0.071
Guianas	468234	9000	0.019
Panama	77082	9000	0.117
Peru	1290000	17143	0.013
Venezuela	912050	20000	0.021

understorey. However, in terms of conservation, it is important to realize that such closely related species may contain little genetic diversity in comparison to more widely separated clades.

Table 6 is a comparison of the niches which species occupy in three well studied forests. Barro Colorado Island in Panama and the Río Palenque Reserve in Ecuador are in the northwestern part of the neotropics which tend to have a higher number of shrubs and herbs with predominantly Andean distributions. The Reserva Florestal Adolpho Ducke is in Central Amazonia where the diversity is in trees with Amazon-centred distributions. The difference in the distribution of types of habit of the species between two areas is quite striking. Large trees make up 70% of the diversity of the Reserva Ducke but only 22% of the flora of Barro Colorado Island and 15% of the flora of Río Palenque. In the Amazon region it is the tree and liana groups that have a high species diversity and these species belong mainly to Amazon-centred genera. The striking difference in the species composition of the northern Andes and Amazonia is further emphasized by the fact that 76% of Amazonian species (14000 species) are endemic to Amazonia (Gentry 1992).

(*b*) *Patterns of neotropical plant distributions*

Whereas most groups of neotropical plants that have been monographed contain a few widespread species, one of the most striking features is the number of species that have extremely limited ranges even within a particular type of vegetation. Only 16.6% of the 349 species of neotropical Chrysobalanaceae could be termed widespread. The remainder are of restricted range or are local endemics. Several factors account for restricted distribution ranges of so many species including edaphic conditions, topography, historic changes in vegetation cover and local climate. Some species are habitat-restricted and occur only in forest on white sand, floodplain forest or montane forest, but even within a more widespread and uniform vegetation type, such as rainforest on non-flooded ground, local endemics are common. The development of adequate conservation plans for any area must involve a detailed knowledge of the distribution of the species of restricted range.

Analysis of the species distributions of any widespread, species diverse, plant family shows that some areas of rainforest have a much higher number of endemic species than others. This has been observed for the distributions of many different organisms (see, for example, Haffer (1969, 1974) for birds'; Brown (1976, 1987) for insects'; Prance (1973, 1979, 1982) for plants). These areas have frequently been equated with forest refugia that remained intact during the drier and cooler periods of climate during glaciation in more temperate latitudes. Whether or not they were refugia, the existence of these centres of endemism has been well established. Their conservation is of great importance because without protection a large number of local endemics would be lost.

The distribution of endemic species in South America has been useful for the definition of phytogeographic regions and phytochoria. Phytogeographic regions were first proposed for Amazonia by Ducke & Black (1954) based on the distribution of a large number of locally occurring species in the region. This was refined by Prance (1977) (figure 1). The conservation recommendations for Amazon proposed by Wetterberg *et al.* (1976) synthesized data from both the centres of endemism of various biogeographers and from the phytogeographic regions of Prance (1977) which are both based on the distributions of species. The proposed conservation areas, some of which have been declared as reserves (Wetterberg *et al.* 1981) include part of each phytogeographic region because each region contains some species of plants that do not occur in other regions.

Figure 2 shows the phytochoria of South America from Prance (1989) slightly modified to incude an extra one for the campos rupestres of eastern Brazil. The phytochoria are defined not primarily by their vegetation type, but mainly as areas within which a large number (over a thousand) of endemic species occur. In addition, some areas are either transitional regions between the main phytochoria or mosaics of species from other regions such as the Pantanal swamp region of Mato Grosso, Brazil (see White (1962) and Prance (1989) for further details). Phytochoria are

Table 6. *A comparison of habit forms between three well studied neotropical areas*

(Data from Croat (1978), Dodson & Gentry (1978) and M. Hopkins (personal communication). All three areas are predominantly lowland rainforest or non-flooded ground.)

	Barro Colorado I Panama	Río Palenque Ecuador	Reserva Florestal A. Ducke, Brazil
area	15 600 ha	167 ha	10000 ha
habit			
trees > 10 cm dbh	291	154	784
small trees and large shrubs	134	99	135
herbs and subshrubs	439	376	90
epiphytes	180	228	51
parasites	8	6	14
lianas	149	87	51
small vines	117	84	20
	1318	1033	1119

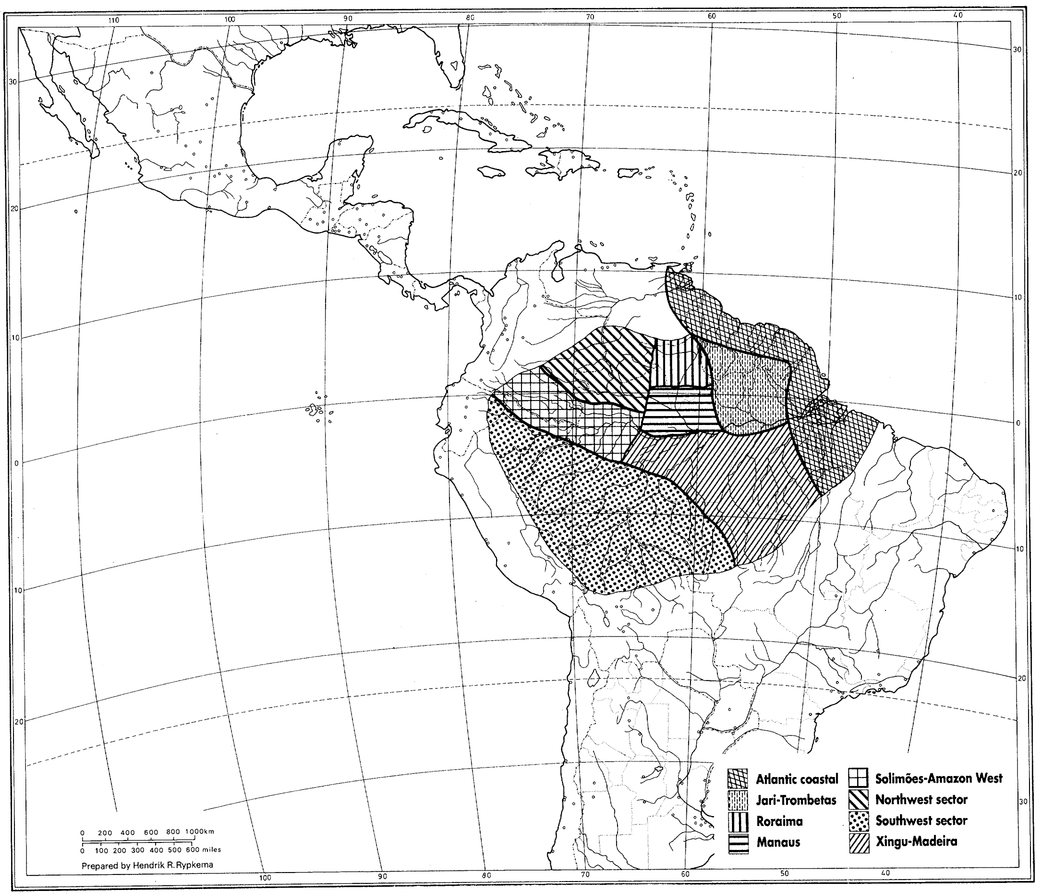

Figure 1. The phytogeographic regions of Amazon as defined by Prance (1977).

either continuous areas or they can be broken up into an archipelago like structure such as many isolated mountain tops of the Guayana Highland or the campos rupestres. In future conservation efforts it is essential to ensure that there are adequate areas of reserves within each phytochorion.

Mori *et al.* (1981) analysed the distribution of 1127 tree species that occur in the Atlantic coastal forests of Brazil. In this analysis 53.6% of the species were shown to be endemic to those forests, 11.8% to the coastal forest and some part of the adjacent Planalto of Central Brazil, and 7.8% disjunct with the Amazon region, and only 26% were widespread. A more recent analysis of the species diversity of Atlantic coastal forests of Brazil that included herbaceous material (Gentry 1992) indicated that there are 9400 endemic species in the region, representing 73% of the total. These figures indicate to conservation planners the high level of endemism of the Atlantic coastal forest and they have been extensively quoted because they quantify the amount of endemism of trees in the region. These studies were based on a simple analysis of the distribution maps of woody species for which data were available from Flora Neotropica monographs.

In addition to plotting a large number of distribution maps based on presence or absence in a grid square, another technique that is most useful for conservation is isoline maps that surround the entire possible distribution of a species. These are of particular use to indicate centres of diversity in large areas of similar vegetation such as within Amazonia.

Figures 3–7 show the distribution of species of Chrysobalanaceae which occur in the Ducke Forest Reserve near to Manaus, Brazil. Some species are eastern Amazonian whose range extends west just to Manaus, some are western Amazonian with a range extending east to Manaus, and some are Guianan species extending south to Manaus. There is a certain amount of endemism in the vicinity of Manaus, but the diversity is particularly high because the species of several regions come together at the extremes of their ranges in this central Amazonian location.

Figure 8 is the result of a workshop held in Manaus in January 1990 where one hundred biologists from different fields such as botany, ornithology, entomology and ichthyology met together to pool their data to define priority areas for conservation. The conclusions were based on data on centres of diversity, centres of endemism, types of vegetation and soil. High priority was given to places where data from more than one group of organisms indicated high diversity or endemism. The end product of a progressive merging of data was a map (Prance 1990; Conservation International 1992) which delimited 94 areas evaluated on a scale of 1–5 in importance for conservation (only three of these levels are shown in figure 8). This provides a synthesis of much of the biogeographic knowledge about the fauna and flora of the Amazon region and is already providing a much more logical basis for future conservation planning throughout Amazonia.

As techniques are refined, more sophisticated

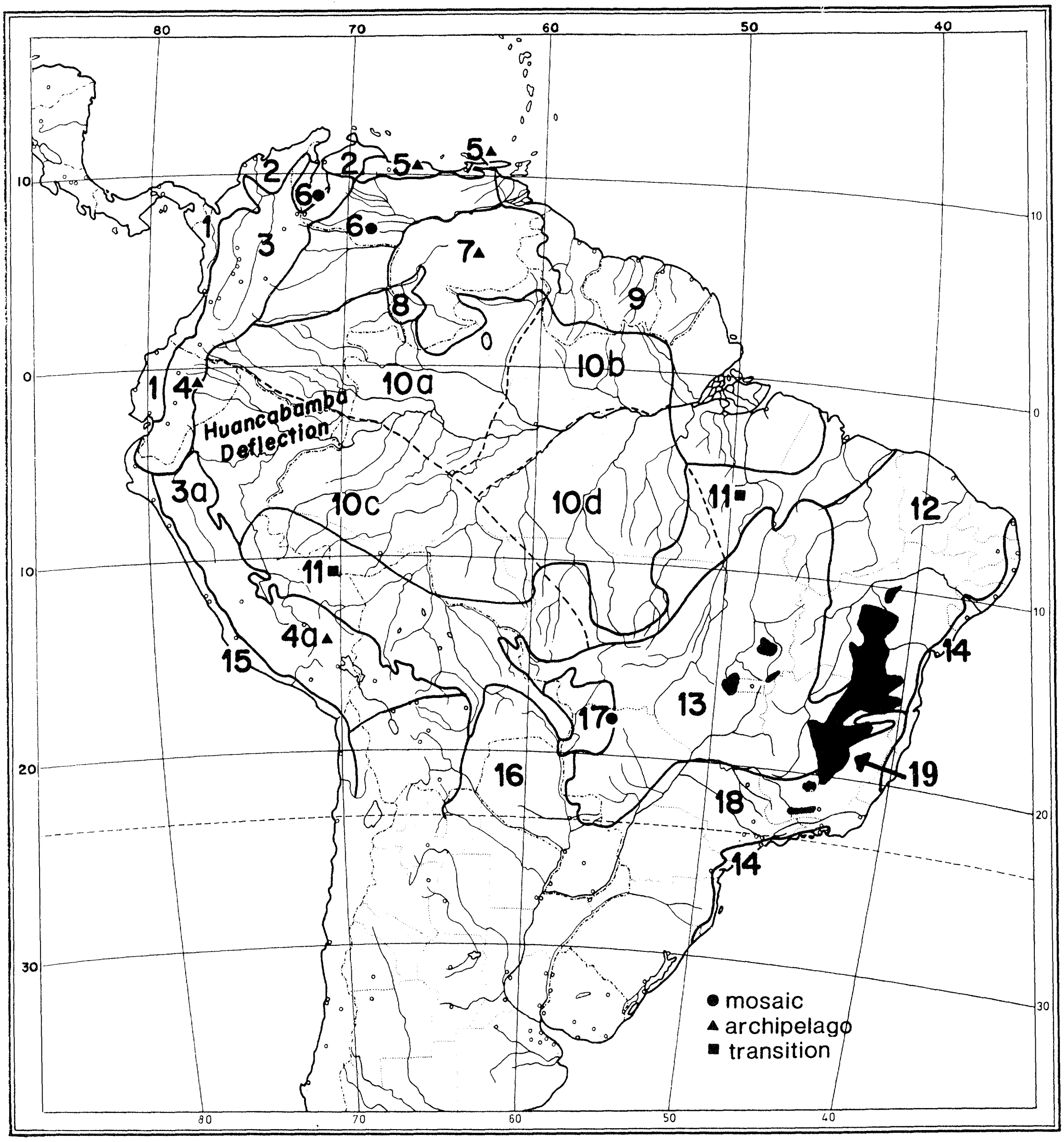

Figure 2. The phytochoria or floristic provinces of South America as defined in Prance (1989). A. Regional centres of endemism with a high percentage of species endemism which are general areas rather than local centres of endemism such as occur within some of these regional centres. 1 = Panama–Chocó; 2 = Magdalena–Venezuelan Gulf; 3 = northern Andean submontane; 3a = southern Andean submontane; 9 = Guiana–eastern Amazonia; 10 = Amazonia; 12 = northeastern Brazil; 13 = Planalto; 14 = Atlantic coastal region; 15 = southern Pacific; 16 = Chaco; 17 = southern Brazil. B. Archipelago-like centres (triangles) of endemism differ from regional centres in their discontinuous distribution, because of their occurrence on isolated mountain tops. The South American centres are: 4 = north Andean montane; 4a = southern Andean montane; 5 = Central Cordillera Venezuela; 7 = Guayana Highland; 19 = shaded area in Atlantic coastal area of Brazil; campo rupestre archipelago. C. Regional transition zones (squares) are regions where there is a gradual transition between two centres, with elements from both types and low endemism. In South America the single such zone of significance is: 11 = Amazon Transition Zone, around the south of Amazonia. D. Regional mosaics (circles) are areas that are not well categorized as centres of endemism or as transition zones. They may or may not be rich in endemic species. In South America the Pantanal mosaic (17) is not rich in endemism, but the other areas are: 6 = Catatumbo–Llanos mosaic; 8 = Venezuelan Amazonas–savannas mosaic.

analyses of species distributions are being made. For example all my distributions of neotropical plant families are now entered in the Worldmap programme (Williams *et al.* 1991; Vane-Wright *et al.* 1991). This makes possible a rapid assessment of areas of high species diversity and of high endemism, and has greatly enhanced analysis at the species level. It is at the species level rather than family or generic levels that these patterns of endemism and of diversity are particularly apparent.

(*c*) *Species diversity at the local level*

Whether Amazon as a whole or a small area such as a hectare is sampled, the species diversity is much greater than in the other major regions of the tropics. Table 7

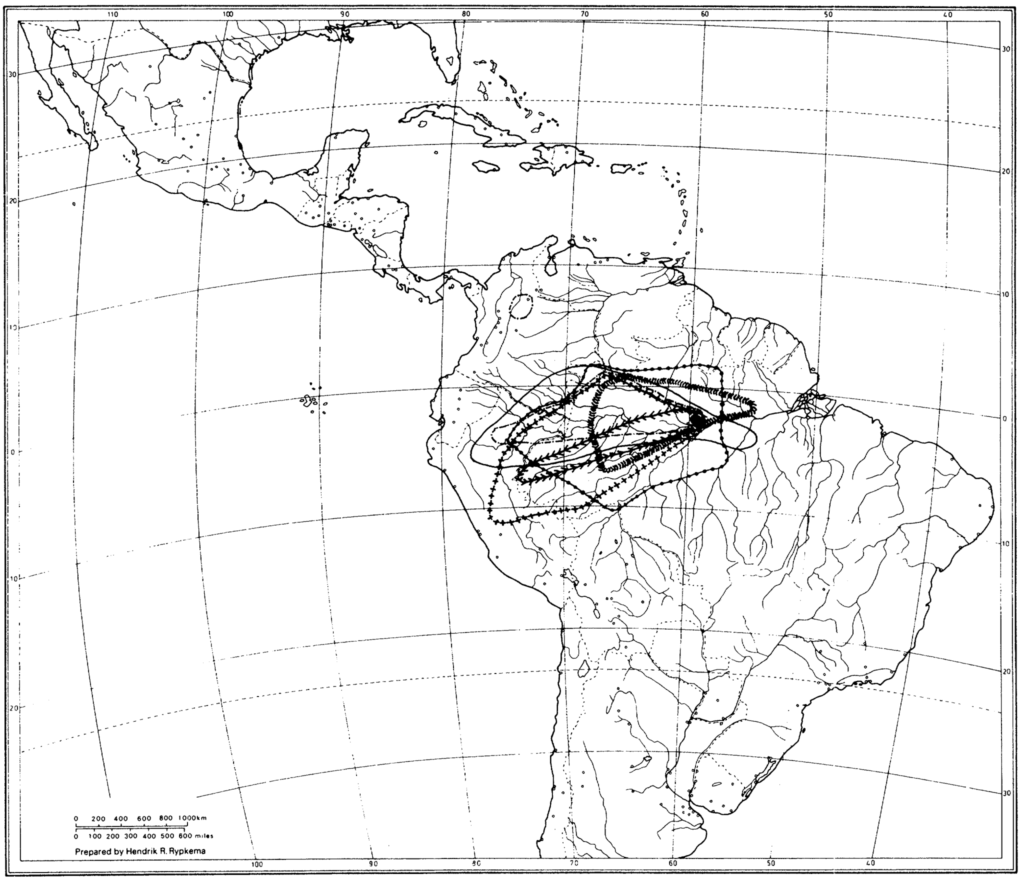

Figure 3. Western Amazonian terra firme forest species of Chrysobalanaceae that also reach as far east as Reserva Ducke.

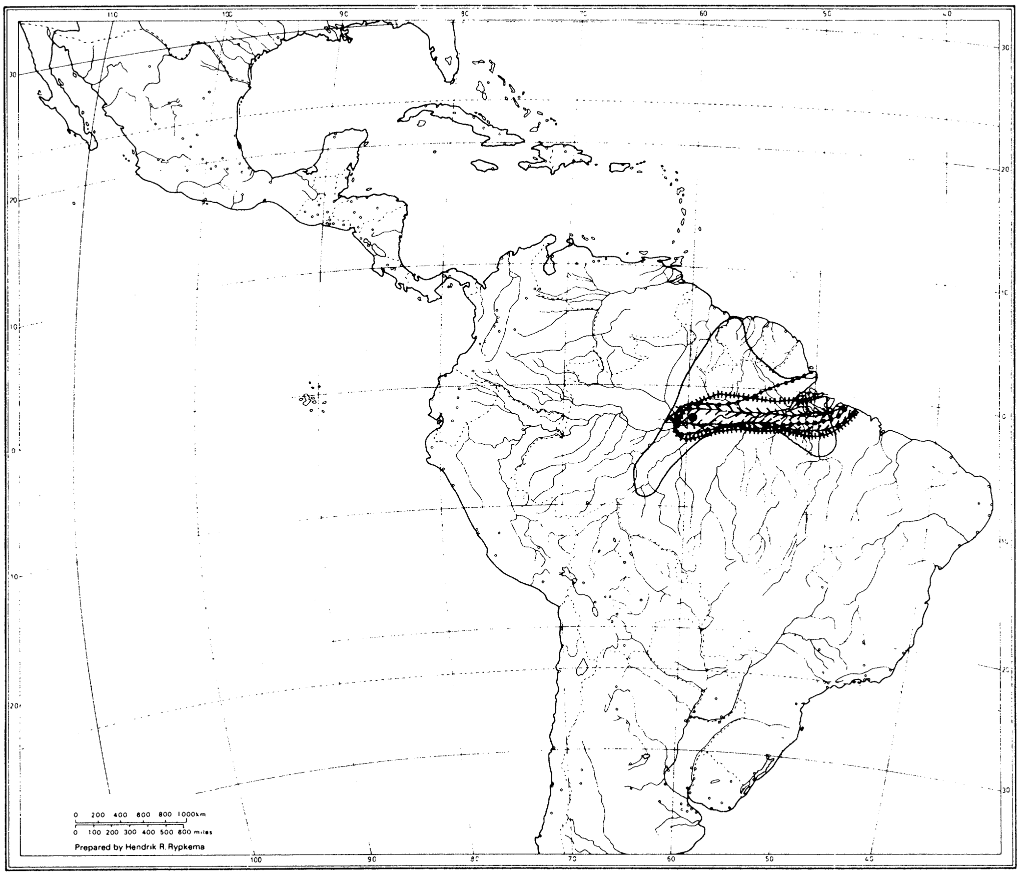

Figure 4. Eastern Amazonian terra firme forest species of Chrysobalanaceae that also reach as far west as Reserva Ducke.

Figure 5. Guianan species of Lecythidaceae that occur in the Reserva Ducke.

Figure 6. Reserva Ducke species of Chrysobalanaceae confined to Central Amazonia.

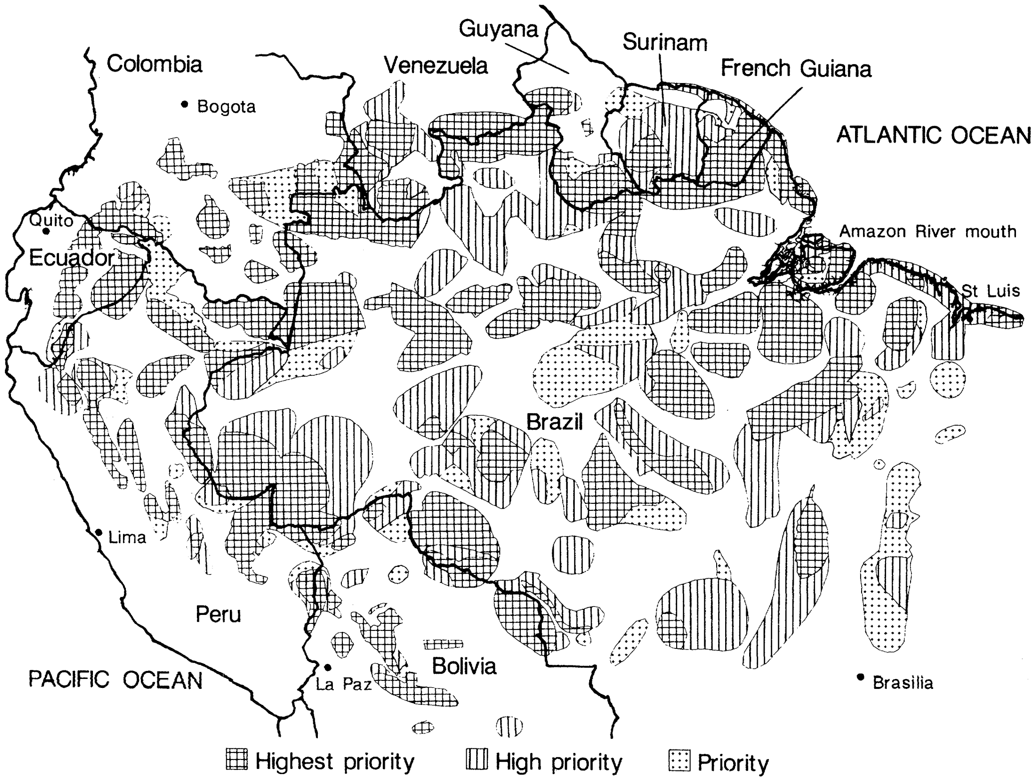

Figure 7. Priority areas for conservation of Amazonia as defined by Workshop 90 in Manaus, Brazil.

presents data from some forest inventories carried out in various parts of Amazonia and it demonstrates the high species diversity. However, there is considerable variation in total species number per hectare because of local variation in soils and climate. Gentry (1982*b*) showed that there is a marked correlation between rainfall and total tree species diversity, hence the higher species numbers in table 7 are from the upper Amazon. Diversity appears to increase up to about 4000 mm of rainfall. The lowest diversity in table 7 is from Alto Ivon in Bolivia which has the lowest rainfall and the most seasonal climate. This Amazonian diversity is often made up of different families, genera and species from those that make up the epiphyte, shrub and herb layers of the northern Andean region.

Table 7 shows the diversity of species that occur together in the same habitat, a single hectare or a few hectares of rainforest on terra firme. Even within such small areas there is considerable niche specialization which apparently allows species of the same genus to coexist, for example, with respect to growth form (emergents, canopy and subcanopy species) and phenology. Species are good indicators of diversity because they tend to be habitat specialists to a much greater extent than the families and genera. Much of the total species diversity of Amazonia is β-diversity or habitat specialization. Table 3 shows how a single genus *Caryocar* has radiated into the major ecosystems available in lowland South America. A common pattern in a genus is that of species pairs with one in the upland non-flooded forest and another often closely related one in the flood plain forest, for example the closely related *Caryocar glabrum* (upland forest) and *C. microcarpum* (floodplain). Table 8 presents data extracted from the inventory of Campbell *et al.* (1986). The left-hand column lists

Table 7. *Data about occurrence of tree taxa at different levels on some quantative inventories of areas of neotropical forest. This shows the enormous species diversity at the local level*

locality	area/ha	min dbh	indiv.	species	gen.	fam.	reference
Brazil: Belém	1	10	423	87	65	31	Black *et al.* (1950)
Rio Xingu	3	10	1420	265	127	39	Campbell *et al.* (1986)
Castanhal	3.5	10	1482	179	130	47	Pires *et al.* (1953)
Manaus	1	5	1561	473	187	54	Valencia *et al.* (1994)
Ecuador: Cuyabeno	1	10	693	307	138	46	Valencia *et al.* (1994)
Añangu	1	10	728	228	126	53	Balslev *et al.* (1987)
Peru: Mishana	1	10	842	275	–	50	Gentry (1988)
Yanamono	1	10	580	300	–	58	Gentry (1988)
Bolivia: Alto Ivon	1	10	649	94	61	28	Boom (1986)
Brazil: Reserve Ducke	100 000[a]	–	7107	1199	510	112	Ribeiro *et al.* (1994)

[a] Sample of 7107 specimens only.

Table 8. *The left-hand column represents all the species found in 0.5 hectare of várzea forest by Campbell* et al. *(1986) and the right-hand column a summary of species found on nearby terra firme forest*

	várzea	terra firme
Anacardiaceae		
	Ancardiaceae sp.	7 other sp.
Annonaceae		
	Duguetia flagellaris	*D. marcgraviana*
	Unonopsis guatterioides	*U. guatterioides*
		5 other species
Chrysobalanaceae		
	Licania canescens	*L. guianensis*
		L. heteromorpha
		6 other species
Clusiaceae		
	Rheedia brasiliensis	*Rh. acuminata*
		Rh. brasiliensis
		1 other species
Erythroxylaceae		
	Erythroxylum sp.	–
Euphorbiaceae		
	Hevea pauciflora	–
	Piranhea trifoliata	*P. trifoliata*
		9 other species
Lecythidaceae		
	Gustavia hexapetala	*G. hexapetala*
	G. poeppigiana	*G. poeppigiana*
		10 other species
Leguminosae		
	Cynometra longicuspis	*C. longicuspis*
	Dialium guianense	*D. guianense*
	Etballia guianensis	
	Macrolobium angustifolium	*M. angustifolium*
	Pithecellobium corymbosum	
	P. cauliflorum	
	P. latifolium	
	Leguminosae 2	Leguminosae 2
	Leguminosae 20	Leguminosae 20
	Leguminosae 22	Leguminosae 22
	4 other species not on terra firme	46 other species
Melastomataceae		
	Mouriri sp.	–
Meliaceae		
	Trichilia sp. 1	*Trichilia* sp. 1
		4 other species of *Trichilia*
		5 other species of Meliaceae
Moraceae		
	Brosimum guianensis	*B. guianensis*
	Sorocea muriculata	*S. muriculata*
		20 other sp.
Myrtaceae		
	Myrtacae sp. 6	16 other sp. of Myrtaceae
Ochnaceae		
	Ouratea acuminata	–
Polygonaceae		
	Coccoloba 2	*Coccoloba* 1
		Coccoloba coronata
Sapotaceae		
	Franchetella anibaefolia	*F. anibaefolia*
	Micropholis truncifolia	*M. venulosa*
		9 other species of Sapotaceae
Tiliaceae		
	Mollia lepidota	*Apeiba membranacea*
		Luehea sp.
Violaceae		
	Amphirrhox surinamensis	*A. surinamensis*
	Leonia glycycarpa	*L. glycycarpa*
	Rinorea juruana	*R. juruana*
	total 17 families (14 on t.f.)	total families 39

all the species found in the area of floodplain várzea forest, and the right hand column shows the species of the same genera that occur on terra firme. It shows that while the várzea forest is much less diverse, it has many species that do not occur on the terra firme. There are many other available habitats such as savannas, white sand caatingas and hill slopes that all contribute the β-diversity of Amazonia. All of this is apparent from the study of species rather than families and genera. An excellent example of phenological separation is given by Hilty (1981) in the genus *Miconia* in the lower montane forest of Colombia.

5. CONCLUSIONS

Although there have been various suggestions that biodiversity can be adequately assessed at higher taxonomic levels than species (Gaston & Williams 1993), for the neotropics at least this would seem to present an inadequate picture for conservation. Whereas higher taxon richness does tend to increase with declining latitude as pointed out by Gaston & Williams (1993) and other authors, within the tropical latitudes this trend is not marked. Important sites for the conservation of biodiversity are the centres of endemism, species diversity and habitat diversity. At the family level few of these centres are evident. There is a slight increase in generic diversity in the centres of high species diversity, but not enough to inform decisions about conservation. In the neotropics there is an extremely high level of endemism and habitat specialization at the species level. There are many centres of species diversity which do not necessarily coincide with centres of endemism. It is, therefore at the species level that we should focus our attention when assessing biodiversity for conservation planning.

REFERENCES

Balslev, H., Luteyn, J., Øllgaard, B. & Holm-Nielsen, L.B. 1987 Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* **92**, 37–57.

Beentje, H.J., Adams, B. & Davis, S.J. 1994 Regional overview: Africa. In *Centres of plant diversity* (ed. S. D. Davis & V. H. Heywood). IUCN/WWF. (In the press.)

Black, G.A., Dobzhansky, T. & Pavan, C. 1950 Some attempts toestimate species diversity and population density of trees in Amazonian forests. *Bot. Gaz.* **111**, 413–425.

Boom, B.M. 1986 A forest inventory in Amazonian Bolivia. *Biotropica* **18**, 287–294.

Brako, L. & Zarucchi, J.L. 1993 *Catalogue of the flowering plants and gymnosperms of Peru.* (1286 pages.) St. Louis: Missouri Botanical Garden.

Brown, K.S. Jr 1976 Neotropical patterns of evolution in Neotropical Lepidoptera. Systematics and derivation of known and new Heliconiini (Nymphalidae: Nymphalinae). *J. Entomol.* B **44**, 201–242.

Brown, K.S. Jr 1987 Biogeography and evolution of Neotropical butterflies. In *Biogeography and quaternary history in tropical America* (ed. T. C. Whitmore & G. T. Prance) (*Oxf. Monogr. Biogeogr.* **3**), pp. 64–104. Oxford: Clarendon Press.

Campbell, D.G., Daly, D.C., Prance, G.T. & Maciel, U.N. 1986 Quantitative ecological inventory of terra firme and várzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* **38**, 369–393.

Chase, M.W. *et al.* 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbc L. *Ann. Missouri Bot. Gard.* **80**, 528–580.

Conservation International 1991 *Workshop 90: biological priorities for conservation in Amazonia.* Map. Washington, D.C.

Croat, T.B. 1978 *Flora of Barro Colorado Island.* (943 pages.) Stanford University Press.

Dodson, C. & Gentry, A. 1978 *Flora of the Rio Palenque Science Center.* Sarasota: Marie Selby Botanical Garden.

Ducke, A. & Black, G. 1954 Notas sobre a fitogeografia da Amazônia Brasileira. *Bol. Técn. Inst. Agron. do Norte* **29**, 1–62.

Gaston, K.J. & Williams, P.H. 1993 Mapping the world's species. The higher taxon approach. *Global Ecol. Biodiv. Lett.* **1**, 2–8.

Gentry, A.H. 1982*a* Neotropical floristic diversity. Phytogeographical connections between central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.* **69**, 557–593.

Gentry, A.H. 1982*b* Patterns of neotropical species diversity. *Evol. Biol.* **15**, 1–84.

Gentry, A.H. 1987 An overview of neotropical phytogeographic patterns with an emphasis on Amazonia. *Ann. 1° Simposio do Tropico Humido, Brasília, Dept. Difus. Tecnologia.*

Gentry, A.H. 1988 Tree species richness of upper Amazonian forests. *Proc. natn. Acad. Sci. U.S.A.* **85**, 156–159.

Gentry, A.H. 1992 Tropical forest biodiversity: distributional patterns and their conservation significance. *Oikos* **63**, 19– 8.

Haffer, J. 1969 Speciation in Amazonian forest birds. *Science, Wash.* **165**, 131–137.

Haffer, J. 1974 *Avian speciation in tropical South America.* (390 pages.) Cambridge, Massachusetts: Publ. Nuttall Ornith. Club. No. 14.

Henderson, A., Churchill, S. & Luteyn, J. 1991 Neotropical plant diversity. *Nature, Lond.* **351**, 21–22.

Hilty, S.L. 1981 Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* **12**, 292–306.

Jacobs, M. 1974 Botanical panorama of the Malesian archipelago. In *Natural resources in humid tropical Asia*, pp. 263– 294. Paris: UNESCO. Natural Resources Research XII.

Johns, R.J. 1992 Biodiversity and conservation of the native flora of Papua New Guinea. In *Papua New Guinea conservation needs assessment*, vol. 2 (*A biodiversity analysis for Papua New Guinea*) (ed. B. M. Bechler), pp. 15–32. Papua New Guinea: Department of Environment and Conservation.

Maas, P.J.M. & Westra, L. 1993 Neotropical plant families. (289 pages.) Koenigstein: Koeltz Scientific Books.

Mori, S.A., Boom, B.M. & Prance, G.T. 1981 Distribution patterns and conservation of eastern Brazilian coastal forest tree species. *Brittonia* **33**, 233–245.

Pires, J.M., Dobzhansky, T.H. & Black, G.A. 1953 An estimate of species of trees in an Amazonian forest community. *Bot. Gaz.* **114**, 467–477.

Prance, G.T. 1973 Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazonica* **3**, 5–28.

Prance, G.T., Rodrigues, W.A. & da Silva, M.F. 1976 Inventário florestal de uma hectare de mata de terra firme km 30 Estrada Manaus – Itacoatiara. *Acta Amazonica* **6**, 9–35.

Prance, G.T. 1977 The phytogeographic subdivisions of Amazonia and their influence on the selection of biological reserves. In *Extinction is forever* (ed. G. T. Prance & T. S. Elias), pp. 195–213. New York: New York Botanical Garden.

Prance, G.T. 1978*a* Floristic inventory of the tropics: where do we stand? *Ann. Missouri Bot. Gard.* **64**, 659–684.

Prance, G.T. 1978*b* The origin and evolution of the Amazon Flora. *Interciencia* **3**, 207-222.

Prance, G.T. 1979 Distribution patterns of lowland neotropical species with relation to history, dispersal and ecology with special reference to Chrysobalanaceae, Caryocaraceae and Lecythidaceae. In *Tropical botany* (ed. K. Larsen & L. B. Holm-Nielsen), pp. 59–88. London, New York: Academic Press.)

Prance, G.T. 1982 Forest refuges: evidence from woody angiosperms. In *Biological diversification in the tropics* (ed. G. T. Prance), pp. 137–158. New York: Columbia University Press.

Prance, G.T. & Campbell, D.G. 1988 The present state of tropical floristics. *Taxon* **37**, 519–548.

Prance, G.T. 1989 American tropical forests. In *Tropical rain forest ecosystems. Ecosystems of the world 14B* (ed. H. Leith & M. J. A. Werger), pp. 99–132. Amsterdam: Elsevier.

Prance, G.T. 1990 Consensus for conservation. *Nature, Lond.* **345**, 384.

Prance, G.T. 1992 New species and new records of neotropical Chrysobalanaccae. *Kew Bull.* **47**, 633–646.

Raven, P.H. 1976 Ethics and attitudes. In *Conservation of threatened plants* (ed. J. Simmons *et al.*), pp. 155–179. New York & London: Plenum Press.

Ribeiro, J.E.L.S., Nelson, B.W., Silva, M.F. da, Martins, L.S.S., Hopkins, M. 1994 Reserva Florestal Ducke: diversidade & composiçáo da flora vascular. *Acta Amazonica.* (In the press.)

Valencia, R., Balslev, H. & Paz y Miño, C. 1994 High tree alpha-diversity in Amazonian Ecuador. (In the press.)

Wetterberg, G.B., Jorge Pádua, de Castro, C.S. & de Vasconcellos, J.M.C. 1976 Uma análise de prioridades em conservação da natureza na Amazônia. (62 pages.) PNUD/FAO/IBDF/BRA 45. Série Técnica No. 8.

Wetterberg, G.B., Prance, G.T. & Lovejoy, T.E. 1981 Conservation progress in Amazonia: a structural review. *Parks* **6**(2), 5–10.

White, F. 1962 Geographic variation and speciation in Africa with particular reference to *Diospyros. Syst. Assoc. Publ.* **4**, 71–103.

Williams, P.H., Humphries, C.J. & Vane-Wright, R.I. 1991 Measuring biodiversity: taxonomic relatedness for conservation priorities. *Aust. Syst. Bot.* **4**, 665–679.

Vane-Wright, R.I., Humphries, C.J. & Williams, D.H. 1991 What to protect? Systematics and the agony of choice. *Biol. Conserv.* **55**, 235–254.