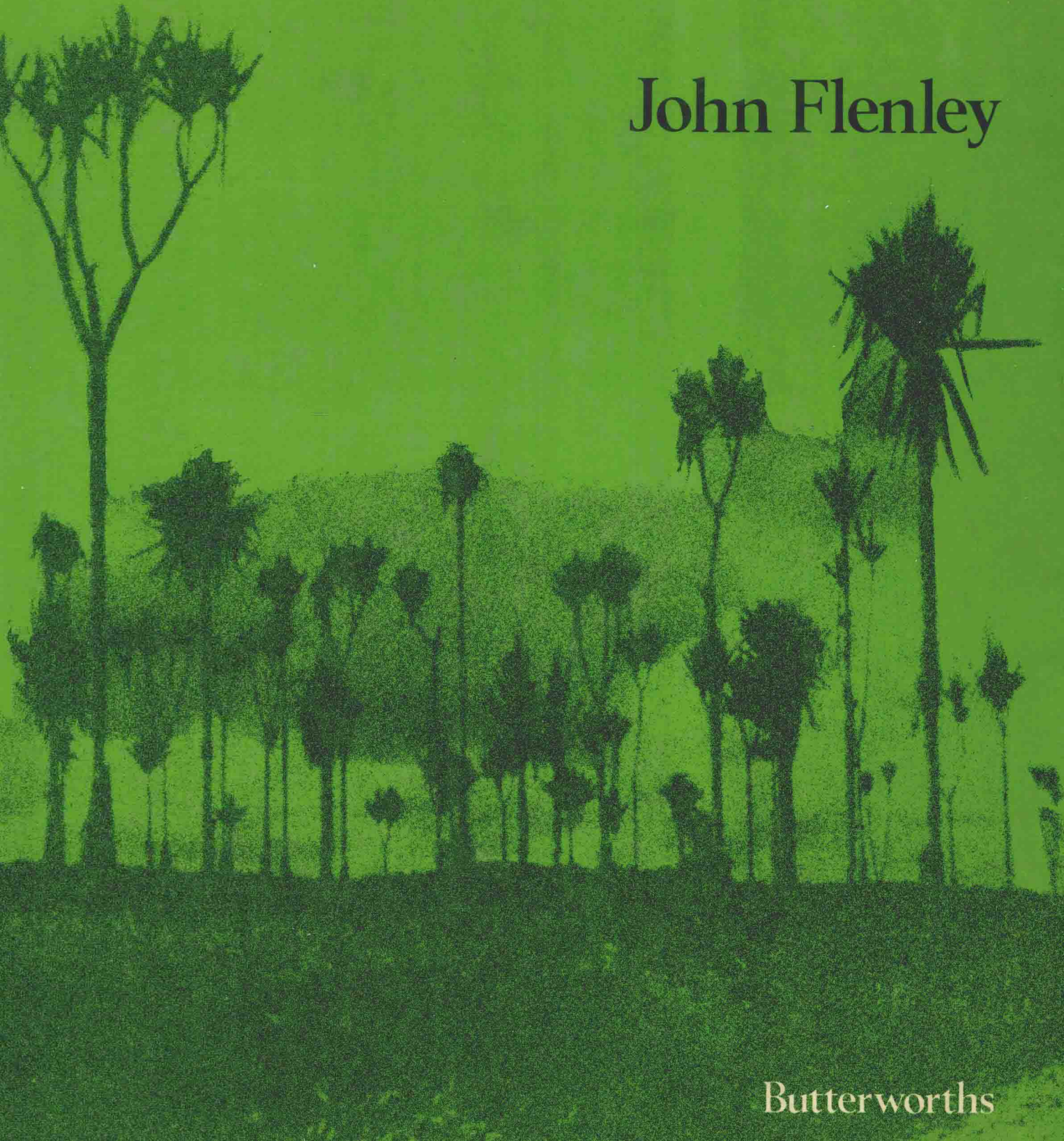


# The Equatorial Rain Forest: a geological history

John Flenley



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and  
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# Preface

Twenty years ago the rain forest was regarded as essentially static, a museum piece, a survival from far into the geological past. The ice ages of temperate regions were thought to have left the tropics substantially unaffected, or to have been reflected there as 'pluvials'. The supposed stability of the rain forest was used to bolster the theory that floristic diversity endowed stability, and the diversity was itself explained in terms of the environmental stability.

Recent research, much of it in the last five years, has shown how wrong were these ideas. The equatorial environment is now believed to have changed markedly in the past, and ice ages in temperate areas were, on the whole, times of aridity in the tropics, not pluvials. The rain forest, and other vegetation of equatorial regions, is now shown to be in a state of considerable instability. The effects of the last major climatic change are still reverberating there, particularly in montane areas.

We have also had to revise our ideas about successional changes in equatorial vegetation. Successions no longer seem to fit into the rigid moulds previously provided for them, and the individualistic behaviour of species is being more widely recognised.

The duration and extent of man's influence on equatorial vegetation has previously been seriously underestimated, but evidence is rapidly accumulating to correct this error.

All these factors encouraged me to write this book. So many decisions are being made at present which will drastically affect the future of equatorial vegetation that I felt it important the facts should be readily available. I hope also that this book will influence a new generation of students, especially in equatorial countries, to study equatorial vegetation

as a dynamic entity with a varied and highly significant history.

Despite its title, this is not a work dedicated only to the study of the geological history of the equatorial rain forest. It also covers the other vegetation types of equatorial regions, and it treats vegetational history not in a purely geological manner, but also from a palaeoecological viewpoint. It is in fact an attempt at a vegetational palaeoecology of equatorial regions.

I could not have written this book without the help and forbearance of my wife Jill and my daughters Eleanor, Frances and Yvonne. I thank Professors D. Walker, H. R. Wilkinson and J. A. Patmore for providing facilities for my work. I wish also to thank Donald Walker for critically reading the whole text, and the following for helpful criticism and/or assistance: K. J. Ackermann, M. Arney, D. Aunela, E. S. Barghoorn, R. R. Dean, S. E. Garrett-Jones, J. Golson, M. Gray, J. C. Guppy, D. Guy-Ohlson, T. van der Hammen, A. J. Hanson, G. S. Hope, M. Horgan, C. A. Joyce, A. P. Kershaw, A. Key, J. G. Lindsay, D. Livingstone, R. J. Morley, J. Muller, J. Ogden, C. D. Ollier, J. S. Pethick, J. M. Powell, M. L. Salgado-Labouriau, H. Salzmann, K. Scurr, G. Singh, A. P. Vayda, N. M. Wace, D. Watts and W. Wilkinson. I am also grateful to those many authors who have permitted the use of their illustrations, which are acknowledged beneath each one. I also thank my publishers, Messrs Butterworths, for their friendly patience and for the award of the Butterworth Scientific Fellowship, 1974, which encouraged me to write and made it financially possible.

J. R. F.  
Canberra



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# Present Vegetation and its Biogeographical Problems

## 1.1 INTRODUCTION

Anyone who has circled the earth in a satellite equipped for time travel need read no further; he will already have seen whole continents migrate and collide, ice sheets expand and contract, sea levels rise and fall, floras evolve and become extinct. The ordinary student, however, must discover the history of vegetation by the more difficult but more satisfying methods employed by Sherlock Holmes, in other words by the collection and assessment of evidence. Nowhere in the world is this study more worthwhile than in the equatorial regions, for it is there that vegetation is at its most complex, previous knowledge at its minimum, and problems about the ecological status and future of vegetation most urgent.

For the purposes of this book, I have considered the regions within about  $10^\circ$  latitude north and south of the equator, which I describe as 'equatorial'. There is no particular theoretical justification for this limitation, nor have I applied it very rigidly; indeed evidence from the whole of the tropics (i.e. up to  $23\frac{1}{2}^\circ$  latitude north and south) and even outside this limit has been mentioned where it seems relevant.

Owing to the major movement of the continents in geological time, the pieces of land between  $10^\circ\text{N}$  and  $10^\circ\text{S}$  have not always been the same pieces. Precisely which continental areas were equatorial at any time, however, is still a matter of some discussion. This book therefore makes no attempt to cover the vegetational history of all these areas, but only of those which are *now* equatorial, wherever they may have been in the past.

There is abundant geological evidence that vegetation we currently regard as equatorial formerly occurred in what are now temperate regions. This is not only the result of continental drift, for in certain periods, such as the Miocene, much of the present temperate regions, as well as the present tropical regions, appears to have borne 'equatorial' vegetation. Climatic change must, almost certainly, be involved here. Although I will mention such occurrences, I will make no real attempt to deal with any vegetation outside equatorial regions.

Twenty years ago scientists regarded the rain forest and most other vegetation of equatorial regions as essentially static, a museum piece, a survival from far into the geological past. They thought ice ages of temperate regions had left equatorial regions substantially unaffected, or had been reflected there as 'pluvials'. They used the supposed stability of the rain forest to bolster the theory that floristic diversity endowed stability, and the diversity itself they explained in terms of the environmental stability.

The aim of this book is to show that all these ideas were wrong. The equatorial environment is now believed to have changed markedly in the past, and I shall present evidence that ice ages were times of aridity in the tropics, not pluvials. In fact the old pluvial theory must be completely abandoned. I shall show that equatorial vegetation, even perhaps the lowland rain forest, has changed dramatically in the geologically recent past, and that the effects of the Pleistocene are still reverberating in this vegetation. I shall conclude that equatorial vegetation is essentially dynamic.

## 1.2 THE PRESENT VEGETATION OF EQUATORIAL REGIONS

History books usually begin, reasonably enough, with history. Why should a book on vegetational history not begin in the same way? The reasons for giving first a brief résumé of present vegetation are threefold. Firstly, the reader may be rather unfamiliar with present-day equatorial vegetation. Secondly, the evidence available to the vegetational historian is much less abundant and clear than that usually used by political, social or economic historians. This means that constant reference to present-day vegetation is necessary for the interpretation of the evidence. Thirdly, a short discussion of present vegetation will permit the recognition of those areas of study where the historical method has the greatest amount to contribute to the interpretation of present vegetation.

This introduction to the vegetation of equatorial regions is necessarily abbreviated and over-generalised, and for more detail the reader is referred to works such as those of Richards (1964), Baur (1964), Walter (1973), Meggers *et al.* (1973), Lind and Morrison (1974), Longman and Jenik (1974) and Whitmore (1975). For simplicity, vegetation is considered under six headings: rain forest, semi-evergreen forest, savannah, swamps, mountain vegetation and secondary vegetation.

### 1.2.1 RAIN FOREST

This vegetation type, which perhaps covers more area than any other in equatorial regions, is to be identified with the *jungle* of many popular authors, although the usual conception of jungle involves the idea of a tangle of lianes more likely to be found in secondary forest. In fact *jungle* comes from the Sanskrit word *jangala*, meaning desert (Ollier, 1974).

The term rain forest has been established in the literature for so long (at least since Schimper, 1903), that it cannot easily be replaced, although it is in many respects an unfortunate term. It implies a relationship with rainy climate which is, of course, generally correct. This is, however, not always so; in Australia and other areas, strips of 'rain forest' occur in the humid environment alongside rivers in areas where there is a pronounced dry season. The term is also unreasonably broad. For example, there are areas which bear a forest vegetation in cool everwet regions, e.g. the west coast of North America. Some people have felt justified in calling this a rain forest; yet it bears so little relationship to its equatorial counterpart that the name does more to confuse than to enlighten. There is, however, no concise alternative term, so we shall continue to use it.

Rain forest has often been divided into tropical, sub-tropical and temperate rain forest. Again, these terms are unfortunate, because they are environmental terms, rather than properties of the forest itself. This results in anomalies; for instance several authors describe the occurrence of tropical rain forest in sub-

tropical regions. This problem need not unduly concern us, however, since all the rain forest within 10° of the equator may be taken to be 'tropical'. To save needless repetition the word 'tropical' in front of 'rain forest' will be omitted.

Rain forest was formerly found in everwet lowland areas almost throughout the equatorial regions. The three principal units there, the American, African and Indo-Malesian\* formations, are distinguished more by their floristic differences than by structural divergence. The forest is usually tall (30m or more) and contains mature trees of many different heights; often there appears to be a fairly distinct 'canopy' with 'emergents' poking through it. Some authors have described other 'strata' below the canopy, but finding these appears to depend largely on subjective choice of site, so that their objective existence is not substantiated. Epiphytes and lianes are often fairly abundant, as are palms and tree ferns. Shrubs and a ground flora of herbs are sometimes present, although the latter may be sparse. Some equatorial herbs are extremely large, e.g. bamboos and many members of the Zingiberaceae. Bryophytes are present, but less abundant than might be expected in the moist environment.

Although many of the trees look alike and have similar entire laurel-like leaves with 'drip-tips', in fact almost every tree found by an observer in the forest turns out to be a different species, for this is the most diverse vegetation type known. Even for large trees alone, the species area curve rises rapidly and fails to flatten off (*Figure 1.1*). Presumably if saplings, lianes, epiphytes, herbs, bryophytes, etc. were included then the curve would rise even more rapidly, although it might eventually flatten more convincingly.

The plant families which occur in rain forest are very numerous but some of the principal ones are: Euphorbiaceae, Leguminosae, Myrtaceae, Burseraceae, Lauraceae, Myristicaceae, Anacardiaceae and Annonaceae. There is considerable regional variation; for instance the Dipterocarpaceae, which are dominant in South-East Asia, are almost absent elsewhere. The above list refers to trees only, but there are also many important herbaceous families such as Orchidaceae.

The taxonomic diversity of the rain forest led to the failure of attempts to classify it by traditional phytosociological methods (e.g. Braun-Blanquet, 1932), and not until the application of statistical methods (Ashton, 1964), and later computer methods (Webb *et al.*, 1967b,c) were satisfactory classifications or ordinations reached. Even now, most of these can only be related to environment in a most generalised way, usually to soil and moisture factors which are not fully independent of each other.

The rain forest has been subjected to shifting cultivation in many areas, and in Africa much forest

\*Indo-Malesia: the Indo-Malesian floristic sub-kingdom of Good (1947), i.e. approximately the political states of India, Bangladesh, Burma, Sri Lanka, Thailand, Laos, Cambodia, Vietnam, Taiwan, Malaysia, Indonesia, the Philippines, and Papua New Guinea. The latinised spelling is adopted to avoid confusion with the political state of Malaysia.



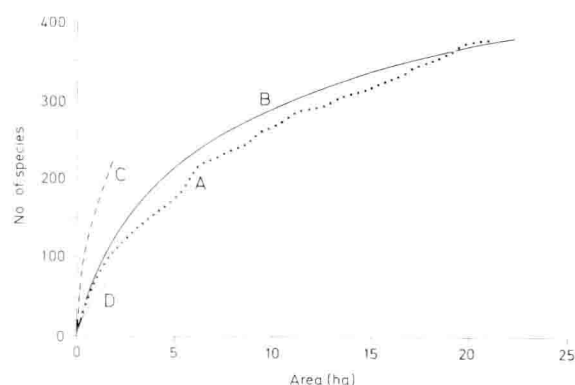


Figure 1.1 Species/area curves from rain forest (lowland Dipterocarp forest) in Malaya.

- A. Additive species/area curve for trees over 28 cm diameter, Jenka Forest Reserve, Malaya.
- B. Curve calculated from the Index of Diversity of the community in Jenka Forest Reserve.
- C. Curve for trees over 10 cm diameter, Sungei Menyala, Malaya.
- D. Curve for trees over 28 cm diameter, Sungei Menyala, Malaya.

The curves fail to flatten off even at large areas. (After Poore, 1964)

previously thought to be 'primary' or virgin, is now regarded as secondary (Richards, 1955). Complete forest clearance has occurred in so many equatorial regions that it is often impossible to reconstruct the original vegetational boundaries from the surviving relict patches with any degree of certainty. Forest clearance is associated with many problems which will be considered in Chapters 6 and 7.

## 1.2.2 SEMI-EVERGREEN AND DECIDUOUS FORESTS

These are forests that contain a proportion (sometimes 30–50%; Richards, 1964) of deciduous and semi-deciduous species. They commonly have far fewer total species than the rain forest, and sometimes a single species may dominate. They also tend to lack epiphytes and bryophytes. These forests grow in areas of pronounced wet and dry seasons, and they are therefore sometimes termed monsoon forests, although this is a misleading term since it assumes the correlation with climate which may not always apply. Semi-evergreen forests are most abundant on either side of the equator, rather than at the equator itself. The principal areas in which they are found are Thailand and Burma (especially the famous forests of teak, *Tectona grandis*); East Java (again teak forests); the Lesser Sunda Isles and southern New Guinea; in East Africa and around the margins of the rain forest areas in West Africa; and around the fringes of the Amazon rain forest in Brazil, Guyana, Venezuela, Surinam and the West Indies.

The semi-deciduous or deciduous nature of the vegetation is of considerable interest. It is possible that the deciduous habit arose in response to seasonal drought in the sub-tropics, and later became an adaptation to seasonal cold in temperate regions. Clearly the habit must have arisen many times in different

taxa, so there is no reason why the cause of its origin should always have been the same.

Shifting cultivation has also been very widely practised in areas of semi-evergreen and deciduous forest.

## 1.2.3 SAVANNAH

Broadly speaking, savannah is a grass-dominated vegetation, with or without scattered trees and shrubs. The term savannah has been applied so differently by so many ecologists that it is difficult to define at all. It is more than likely that fire, lit by man, is responsible for the maintenance, and even the formation, of many savannahs. There is good geological evidence, however, that some savannahs have existed in tropical regions since before man is known to have evolved, and are therefore a 'natural' vegetation type.

There are vast areas of savannah in South America, especially the cerrados, south of the Amazon rain forest, and the llanos, to its north. In Africa, savannahs are also widespread, especially to the south of the Sahara and in East Africa. In Indo-Malesia savannah is restricted to smaller areas such as the patanas of Sri Lanka, the cogonales of the Philippines, and the kunai of New Guinea.

## 1.2.4 MOUNTAIN VEGETATION

The rain forest of the lowlands does not give way sharply to mountain vegetation. Indeed the change is so gradual, and occurs at such a wide range of altitudes, that any boundary must be considered arbitrary. It is true that workers in South America (Cuatrecasas, 1958; van der Hammen, 1974), in Africa (Hedberg, 1951; Troll, 1959), and in South-East Asia (van Steenis, 1972), have considered 1000m as a suitable boundary, but this can be taken as only the vaguest of guides.

The mountain forests are evergreen but less diverse than the lowland forest; they are also usually less tall but richer in epiphytes and tree ferns. Epiphytic bryophytes may be particularly abundant at higher elevations, clothing every branch and trunk to produce the so-called 'mossy forest'. The boundary between the Lower and Upper montane forests is often fairly clear (Whitmore, 1975).

At elevations above about 3400m, or frequently somewhat lower, the forest is replaced by non-forest vegetation, often dominated by genera with temperate affinities, the so-called stenotherm or microtherm genera (van Steenis, 1934–36). Frequently there is an intermediate zone of shrubs in which the Ericaceae may be prominent. Isolated small trees may be found at higher altitude, so it is best to distinguish between the forest limit, where closed forest ceases, and the tree line, above which no isolated trees occur.

Above the forest limit the vegetation is extremely variable. On some mountains, for example Mt Kinabalu, Borneo, you emerge from the forest onto almost bare rock. More usually there is a herbaceous vegetation in which grasses dominate to a greater or lesser extent.

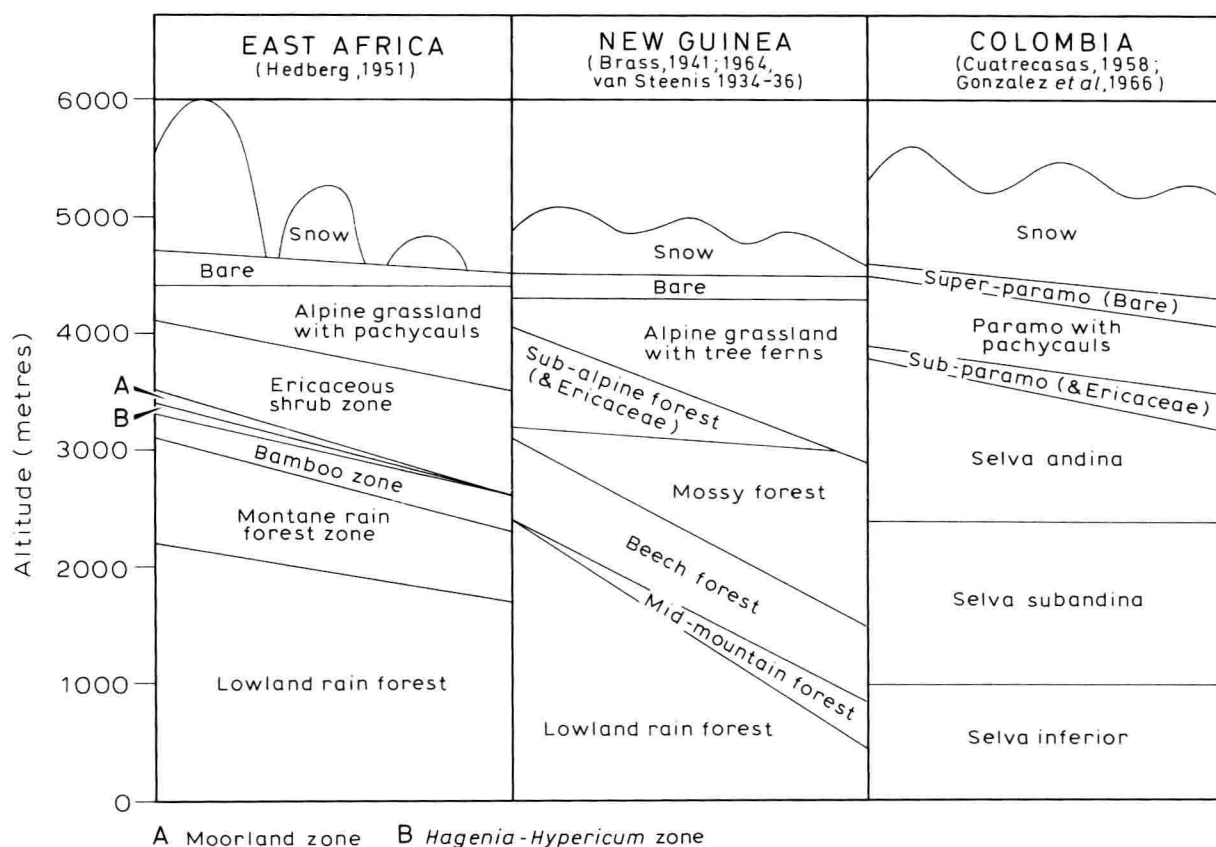


Figure 1.2 Altitudinal zonation of equatorial vegetation. There is a broad parallelism between zonation in all three regions. (After Flenley, 1967; Troll, 1959 and other authors shown in the diagram)

This has often been called 'alpine' by analogy with the Swiss Alps, but this term suggests a comparison which may not be justified. The term 'tropicalpine' seems less open to objection.

The snow line on equatorial mountains is at about 4500m (Troll, 1959). There is considerable variation in relation to precipitation, and valley glaciers may come well below the regional snowline. Seasonal variation in snow deposition and accumulation is at a minimum, in line with the pronounced lack of seasonality in the climate.

Many attempts have been made to subdivide mountain vegetation on an altitudinal basis, e.g. Cuatrecasas (1958) for South America, Hedberg (1951) for Africa, and van Steenis (1934-36) and Robbins (1958) for South-East Asia. Their results have been summarised in Figure 1.2. None of these attempts is entirely satisfactory for a variety of reasons. In the first place, vegetation, if it obeys any laws at all, obeys statistical ones. Any zones, therefore, can only be regarded as areas of high probability for the occurrence of a particular vegetation type (e.g. Walker and Guppy, 1976). This may be illustrated by data showing the number of tree species recorded in plots at various altitudes in New Guinea (Figure 1.3). It is clear that at any given altitude this number may take quite a range of values. It is, of course, equally clear that there is an overall trend of decline in diversity with increasing altitude.

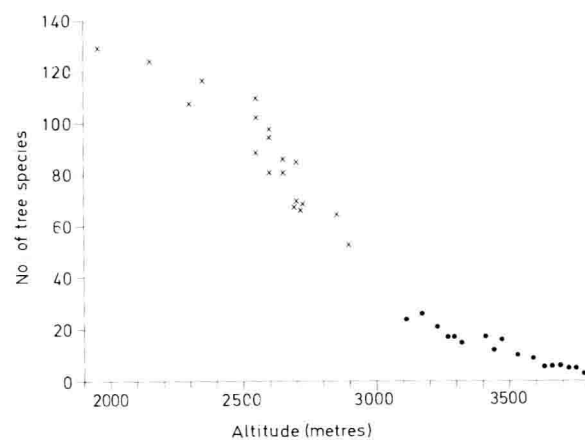


Figure 1.3 The numbers of tree species in plots at various altitudes in New Guinea.

x, Plots of 5000 m² in the Wabag Region (Flenley, 1967; 1969).

•, Plots of 100 m² on Mt Wilhelm (Wade and McVean, 1969).

There is a marked decline in number of species with increasing altitude. The small plots used at high altitude are adequate for the relatively undiverse forest there. (Original)

A second reason for difficulty in zonation is the fact that zone boundaries tend to occur at lower altitudes on small isolated peaks near the sea than on large mountain masses inland. This is the Massenerhebung effect, first noted in the Alps. The effect is particularly marked in South-East Asia (Figure 1.4). Among the many explanations advanced for the Massenerhebung are the accumulation of cloud over mountains (Brass, 1941; Grubb and Whitmore, 1966), the effect of wind near the sea (Beard, 1946), the excessive decline in soil fertility with altitude on small isolated peaks (Grubb, 1971), and the differing temperature lapse rate over large mountain masses (Hastenrath, 1968).

It is very desirable that lapse rates should be measured in more places. Few people have the time to take a year's observations and fewer still to take several years', yet variation from year to year may be important. It is to be hoped that the more general availability of automatic apparatus will eventually yield more data. Among the simplest of such devices is the thermal cell developed by Ambrose (1976). Failing all else, those

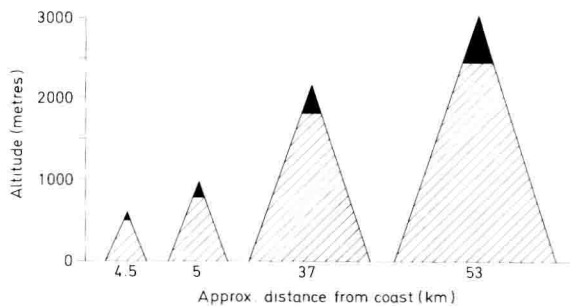


Figure 1.4 The Massenerhebung (mass elevation) effect illustrated by the occurrence of mossy forest on mountains in Indonesia. From left to right: Mt Tinggi (Bawean), Mt Ranai (Natuna Is.), Mt Salak (W. Java) and Mt Pangerango (W. Java). The small mountains near the sea have mossy forest at lower altitudes than the large mountains inland. (After van Steenis, 1972)

on short visits to mountains could do worse than measure the soil temperature at depth. As seasonal variation is slight, and diurnal variation almost eliminated below 30 cm, a probe inserted to 1 m depth gives an approximation to mean annual temperature (Mohr and van Baren, 1960; Schulz, 1960). Preliminary results suggest different lapse rates on different mountains in western Malesia\* (Morley, 1976).

Clearly the question 'why do zonations differ on different mountains?' invites the question 'why is vegetation zoned altitudinally at all?'. In answer to the second question there is general agreement, but no proof, that the primary control is temperature. In some cases direct damage by frost affirms the importance of temperature (van Steenis, 1968). It is also true

\*Malesia: The Malaysian floristic region of Good (1947), i.e. approximately the political states of Malaysia, Indonesia, the Philippines and Papua New Guinea. The latinised spelling is adopted to avoid confusion with the political state of Malaysia.

that a few transplantation experiments have shown that species rarely flourish outside their ordinary altitudinal range (van Steenis, 1962a), but this could be due to other factors which vary with altitude such as ultraviolet radiation. Phytotron experiments are what is really needed. Even if, as does seem likely, temperature is the causal factor, precisely how it operates is not clear. Brunig (1971) has shown that physiological drought may be likely at high altitudes, due to diurnal variations in leaf temperature, while Grubb (1974) has shown that transpiration may be impaired due to the foggy conditions prevalent on mountains.

#### 1.2.5 SWAMP VEGETATION

Equatorial swamps come in two main kinds: salt and brackish water (mangrove) swamps, and freshwater swamps. There is, of course, no real dividing line between the two, and the vegetation forms a continuum.

Mangrove swamps are vegetated by woody species (mangroves) of several plant genera, for example *Rhizophora*, *Avicennia* and *Bruguiera*, all of which can withstand degrees of inundation by tidal water. The most well-known growth form is that in which abundant aerial roots emerge from the trunk, making an almost impenetrable barrier. Although mangroves may occur on a variety of substrata including coral, they are usually found on silty and clayey deposits. Mangrove propagules are, not surprisingly, adapted to marine dispersal; for example, in *Rhizophora* the seed germinates while still on the tree to produce a vastly enlarged radicle up to 30 cm long, and capable of supporting the seedling in sea-water.

Mangrove swamps are zoned approximately according to the amount of inundation, the salinity of the water, exposure and other factors; the situation is somewhat analogous to the zonation of a temperate salt marsh. A good example is that from the west coast of West Malaysia (Watson 1928).

Freshwater swamps bear vegetation which varies according to altitude, water depth, nutrient status and other factors. Water which is regularly over 2 m deep normally bears either submerged aquatics, or a *schwingmoor* (floating mat), frequently with Cyperaceae as the main structural basis. Shallow water may be dominated by Cyperaceae or Gramineae or by trees and shrubs. Swamp forest may be present in shallow water or where the water table fluctuates. Vast areas in the Amazon Basin, the Irrawaddy floodplain and the lowlands of Borneo, Sumatra, and New Guinea, support swamp forests of various kinds.

A remarkable development found particularly in South-East Asia is the peat-swamp. These gently domed areas of peat may be many kilometres across, and are analogous to the raised bogs of temperate regions (Anderson, 1963, 1964). They are entirely forested, but there is a steady decline in diversity, from over 50 species at the edge, to only 20–30 species in the centre (Anderson and Muller, 1975). Indeed single-species dominance (as by *Shorea albida*) is common.

The successional relationships of these many types of swamp vegetation will receive attention in Chapter 6.

### 1.2.6 SECONDARY VEGETATION

Most of the vegetation types so far described may be regarded as primary, in the sense that they are believed to be part of the original pattern of vegetation types before man began to affect vegetation. But there is another whole suite of vegetation types which are believed to result directly or indirectly from human activities and are therefore secondary. The term anthropogenic is sometimes applied to such vegetation, but as this literally means 'man-producing' rather than 'man-produced' it is an unfortunate term and best replaced by 'man-made'. The impact of man in equatorial regions as in temperate regions appears to have been principally through felling, burning and agriculture (Thomas *et al.*, 1956). The effect of various minor activities in the forests, such as hunting and the gathering of food and lianes, has remained largely unassessed.

The vegetation of plots abandoned after clearing falls into a sequence of stages which vary enormously depending on the proximity of forest, the duration of clearance, the type of cropping and other factors. The act of clearance exposes the soil to the sun, resulting in direct oxidation of organic matter. If fire is used in the clearance further loss of organic matter results. Most of the nutrients in a tropical land ecosystem are stored not, as in temperate systems, in the soil, but in the biomass, principally the vegetation. Burning results in the gaseous loss of some elements such as nitrogen and the conversion of others to mineral ash which is rapidly leached by the tropical rainfall. Clearance therefore tends to lead to soil degradation and infertility. The result is that primary forest trees are, in many cases, unable to invade cleared land immediately it is abandoned, for their seedlings seem to require higher nutrient status and, in many species, shade. Early dominants of secondary vegetation are therefore usually grasses, tree ferns and small trees. The trees concerned are adapted to the secondary habitat by rapid growth, good seed dispersal, ability to germinate in the open and ability to flourish on poor soils (sometimes the result of nitrogen-fixing root nodules as in *Casuarina* spp. and *Trema* spp.). The secondary trees are considered to have been, before man's activities, 'nomads' in the forest, dependent on rare natural events for their survival (van Steenis, 1958a). Successional aspects of this secondary vegetation will be considered in Chapter 6.

### 1.2.7 THE GEOGRAPHICAL DISTRIBUTION OF PRESENT VEGETATION

Most vegetation types occur where ecological considerations would lead you to expect them (*Figure 1.5*). Secondary vegetation and agricultural land alone do not follow these relatively simple trends. In general,

man has used the land close to the sea, rivers and other access routes. The latest example is the clearance of land on both sides of the new Amazonian roads. Sometimes geological considerations have been important to man, for instance much of the east coastal plain of W. Malaysia has been cleared during tin-mining operations. The greater clearance of land in lowland Java than in lowland Sumatra is related closely to the much greater population density on Java. Whether land remains in cultivation or reverts to secondary vegetation again depends on complex factors. Soil fertility is important, but economic or other factors may also be very significant. In the New Guinea Highlands, valley bottoms were deserted possibly because malaria was more prevalent there; alternatively they may have been relinquished because they were difficult to defend when population pressure led to increased inter-tribal warfare (Brookfield, 1964).

### 1.3 THE VALUE OF VEGETATIONAL HISTORY

The study of present vegetation raises a number of problems. Some may be wholly or partially solved by vegetational history. Past vegetation changes may also be evidence of great importance for other sciences such as climatology, geomorphology, stratigraphy, geophysics, archaeology and human geography. Topics to which vegetational history in equatorial regions may have particular relevance are briefly mentioned below.

#### 1.3.1 ANOMALOUS RANGES

The theoretical distribution range for a taxon (a unit of classification such as a species, genus or family) is a circular one resulting from a spread outwards from its centre of origin; the size of the circle would relate to the age of the taxon (Willis, 1922). Distributions fail to reach this theoretical ideal to various extents, and when they depart markedly from it they may be called anomalous. The modes of departure are various, and some are susceptible to historical investigation; a few examples are given below:

##### *Relict ranges*

If there are grounds for thinking a taxon to be ancient, for instance if it is taxonomically isolated or morphologically primitive, then it should have a wide range. If it has a restricted distribution, there is a strong possibility that it is a relict and was formerly more widespread. Fossil evidence of this may be readily available if it is a morphologically distinct taxon. Thus the conifer genus *Metasequoia* is restricted now to a single area of China, but occurred also widely in North America and Europe in the Mesozoic and Tertiary Eras.

##### *Disjunct ranges*

The range of a taxon is disjunct when the taxon occupies two or more well separated geographical areas. Between these areas barriers of different kinds

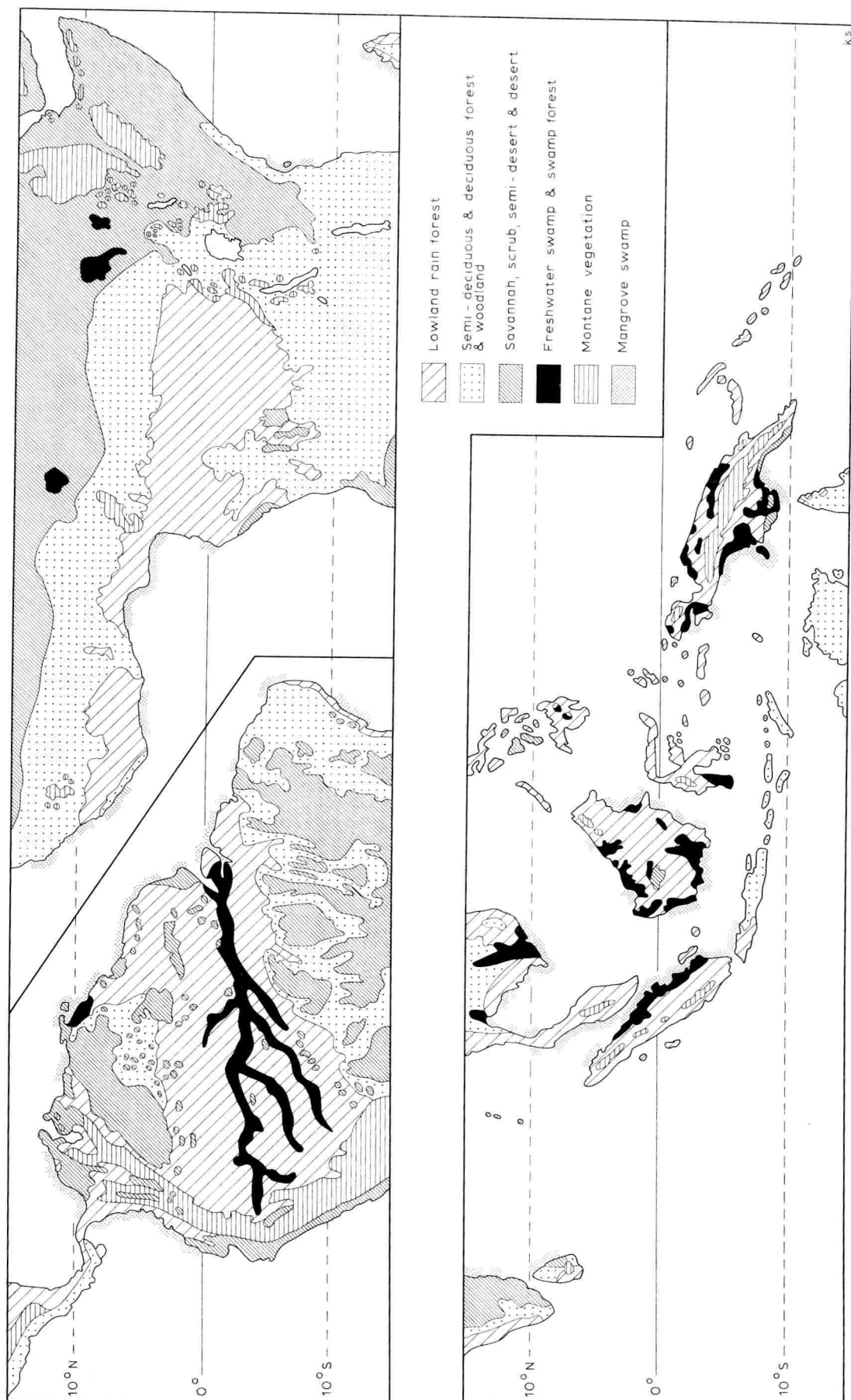


Figure 1.5 The present vegetation of equatorial regions (ignoring recent forest clearance). Compiled from various sources including van Steenis (1958b), Clark (1967), Livingstone (1975), van der Hammen (1974), Eiden (1974) and Hueck and Seibert (1972)



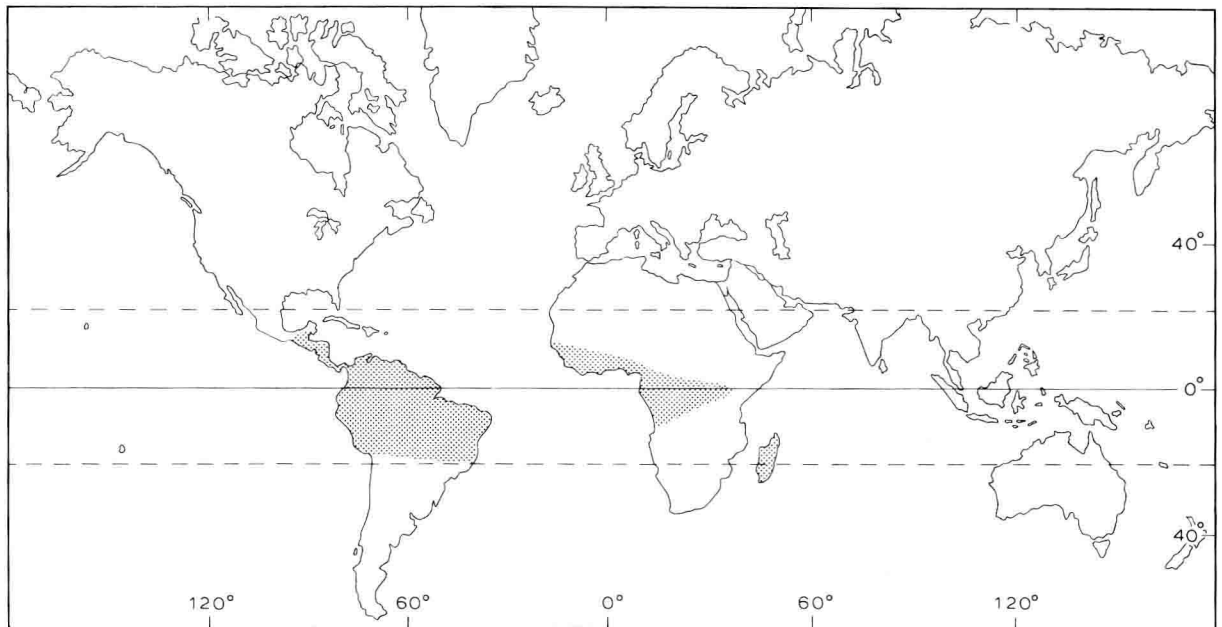


Figure 1.6 Distribution of the genus *Symphonia*. A distribution in accordance with plate tectonic theory. (After Good, 1947)

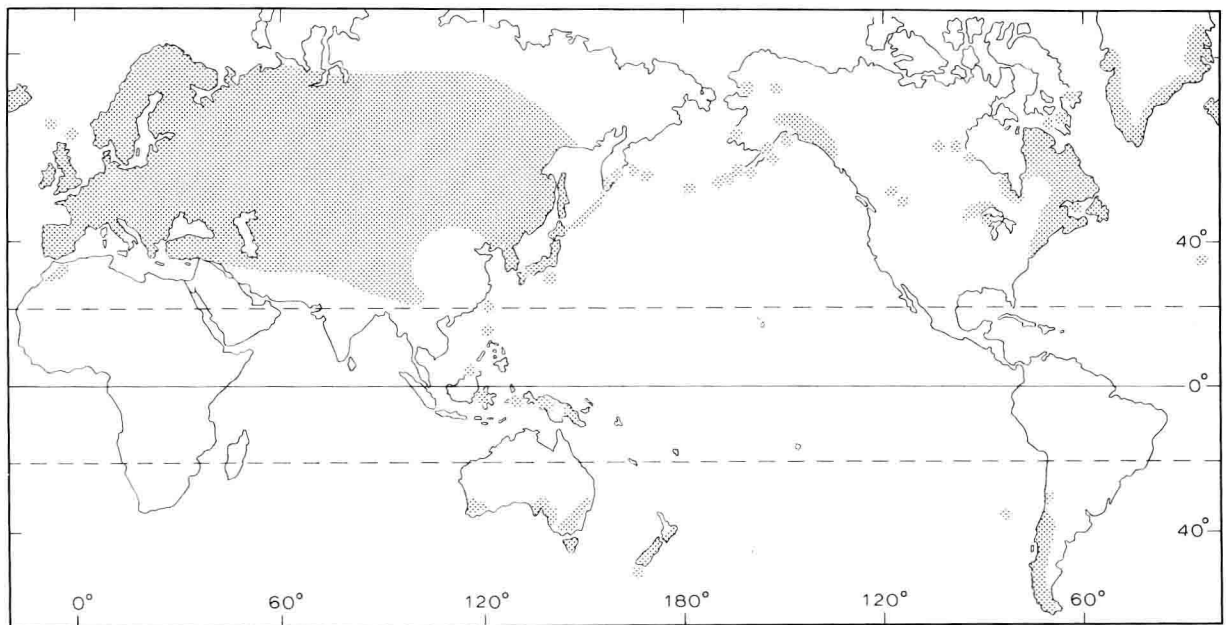


Figure 1.7 Distribution of the genus *Euphrasia* showing equatorial occurrences (on mountains) of a mainly temperate genus. (After van Steenis, 1971)

are normally present. The most common barrier is the ocean, as with the genus *Symphonia* (Figure 1.6), that is present in the African and South American tropics, separated by the Atlantic. Another common barrier is a mountain range: for example, differences in plant communities on either side of the Rocky Mountains of North America cannot all be explained by climatic differences. The reverse is the situation for mountain plants, which can be regarded as living on islands in a sea of lowland vegetation. The genus *Euphrasia* is present on numerous high mountains in South-East

Asia (Figure 1.7) but totally absent in the intervening lowlands. In the last two cases the barrier is presumably a climatic one: lowland species cannot grow in the mountains and *vice versa*. Another example of climatic disjunction is that exhibited by many taxa in the semi-evergreen forests of South-East Asia (Ashton, 1972). These forests occur in the monsoon climate, with a pronounced dry season, in Thailand and East Java, but are absent from the everwet areas in between (Figure 1.5). In some cases land itself is a barrier; the mangrove swamps on both sides of the Isthmus of

Panama show similarities and differences which are probably closely related to their history.

The contribution of historical data in these cases could well be crucial. In the case of major disjunctions between continents, a demonstration that the taxon had a long history on both sides of the barrier might well, in conjunction with geological evidence for continental drift, solve the problem completely. In the case of mountain barriers it would again be relevant to know the history of the disjunct taxon in relation to the age of the mountain range. Did the plant, for instance, exist on both sides before the orogeny, or did it succeed in crossing the barrier in some way?

The problem of mountain floras has long been of interest to biogeographers. In temperate regions it has been shown that historical evidence is decisive; for example in Britain the Late-glacial lowland flora included many Arctic-alpine species which became restricted to mountains during the Post-glacial forest period (Godwin, 1956). In the tropics close relationships between the floras of separate peaks have been established in Africa (Hedberg, 1964) and in South-East Asia distinct 'migration tracks' have been recognised (van Steenis, 1934–36). In South America the various cordilleras of the Andes form the clear migration routes. All tropical montane floras have distinct relationships with temperate floras. Darwin (1859) clearly enunciated the possibility that a former cooling of climate had been very important in aiding the migration of species to tropical peaks from temperate areas, and the idea was thoroughly espoused by Wallace (1869). Not all later workers have agreed with this. Van Steenis (1934–36) for example, preferred the possibility that former continuous mountain chains had existed, although there is little geological evidence for this. The body of data relevant to the tropical mountain floras is now considerable (see Chapters 3–5).

In the case of disjunction in the lowlands between two blocks of rain forest, historical evidence could possibly show the former similarity of the now separated blocks.

#### *Vicarious ranges*

When two closely related taxa occupy the same ecological niche in different geographical regions, they may be termed vicarious (Good, 1947). There is always a strong supposition that such taxa have a common evolutionary origin and have diverged following isolation. It would be desirable to check this hypothesis against the fossil record, although this does not yet appear to have been done successfully.

### 1.3.2 SUCCESSIONAL CHANGES

The classical accounts of successions (Clements, 1916; Tansley, 1920) are all related to temperate examples. Tropical successions remain little studied, although they are clearly very different from temperate ones. Even in temperate areas it is impossible to obtain certain knowledge of the precise sequence of events

without historical information. It is very tempting to examine, say, a series of concentric zones in the hydrosereal vegetation around a lake, and to conclude that the zones also represent successive stages in a temporal sequence. Unfortunately this may be an incorrect conclusion, and it is necessary to examine fossils in the lake deposit before the actual succession is revealed. This technique has led to a critical re-evaluation of many earlier ideas about the temperate hydrosere (Walker, 1970b). In the case of a xerosere, the pages of history are not so well preserved; it is necessary to choose a site of sediment accumulation lying within the area of land under study. One particular type of xerosere, the vulcanosere, is quite abundant in some equatorial regions and may be studied by analysis of deposits from crater lakes.

When the direction in which a succession is moving is known it is still very difficult to know the rate of change. This may have important applications, for example the time needed for secondary forest or logged forest to revert to a forest similar to the primary forest is essential knowledge in planning any sensible use of forest resources. Vegetational history may be able to provide this information.

### 1.3.3 DIVERSITY

Diversity may be defined in several ways, but is usually some measure of the richness in species of an area, a community or a flora. Whatever criteria are used, tropical lowland forests emerge as very diverse compared with those from semi-arid, temperate or montane habitats. Indeed there is, with many exceptions, a general decline in diversity from equator to pole and from sea-level to the snow line. The more one thinks about this the less obvious appear the reasons for it. The number of plant species in any defined area is the resultant of two factors: the rate of acquisition of species by immigration into the area or by speciation, and the rate of extinction or emigration of species once there. A balanced, but dynamic, equilibrium is achieved when these two rates are equal. This was understood by Darwin (1859), and has been put in more mathematical terms by MacArthur and Wilson (1967). In the case of small islands near a continent, immigration may be the main means of acquiring new species, but in the case of large land areas speciation is usually more important than immigration.

The theories which try to explain the incredible variations in diversity throughout the globe may be grouped as shown in *Table 1.1*. It must be emphasised that the theories are not mutually exclusive. It is clear from *Table 1.1* that several of the theories could be tested if sufficient historical data were available. The non-equilibrium hypothesis, for example, requires that all but the most diverse communities should have a still increasing diversity. Similarly the theory that tropical populations are more sedentary should be susceptible of historical investigation, as perhaps should the idea that speciation rates are high in the tropics. The whole concept of the stability of tropical

**Table 1.1** AN OUTLINE OF THE BASIC HYPOTHESES CONCERNING SPECIES DIVERSITY, PARTICULARLY THE INCREASED SPECIES DIVERSITY IN THE TROPICS COMPARED TO TEMPERATE AND ARCTIC REGIONS. (AFTER RICKLEFS, 1973)**NONEQUILIBRIUM HYPOTHESIS**

Time — the tropics are older and more stable, hence tropical communities have had more time to develop.

**EQUILIBRIUM HYPOTHESES**

- I. Speciation rates are higher in the tropics.
  - A. Tropical populations are more sedentary, facilitating geographical isolation.
  - B. Evolution proceeds faster due to
    1. a larger number of generations per year.
    2. greater productivity, leading to greater turnover of populations, hence increased selection.
    3. greater importance of biological factors in the tropics, thereby enhancing selection.
- II. Extinction rates are lower in the tropics.
  - A. Competition is less stringent in the tropics due to
    1. presence of more resources.
    2. increased spatial heterogeneity.
    3. increased control over competing populations exercised by predators.
  - B. The tropics provide more stable environments, allowing smaller populations to persist, because
    1. the physical environment is more constant.
    2. biological communities are more completely integrated, thereby enhancing the stability of the ecosystem.

environments (non-equilibrium hypothesis and equilibrium hypothesis IIB in *Table 1.1*) is also capable of investigation by vegetational history.

**1.3.4 STABILITY OF COMMUNITIES**

A popular recent hypothesis has been that the more diverse a community is, the more stable it will be (MacArthur, 1955). There are some good reasons for believing this: for instance, the populations of a predator and its prey in a simple community often fluctuate wildly, but in a more complex one the predator can use various prey and fluctuations are thus damped down. The hypothesis has often been bolstered, however, by quoting the rain forest as an example of great stability through geological time. If it could be shown that tropical forests, despite their diversity, have changed markedly in distribution in the Quaternary, and are therefore not particularly stable, this would argue against the hypothesis.

**1.3.5 THE EFFECT OF MAN ON VEGETATION**

Man is an animal and like all animals he affects his environment to some extent, but the effects of man are astounding. Even primitive man at an early level of evolution may have had sufficient knowledge of tools and fire to affect forest cover, and the activities of prehistoric modern man in this direction are well known. Mesolithic cultures have left tree trunks with the marks of the axe which felled them and forest clearance of this age can be detected now in British pollen diagrams. The activities of neolithic cultures are even clearer; forest destruction becomes obvious and even the pollen grains and fruits of the cultivated plants have been recovered from organic deposits and archaeological sites. Agriculture is also indicated by the presence of weeds, recorded as both pollen and seeds. Indeed, it is even possible to conclude, from the assemblages of weeds present, whether a particular agricultural phase was primarily pastoral or arable.

The success of this historical approach in elucidating the origins of farming and of secondary vegetation in temperate regions encourages one to expect much of it in the tropics. This is particularly so in view of the significance of tropical regions for the origin of cultivated plants. In his classic work on this subject, Vavilov (1951) distinguished eleven centres of origin for cultivated plants. Five of these are wholly or partially in the equatorial regions. There is a good chance, therefore, that the vegetational history of equatorial regions holds important evidence regarding the origins of agriculture.

Several equatorial vegetation types, especially savannahs and grasslands, are of possible secondary origin, or at least maintained by man, and there is every possibility that the factual data provided by the historical approach can also throw light on this field of study, which until now has been dominated by speculation.

The effects of man on vegetation will be reviewed in Chapter 7.

**1.3.6 CLIMATIC CHANGES**

It is sometimes said that if one examines a set of vegetational changes — as recorded, for example, in a pollen diagram — and removes the effects of natural successions, soil maturation and human and animal activity, then what is left must be due to climatic change. This statement needs several caveats, but it adequately expresses an important viewpoint, that is, the reluctance of reputable biogeographers to attribute vegetational changes too readily to climatic change. There is, of course, unimpeachable evidence for climatic change in the Quaternary, especially from temperate regions. From the equatorial regions the evidence is much less strong. I do not intend to review other than vegetational evidence, but it is perhaps desirable to mention it very briefly:

*Glaciation*

Most tropical mountains over about 3800 m high bear

evidence of Pleistocene glaciation. Deglaciation has in some cases been dated to between 8000 and 15 000 B.P. (Livingstone, 1962; Gonzalez *et al.*, 1966; Hope and Peterson, 1975; Flenley and Morley, 1978).

#### Lake levels

Several lakes which are centres of internal drainage show evidence of former higher levels, e.g. the surface of Lake Nakuru in Kenya was formerly 180 m higher than at present (Washbourn, 1967).

#### $^{16}\text{O}/^{18}\text{O}$ ratios

The measurements made by Emiliani (1955) claimed to show that the tropical Atlantic surface water was  $6^{\circ}\text{C}$  cooler during the late Pleistocene. Unfortunately it now seems likely that these ratios indicate not so much the temperatures as the amount of water incorporated in world ice sheets at the time, which can only be an indirect indication of tropical temperatures (Shackleton, 1967).

#### Soils and weathering

In some areas the soil is one which is known to form only under a different climatic régime from that obtaining in the area at present, e.g. some lateritic soils of the Lesser Antilles, India, Senegal and Queensland (Mohr and van Baren, 1960).

#### Geomorphology

Some physical features of the landscape can only form under certain climates, for example, dunes usually require desert conditions. In some cases present climate does not conform with landforms at all; in Amazonia, Tricart (1974) describes dune systems seen, on satellite photographs, in savannah areas where there is no possibility of dune formation today.

Alluviation has been taken to imply certain climatic conditions, but it is difficult to interpret this evidence since high values for suspended solid matter may be characteristic of rivers in both high and low rainfall areas (Douglas, 1967).

#### Animal distributions

Many animals show distributions only explicable in terms of climatic change, possibly combined with other geological changes. For instance, in the opinion of Simpson (1971), the bird fauna of the Amazon can only be explained if the Amazon rain forest was divided into several separate blocks during the Pleistocene.

#### Theoretical considerations

Modern theories of climatic change are legion (Flint, 1971). Some of these, such as Milankovitch's theory, would require little or no climatic change in the tropics. Others, such as the theory of variation in solar output, imply considerable world-wide changes, although it is likely that the high albedo of the glaciated temperate regions would have led to exaggerated change there compared with the tropics. In arid regions there is a possibility that the so-called 'pluvials', if they occurred at all, occurred at quite different times depending on the latitude, for if a general

cooling led to decreased atmospheric circulation, all climatic belts might move towards the equator. Thus pluvials near the equator would tend to coincide with interglacials, while those further away would be more prone to occur along with glacials. Figure 1.8 shows several suggested models for climatic change near the equator.

When climate changes it is likely to do so in an extremely complex manner. A lowering of solar output, for example, might result in a lessening of

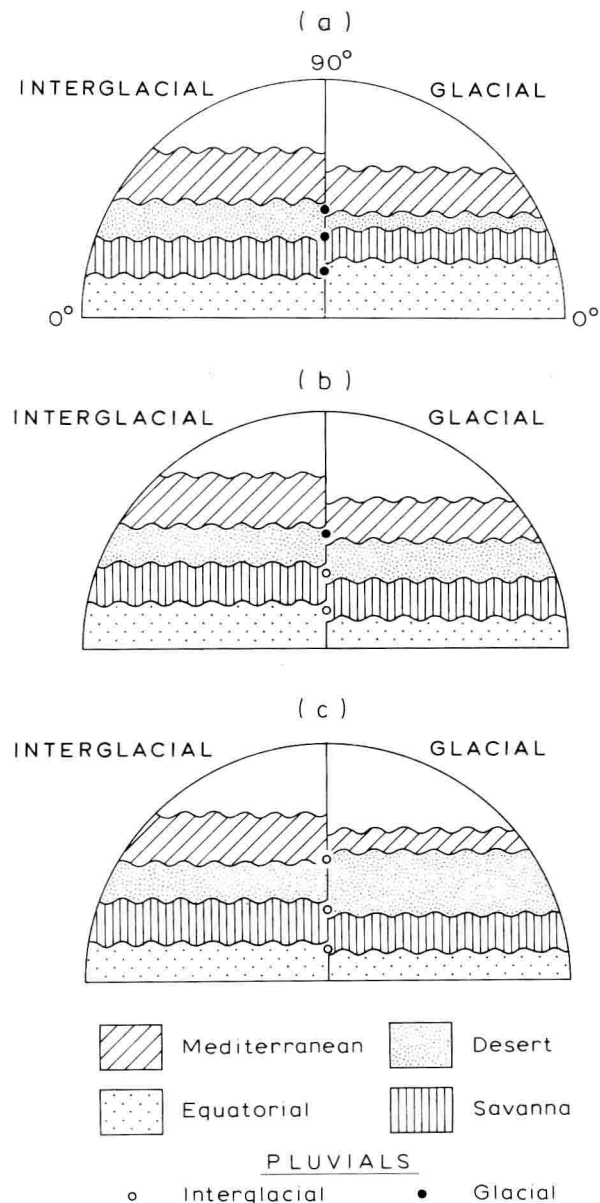


Figure 1.8 Some theoretical schemes for the glacial/interglacial cycle in low and middle latitudes.

(a) The 'old pluvial' theory. All pluvials are synchronous with glacials.

(b) All climatic belts move towards the equator in glacial times. Some pluvials are synchronous with glacials, others with interglacials.

(c) Deserts expand during glacial times. All pluvials are synchronous with interglacials.

Several other such schemes have been proposed. Present evidence favours (c). (Original)