CHAPTER 5

FOREST ECOLOGY

CHAPTER OUTLINE

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5.1 INTRODUCTION

This chapter aims to provide the reader with the ecological knowledge that is considered important for anyone seeking to develop a working understanding of conservation and of natural forest management. Although it is possible to manage natural forests without in-depth ecological understanding, experiences from around the world suggest that, in the long term at least, such management will fail. No-one would suggest that forests are best managed exclusively by ecologists, but in ecology must play its part. In today's forestry, with its emphasis on multiple values and sustainability, it is more vital than ever before that foresters have a broad understanding of ecology.

5.1.1 What is ecology?

Ecology is the study of the processes and interactions between organisms and their environment, both **biotic** (living) and **abiotic** (non-living), and their resultant patterns of distribution and abundance.

5.1.2 Why do we need to know about ecology?

Nature conservation can be interpreted at many levels. For some people, it may mean the conservation of particular species of plant or animal, for instance ones which are particularly rare or threatened. But it is impossible to divorce any one species from its natural environment, so to conserve any species successfully we need to know something about its environment too. Ecology is concerned with distribution and abundance, and helps to explain why particular organisms are where they are, and in what quantity.

Likewise, we may want to manage the natural environment to meet our own needs or desires, for instance for timber or for bush meat, or for multiple use. Even man-made ecosystems, such as plantations, still have to obey basic ecological principles. We risk running into problems if we try to manage any ecosystem this way without a good understanding of the processes and interactions that are going on between organisms in that environment, and between organisms and the environment around them. Understanding ecology enables us to make predictions about the likely impact of any management on both the target species or area and those with which the species or area interacts. An understanding of ecology is therefore essential if we are to make informed decisions about management.

It is therefore in our own self-interest, and in the interests of conservation, that we know something about the ecology of the environments around us and in which we are working.

5.2 SOME BASIC ECOLOGICAL CONCEPTS

There are many things about the natural world that we need to understand. First, we must look for patterns in the natural world. We must appreciate that the natural world is diverse and complex; that it is dynamic but also stable and self-replenishing; that it is organised by physical and biological processes; and that to study it we need to use observation, theory and experiment. Even then, our understanding of nature will never be perfect, limited as it is by our very human perception. These are the basic premises underlying ecology (Krebs, 1985).

Ecology has its own vocabulary to express certain concepts. If we were to study the relationship of an individual organism to its non-living (physical and chemical) environment then we would be looking at the **biology** of that type of organism or species. However, organisms do not usually live in isolation. If any particular area is studied, it will be clear that species form **communities** consisting of large numbers of **populations** of several or many different species (plants, animals and micro-organisms). The relationship of each community with its non-living environment makes up an **ecosystem**. Ecosystems are the fundamental unit of study in ecology, but they can be as small as isolated swamps or as large as an entire forest zone depending on where one chooses to draw the line of study. More pragmatically, it is much more easy to describe an ecosystem by using only its visible structure, i.e. the plant community, or more usually the dominant vegetation type, for example forest or grassland. In practice, many ecologists now use the word **habitat** to describe such features, although the term originally meant the particular environment or home inhabited by a particular species, such as fungi on rotting wood.

Since we have seen that ecology is primarily about processes and interactions, let us look first at some of these interactions.

5.3 INTERACTIONS BETWEEN SPECIES AND THEIR ENVIRONMENTS

No ecosystem has ever been found to consist of just a single species, and most consist of many thousands or even hundreds of thousands. So in any ecosystem, there will be numerous interactions going on between species. These are known as **interspecific interactions**. Each individual organism belonging to each species is striving to maximise production of its own kind. Sometimes this results in competition with other species, sometimes one species will take advantage of another (such as predators and their prey), and sometimes two or more species will act in a way that is mutually advantageous. Many interactions are still not fully known.

Whatever the form that the interaction takes, it means that the destinies of species in an ecosystem are often intricately linked, one with another: the loss of one link can easily have knock-on effects on other species. Broadly speaking, interactions may be classed as either positive or negative. In **positive interactions**, one or both species benefit from the arrangement, and neither is harmed. In **negative interactions**, one or both species is harmed by the arrangement. Table 5.1 outlines a classification of interactions with some examples.

5.3.1 Fig pollination and dispersal

Because tropical forests contain so many species, they are particularly rich in interactions too. Some of these interactions are highly specialised. A classic example of this is the mutualistic relationship between fig trees and their fig wasps (Pomeroy and Service, 1986; Whitmore, 1990). The fruits of fig-trees (*Ficus* spp.) are remarkable structures, highly adapted to their associated fig-wasps (insects of the order Hymenoptera: family Agaonidae). The fruit is derived from an inverted flower-head, forming a hollow structure (the synconium) which has only a narrow opening to the outside, called the ostiole. Every species of fig-tree is pollinated by a single species of fig-wasp. Thus Budongo Forest, which supports over twenty fig species (Synnott, 1985), may also support the same number of species of fig-wasp.

A female fig-wasp enters the synconium by squeezing through the ostiole. Once she is inside, she lays eggs in some of the female flowers. She also pollinates other female flowers with pollen brought in her pollen sacs from the synconium where she was born, and in this way cross-pollinates the tree. The female wasp dies, but the female flowers containing eggs enlarge into galls, providing food and shelter for the next generation of wasp larvae.

After pupation the adult wasps emerge, first the wingless males, and then the females. They mate, and the male then makes a hole through the wall of the synconium, after which he dies. The hole enables the female to escape, but before she goes she collects pollen from stamens which have ripened later than those previously visited by her mother. Female fig-wasps pollinate more flowers than they lay eggs in, so the synconia produce seeds and their flesh ripens. The process of pollination stimulates the ostiole to close, thus excluding more wasps from entering, whilst the presence of eggs in the female flowers inhibits the fruit from ripening too quickly or dropping. Eventually it does ripen, but not before most of the wasps have emerged.

Table 5.1.
A classification of species interactions. After Pomeroy and Service (1986).

POSITIVE INTERACTIONS one or both species benefit, neither is harmed			
MUTUALISM both species benefit		COMMENSALISM one species benefits, the other is unaffected	
Facultative mutualism	**Symbiosis (obligate mutualism)**	**Normal commensalism**	**Phoresy**
relationship is temporary	one species cannot exist without the other	the benefiting species obtains food or shelter from the arrangement	the benefiting species uses the other for transport
example: *monkeys and the trees whose seeds are usually consumed by them but are occasionally dispersed by them.*	***example:*** *fig tree and fig wasp; termites and the wood-digesting protozoans living in their guts.*	***example:*** *mites living in the roots of primate eyelashes*	**example:** *soil mites that disperse by clinging to insect legs; sticky seeds or burrs from plants growing along tracks sticking to animal fur*

NEGATIVE INTERACTIONS one or both species is harmed				
Harmed species often dies			**Harmed species normally survives**	
Predation	**Parasitoids**	**Competition (interspecific or intraspecific)**	**Parasitism**	**Grazing and browsing**
one organism consumes another	kill their hosts while completing their life-cycles	sometimes leading to death of the loser	the host is not normally killed while the parasite completes its life-cycle	by animals on plants
example: *leopard preying on duikers*	***example:*** *ichneumon wasp larvae developing inside caterpillars*	***example:*** *two cockerels fighting; paper mulberry displacing other pioneer trees; strangler fig on host tree*	***example:*** *cassava leaf mosaic virus, or malaria*	***example:*** *bush buck eating grass; caterpillar eating leaves*

It seems there is a species to exploit every opportunity that exists in nature. For example, the developing wasp larvae inside the fig synconium are "sitting targets" for attack by tiny parasitoid wasps. Females of these parasitoid wasps have extremely long ovipositors, several times the length of their own bodies. They settle on the outside of the young fig and insert their ovipositors through the fig until they pierce a developing fig-wasp larva within. An egg is then laid inside the larva, and, on hatching, the parasitoid's larva consumes the living tissue of the fig-wasp larva, eventually killing it before pupating inside the fig. If a fallen fig is opened, it is often possible to see all the players in this series of interactions: the male fig-wasps (many of them dead), an occasional newly-emerged female fig-wasp, and usually many female parasitoid wasps, easily identifiable by their ovipositors.

Many species of fig that live in tropical forests are known as *stranglers*. Once a fig from such a species has ripened, another mutualistic relationship comes into play. Figs are a highly favoured food for many primates and larger birds, who gorge themselves on the fruit as soon as they are ripe, and end up dispersing the fig's seeds. The flesh surrounding the seeds is easily digested, but the seeds themselves normally pass through the gut intact, and are passed out in the faeces. Since many of the animals that eat figs are arboreal (that is, they spend their lives up in the forest canopy), many of the seeds end up falling into crevices in tree branches. On germinating in the humus in these crevices, a fig seedling will send a long root down the side of the branch and trunk of the host tree. Once it reaches the soil, growth becomes more rapid, and more and more roots descend. At this stage, the fig tree itself becomes a competitor with the host tree, and usually it will succeed in gradually weakening the host tree by a combination of strangulation of its trunk and root system (hence the term "strangler fig") and shading out, until the host is killed off and its space taken by a mature fig tree.

So we can see that for its survival through a single generation, a fig tree requires the presence of at least three other species: a host tree in which to germinate, a fig-wasp to pollinate its flowers, and a frugivorous bird or mammal to disperse its seeds. And each of those species may have equally intricate interactions with a range of other species in the forest, and so a whole web of interactions is maintained.

5.3.2 Food chains and food webs

All organisms need energy to survive and reproduce. There are two main potential sources of energy: the sun, and other organisms, either living or dead. The terms used to describe the sorts of organisms that get their energy from these different sources, along with some examples, are shown in Table 5.2.

The process whereby energy is transferred from the sun to primary producers to primary consumers to secondary consumers, is known as a **food chain**. Transferring energy from one trophic level to another is not very efficient. Generally, only about 10% of the energy in a given source is converted into living matter; the rest is lost mostly as heat.

Table 5.2.
Feeding relationships. Adapted from Pomeroy and Service (1986)

Feeding, or trophic, level	Examples
Primary producers (autotrophs) derive energy directly from sunlight by photosynthesis	Green plants; autotrophic bacteria
Primary consumers (herbivores) derive energy by consuming primary consumers	Grazers: eat low-growing herbage *(e.g. cattle)* Browsers: eat leaves and twigs *(e.g. duikers, colobus)* Frugivores: eat fruit *(e.g. hornbills, chimps)* Granivores: eat small seeds *(e.g. mice)* Nectarivores: eat nectar *(e.g. sunbirds)* Sap-feeders *(e.g. aphids)*
Secondary consumers (carnivores) derive energy by consuming primary consumers or other secondary consumers	Insectivores: eat insects *(e.g. many small birds)* Piscivores: eat fish *(e.g. otters)* Cannibals: eat members of their own species *(e.g. occasionally reported in monkeys)*
Decomposers derive energy by consuming dead producers or consumers or their waste products	Detritivores: eat small particles of organic matter *(e.g. earthworms)* Saproxylics: eat dead wood *(e.g. termites and some beetles)* Coprophages: eat dung *(e.g. dung-beetle)* Saprophytes: plants that get some of their energy as decomposers *(e.g. some forest floor orchids)*

This means that there is only a limited amount of energy available for life in any ecosystem, and most of the energy originally absorbed from the sun by plants will have been lost by the time it has passed through a food chain to the secondary consumers. This is the main reason why carnivores and other so-called **top predators**, which sit at the top of the food chain, are normally much rarer than herbivores, which are in turn rarer than green plants. This effect is known as a **pyramid of numbers**, or, since it is not so much numbers as mass which is important, a **pyramid of biomass** (Figure 5.1).

Because many animals do not restrict their feeding to one food source, feeding relationships in any ecosystem consist of numerous inter-linked food chains, called a **food web**. For example, crowned eagles will normally feed on forest primates (which are primary consumers), but sometimes they will also eat insectivorous birds (which are themselves secondary consumers). Humans are even less choosy: we eat plants, herbivores such as goats and duikers, and occasionally carnivores such as dogs, and decomposers such as fungi. As such, we are called **omnivores**.

Food chains and food webs do not stop at the top predator, of course, because even predators are food to decomposers when they die, and, like all animals, are constantly producing waste products while they are alive, which still contain enough energy to feed other decomposers. Without the decomposers, the whole ecosystem would grind to a halt as dead plants and animals and waste products would just accumulate rather than being decomposed and recycled.

It is impossible to represent all the possible feeding relationships that exist in a forest, but Figure 5.2 attempts to do this for a small selection of forest organisms.

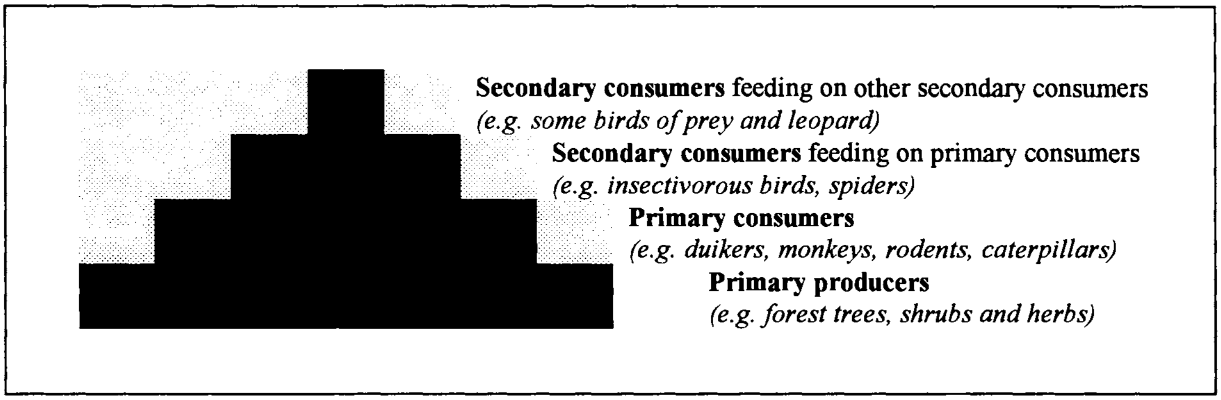


Figure 5.1. A simplified pyramid of biomass for an African tropical forest food chain.

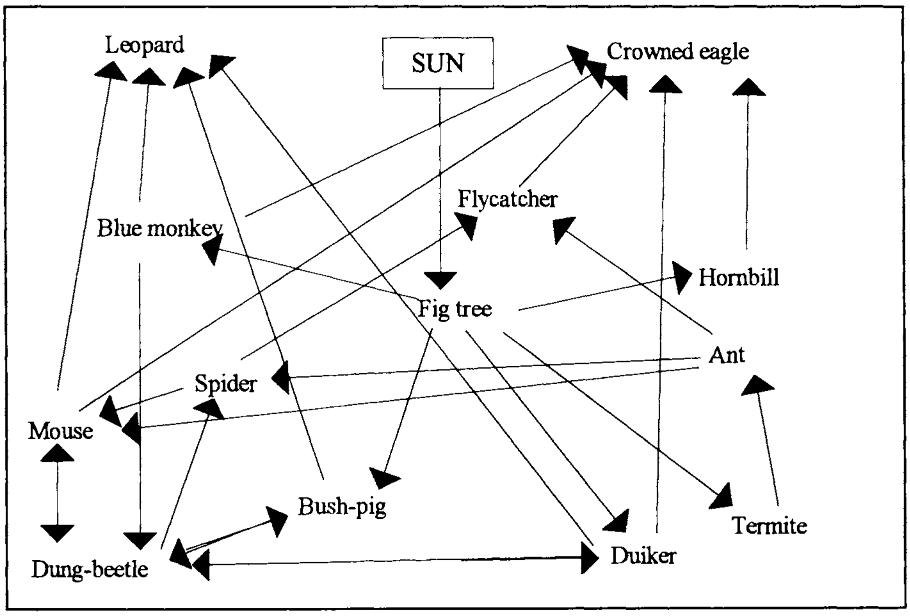


Figure 5.2. A simplified food web for an African tropical forest ecosystem. The arrows point from the consumed to the consumer.

5.3.3 Ecological cycles

Organisms interact with their environment in numerous ways. Perhaps the most important are the various cycles, such as nutrient cycles (involving nitrogen and other elements essential for life), carbon cycles and water cycles. If it were not for living organisms, many of these cycles would not be possible; likewise, if the cycles are interrupted or disrupted by human activities, then whole ecosystems can suffer. Since we are part of those ecosystems, then we need to be aware of the consequences of any disruption. This is not the place to discuss these cycles in detail, but some of the more important cycles are summarised below. See Desmukh (1986) or Pomeroy and Service (1986) for fuller accounts.

5.3.31 Nutrient cycling

There is not space here to go into this subject in detail, but it is worth noting that the main contributors to the recycling of nutrients in any ecosystem, and particularly forests, are the **decomposers**. In a tropical forest, most of the available nutrients normally reside at any one time in living plants and animals; the soil is normally quite deficient even though this is the original source of much of the nutrients. Thus the main way that nutrients can become available for new plant growth is when old plants die. A study reported by Swift, Heal and Anderson (1979) recorded a "litterfall" (leaves, twigs, fruit and flowers etc.) rate beneath lowland tropical rainforest of about 890 $g/m^2/yr$. Once dead, whether it be whole trees or just leaves, a whole army of decomposers, such as bacteria, earthworms, termites and many insects, get to work. The same study also recorded 5,000,000 bacterial cells per gram of soil beneath a tropical rainforest, plus 65,000 organisms classed as microfauna, 22,000 mesofauna and 1,650 macrofauna per square metre. Most of these organisms are involved in decomposition. Thus in quite a short time, most of the nutrients and energy will have been extracted from the plant remains. Animal remains and waste products will be treated in the same way. Some of the nutrients thereby released will be consumed by animals consuming the decomposers, while some will eventually end up in the soil. Almost as soon as they arrive there in a mineral form, plant roots, often aided by symbiotic associations with fungi (called mycorrhizae), will take up those nutrients and build them into their own tissues, so completing the cycle.

Human activities can easily interfere with these cycles. If forest is burnt, or excessive timber, firewood or charcoal is removed, then a sizeable proportion of the nutrients will be lost too, and subsequent regeneration of the forest will be less vigorous than otherwise. If the soil is also exposed and nutrients lost through leaching and run-off, the results can be severe. Many parts of the world which should be able to support forest do not do so because they have lost too many of their nutrients. Sometimes those nutrients end up in other ecosystems. If the land receiving the nutrients is farmland, then this can be put to good use. An example is the very fertile valleys that lie below the eroded slopes of Kigezi, or the West Usambaras in Tanzania. But if there are too many nutrients around, then conditions are said to be *eutrophic*, and only a limited range of plant species will thrive under such conditions.

5.3.32 Carbon cycling

Carbon, in the form of sugars, is the means used by most organisms to store energy. As such, it is passed through the ecosystem when one organism consumes another. Plants initially fix (assimilate) carbon from atmospheric carbon dioxide during photosynthesis; both plants and animals ultimately return carbon dioxide to the atmosphere during respiration, thereby releasing the energy contained in the sugars for other uses. Without green plants constantly absorbing carbon dioxide during photosynthesis, the level in the atmosphere would keep rising.

Recently, levels of carbon dioxide have been rising anyway. This is partly attributed to the loss of forests and vegetation worldwide as a result of human activities, and partly to the burning of fossil fuels which contain carbon that has been "locked away" for millions of years. It is now feared that the increase in carbon dioxide in the atmosphere may lead to global warming through the so-called "greenhouse effect". It does not take much ecological understanding to see that this could have profound effects on ecosystems worldwide, and ultimately on our own species. One solution to this problem that is being given support now is reforestation, to "sequester" or lock away some of the excess carbon dioxide. Since forests grow quickest in the tropics, this is where we can expect to see most reforestation effort. Recent plans for afforestation on Mount Elgon and elsewhere by FACE (a Dutch energy consortium) are part of this concern. It should be remembered, however, that the beneficial effects of afforestation only last as long as the wood: if the wood is burnt or rots, the carbon is again released back to the atmosphere.

5.3.33 Water cycling

Water is essential for life; the wettest places on earth support more species and more biomass than places where water is a limiting factor. The main reservoirs of water are the oceans and lakes. Living plants also act as a reservoir since water is a product of respiration and is constantly lost by plants during transpiration. Through evaporation and transpiration, water ends up in the atmosphere, eventually to fall to earth as rain or snow.

It has long been argued that without forests, there would be less rain. Whether this is true seems to depend on the area in question. For somewhere the size of the Amazon forests, or possibly even the forests of Zaire, it may be so. Clark (1992) found that annual rainfall may decrease by 650-800 mm over large areas that have been deforested, accompanied by a rise in surface temperatures of about 3°C and reduced cloud cover. In Banjul, The Gambia, annual rainfall fell from 1240 mm in 1965, when the surrounding land was well forested, to 650 mm in 1988, when deforestation was almost complete (Sayer et al, 1992). Despite these claims, many people now argue that smaller areas of forest contribute an insignificant amount of moisture to the atmosphere. Sometimes the arguments seem rather circular: for instance, does the high rainfall over Budongo Forest compared to adjacent areas (Figure 5.3) reflect the rain-making properties of the forest, or is the forest there and not elsewhere because the rainfall is higher, due to some other reason such as geographical location? Some people think that it is possible that in areas where most rainfall is convectional (as in much of Uganda), even relatively small forest areas (such as Budongo) might enhance convection sufficiently (because of the "rough" surface of forests and their darker, more heat-absorbing colour) to trigger showers.

It is also argued that some forests, particularly on watersheds, act as sponges, absorbing the impact of heavy or seasonal rains and allowing water to percolate through to the water-table rather than over the surface, and allowing year-round flows in rivers (Hughes, 1950). Since watershed protection is one of the main functions of many of Uganda's forest reserves, it is worth examining this more closely. Generally, anecdotal evidence supports the view that some forests may act in this way. For example, when the forested area of the Parc National des Volcans in the Rwandese Virungas was reduced by 40% in the 1970s (mostly for a pyrethrum-growing project), several of the streams that had previously fed the intensively farmed land below dried up (Ehrlich and Ehrlich, 1990). Similarly, long-term residents of the East Usambara mountains in Tanzania have reported that streams and springs in deforested areas are now dry, and that the climate in general has become hotter and drier (Hamilton, 1989).

A further possibility is that forests produce "occult precipitation", that is, they induce water to settle out of fogs and mists. Nicholson (1930) concluded from studies in Africa and India that in East Africa, occult precipitation was likely to account for about 25% of rainfall in mountain forests.

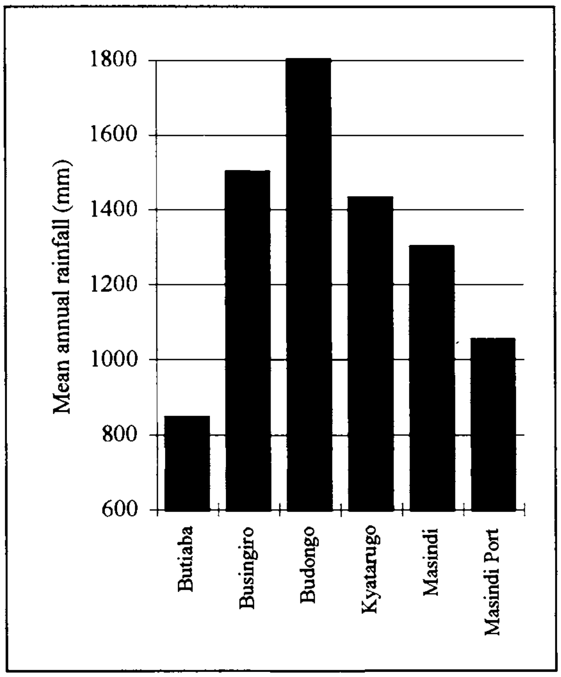


Figure 5.3. Variation in mean annual rainfall in part of north-west Uganda, from west (Butiaba) to east (Masindi Port), through Budongo Forest. Rainfall peaks in Budongo Forest, and declines towards the forest edge at Busingiro and Kyatarugo, apparently tailing off further with distance from the forest. Data are from Eggeling (1947), and refer to ten-year averages to 1943, apart from the figure for Budongo which was a temporary station in the centre of the forest recorded from 1939-1941 only. It is possible that these three years were unusual: more systematic rainfall recording and analysis would be needed to be sure of the apparent trend.

5.4 ECOSYSTEMS AND VEGETATION TYPES

An **ecosystem** is *a functioning, interacting system composed of one or more living organisms and their effective environment, both physical,* of the ecosystem can be used at a variety of scales, since its main value is that it enables us to delineate areas into manageable sizes. How big those areas are depends on what we want from the information.

5.4.1 Biomes

The widest possible scale at which the ecosystem concept applies is the **biome**. Biomes are the major ecological zones of the world, such as tropical rainforest, tropical dry forest, savannah, temperate deciduous forest, tundra and so on. Uganda has three main terrestrial biomes, comprising the first three in this list. One problem is that there is no universally agreed classification. Where, for instance, do we draw the line between tropical rainforest and tropical dry forest? Should we base the classification on what grows there, or on climate? If we just used climate, we would find that some of the savannahs of Africa would have to be grouped with eucalyptus forest in Australia, because eucalypts seem to be able to survive in climatic conditions that in Africa can only support savannah. This means that we still do not know how much of each biome exists on earth. Maps showing the global extent of tropical rainforest differ markedly depending on the classification adopted. Some show tropical rainforest in Uganda, while others do not. Figure 5.4 shows a classification for Africa.

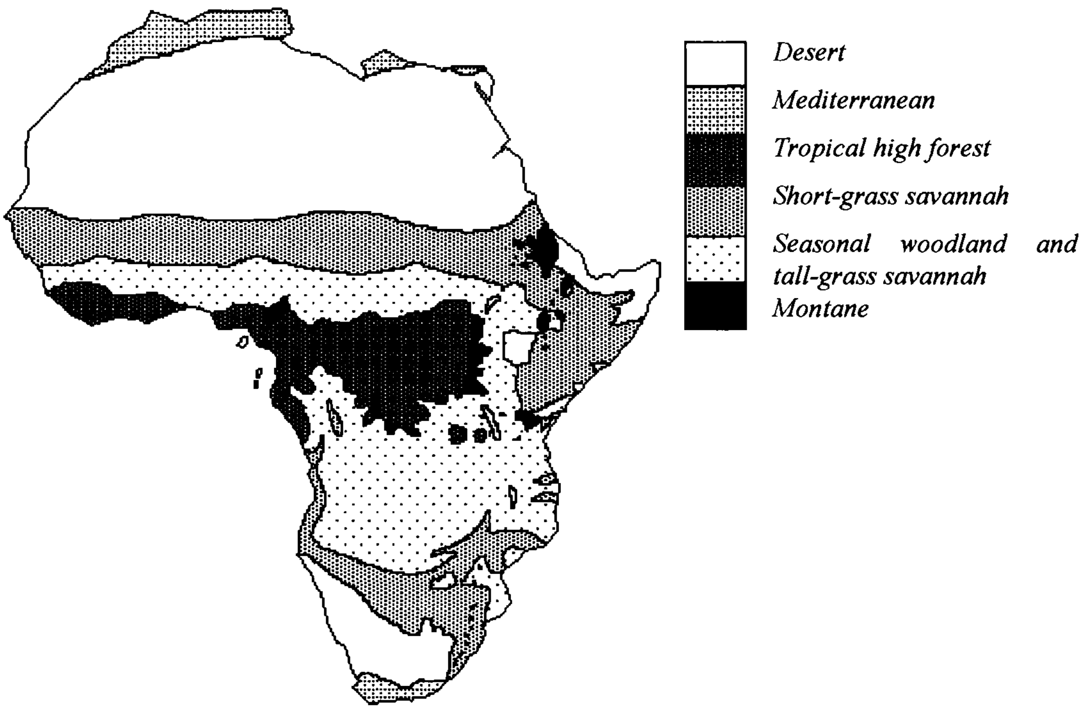


Figure 5.4. A map of the main biomes in Africa. After White (1983).

5.4.2 Vegetation types

Looking at a vegetation map on a finer scale, such as that of Uganda produced by Langdale-Brown, Osmaston and Wilson (1964) (Figure 5.5), one can see that the country is divided into numerous **vegetation types**. These are classified by which plants grow together there, with a particular emphasis on the most dominant types. As such, they are not a full description of the ecosystem, but are descriptions of **plant communities**. Although such a classification does not consider what animals live there, it is often the case that if one can label an area by its vegetation type, one will also be enabling others to know what animals can be expected there too. Box 5.1 outlines Langdale-Brown, Osmaston and Wilson's classification of the vegetation of Uganda. Figure 5.5 is a very simplified interpretation of this classification.

Box 5.1
A classification of the vegetation of Uganda (Langdale-Brown, Osmaston and Wilson, 1964)

A	**High Altitude Moorland and Heath**
A1	*Alchemilla-Helichrysum* moorland
A2	Ericaceae-*Stoebe* heath
B	**High Altitude Forests**
B1	*Pygeum* moist montane forest
B2	*Hagenia-Rapanea* moist montane forest
B3	*Juniperus-Podocarpus* dry montane forest
B4	*Arundinaria* montane bamboo forest
C	**Medium Altitude Moist Evergreen Forests**
C1	*Piptadeniastrum-Uapaca*
C2	*Piptadeniastrum-Albizia-Celtis*
C3	*Parinari*
D	**Medium Altitude Moist Semi-Deciduous Forests**
D1	*Celtis-Chrysophyllum*
D2	*Cynometra-Celtis*
D3	*Albizia-Markhamia*
D4	*Albizia-Chlorophora*
F	**Forest/Savannah Mosaics**
F1	at high altitudes
F2	at medium altitudes
G	**Moist Thickets**
G1	Undifferentiated semi-deciduous thicket
G2	Riparian
G3	Lowland bamboo
G4	Montane
H	**Woodlands**
H1	*Vitex-Phyllanthus-Sapium-Terminalia*
H2	*Terminalia*
H3	*Isoberlina-Daniellia*
H4	*Albizia-Combretum*
J	**Moist Acacia Savannahs**
J1	*Acacia-Albizia-Beckeropsis-Cymbopogon*
J2	*Acacia-Albizia-Chloris-Panicum*
K	**Moist Combretum Savannahs**
K	*Combretum-Terminalia-Albizia-Hyparrhenia rufa*
L	**Butyrospermum Savannahs**
L1	*Butyrospermum-Daniellia-Hyparrhenia*
L2	*Butyrospermum-Hyparrhenia rufa*
L3	*Butyrospermum-Hyparrhenia dissoluta*
M	**Palm Savannahs**
M1	*Borassus-Hyparrhenia rufa*
M2	*Borassus-Hyparrhenia dissoluta*
N	**Dry Combretum Savannahs**
N1	*Combretum-Terminalia-Loudetia*
N2	*Combretum-Hyparrhenia*
N3	*Combretum-Cymbopogon*
N4	*Combretum-Oxytenanthera-Hyparrhenia*
N5	*Combretum-Acacia-Hyparrhenia*
N6	*Combretum-Acacia-Lasiurus*
N7	*Combretum-Acacia-Heteropogon*
N8	*Combretum-Acacia-Themeda*
N9	*Combretum-Acacia-Commiphora*
N10	*Boswellia-Fagara-Heeria*
N11	*Acacia-Combretum*
N12	*Acacia-Heeria-Terminalia*
N13	*Lannea-Combretum-Lonchocarpus*
P	**Dry Acacia Savannahs**
P1	*Acacia-Cymbopogon/Themeda* complex
P2	*Acacia-Hyparrhenia-Themeda*
Q	**Grass Savannahs**
Q1	Moist *Hyparrhenia*
Q2	*Hyparrhenia* grass savannah derived from Type L
Q3	Dry *Hyparrhenia*
Q4	*Themeda-Chloris*
Q5	*Themeda-Loudetia*
Q6	*Themeda-Heteropogon*
Q7	*Eragrostis-Loudetia*
R	**Tree and Shrub Steppes**
R1	*Acacia*
R2	*Lannea-Acacia*
S	**Grass Steppe**
S	*Chrysopogon*
T	**Bushlands**
T1	*Acacia mellifera*
T2	*Acacia-Commiphora-Lannea*
T3	*Acacia-Commiphora*
T4	*Acacia reficiens-Commiphora*
T5	*Commiphora-Euphorbia-Lannea*
T6	*Lannea-Acacia-Balanites*
T7	*Acacia-Albizia-Dichrostachys*
T8	*Acacia mellifera*
T9	*Acacia seyal-Acacia nilotica-Pennisetum mezianum*
V	**Dry Thickets**
V1	Undifferentiated deciduous thicket
V2	*Acacia-Euphorbia*
V3	*Acacia-Commiphora*
V4	*Acacia nubica*
V5	*Acacia mellifera*
W	**Communities on Sites with Impeded Drainage**
W1	*Echinochloa* grassland
W2	*Sorghastrum* grassland
W3	*Brachiaria-Hyparrhenia* grassland
W4	*Acacia-Imperata* savannah
W5	*Combretum-Acacia-Hyparrhenia* savannah
W6	*Combretum-Acacia-Hyparrhenia* savannah
W7	*Acacia-Themeda* savannah
W8	*Acacia-Setaria* savannah
X	**Swamps**
X1	*Cyperus papyrus*
X2	*Miscanthidium*
Y	**Swamp Forests**
Y1	*Rauvolfia-Croton* seasonal swamp forest
Y2	*Baikiaea-Podocarpus* seasonal swamp forest
Z	**Post-Cultivation Communities**
Z1	*Imperata-Panicum-Hyparrhenia*
Z2	*Cymbopogon-Imperata*
Z3	*Hyparrhenia-Pteridium*
Z4	*Eragrostis-Chloris-Hyparrhenia*

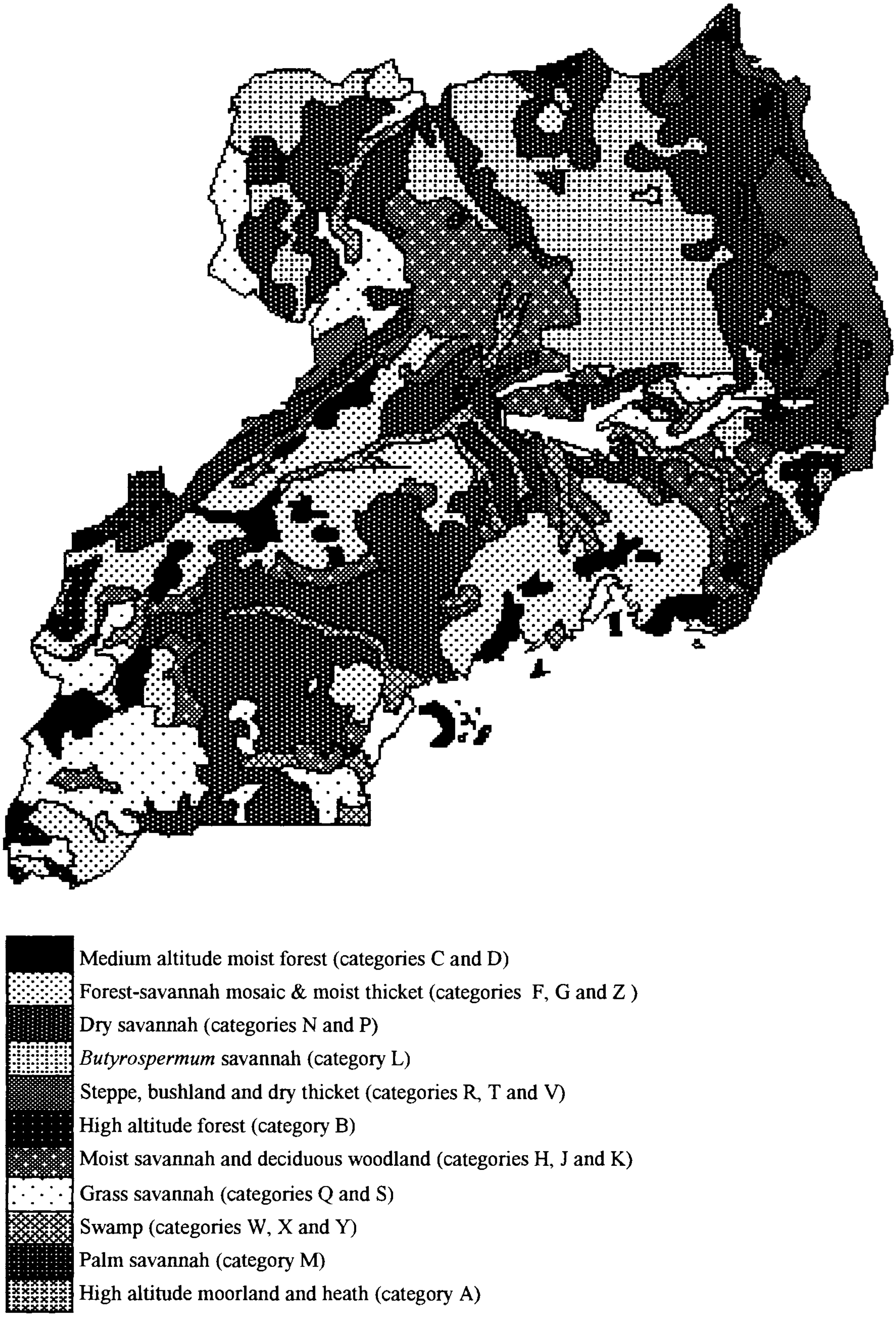


Figure 5.5. A simplified version of Langdale-Brown, Osmaston and Wilson's vegetation map of Uganda. Redrawn from Atlas of Uganda (1967). See Box 5.1 for details.

5.4.21 Why classify vegetation types?

If we know what vegetation types exist in an area, and how common or rare each vegetation type is either locally, nationally or internationally, then we are in a better position to make a rational plan for conserving as wide a variety of vegetation types (and therefore ecosystems and species) as possible. A map of vegetation types also provides a "snapshot" of the situation at the time of the survey, against which future changes in vegetation types can be monitored. Vegetation may subsequently change for natural or human-induced reasons, and comparing standardised surveys made at different times may make it possible to quantify the change and may have implications for management.

5.4.3 What controls the distribution of vegetation types?

Various factors control what grows where. Some of them are shown in Figure 5.6.

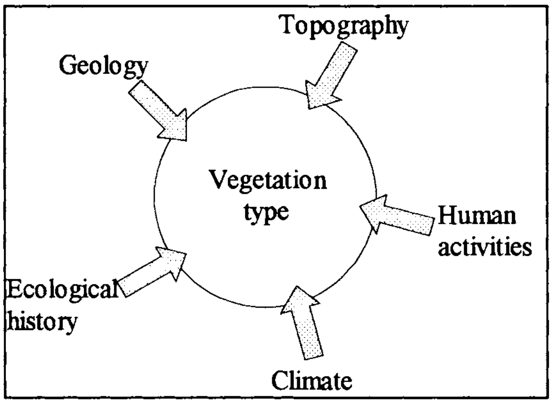


Figure 5.6. Some of the main environmental factors controlling vegetation types. See text for details.

5.4.31 Geology

The nature of the bedrock and soils has some influence on what vegetation can be supported. For instance, there is a large difference between vegetation types growing on calcareous or base-rich bedrock and those on rocks poor in calcium. This is why, for instance, heathland dominated by ericaceous shrubs (A2 in the 1964 classification) is common on the Rwenzoris, where the granite bedrock is extremely base-poor, and rare on the Virungas, where the volcanic bedrock is more base-rich. This means that a conservation area on the top of the Rwenzoris will protect a different range of species from an apparently similar area on the Virungas. Porous bedrocks often support drier vegetation types than impermeable ones for any given set of climatic conditions, although sometimes porous rocks may act as aquifers (underground reservoirs of water) that may enable deep-rooted trees to survive in what appear to be rather dry conditions. Other elements also have some effect on vegetation, but these are not well documented in Uganda, and are likely to be local in effect.

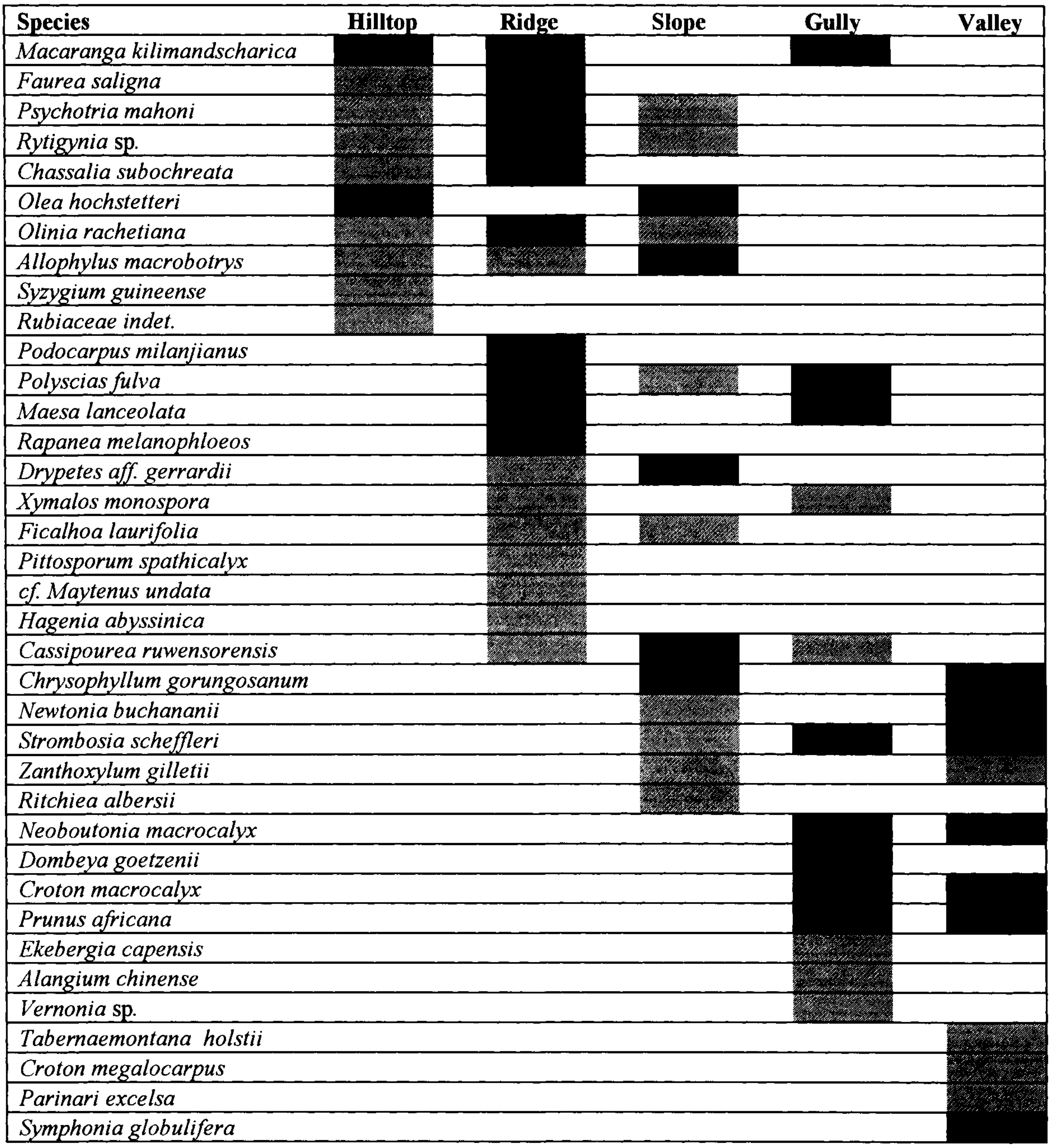
5.4.32 Topography

The biggest influence that topography has is on rainfall and temperature, which are considered under climate below. The way the land slopes also has more local effects on what grows there. Forested slopes often support more light-demanding or short-lived species than flat ground, and swamps in valleys support a different forest type again. Figure 5.6 shows the distribution of various tree species in Bwindi, from a study by Hamilton (1969). It is clear from this study that forest composition changes dramatically according to topography. This means that a conservation area encompassing, for example, just the hilltops and ridges of a forest will be unlikely to protect all the species of that forest, since many species confined to gullies or valleys will be missed.

5.4.33 Climate

Climate is undoubtedly the main factor controlling the distribution of vegetation types at a global and even national scale. The two main climatic factors responsible are **temperature** and **rainfall**.

Global temperatures are, of course, warmest in the tropics and decline towards the poles. This has major implications for vegetation. Polar regions may have sub-zero temperatures year-round, and cannot support vegetation, whereas temperatures in the tropics may be around 30^0C year-round, and can support lush vegetation. Most areas in between these extremes have strongly seasonal climates which favour certain plants over others. Most species of plants (and animals) are dependent on warm conditions, so many are absent from cooler climates. However, some prefer cooler conditions, and cannot tolerate growing in warm regions.



Species	Hilltop	Ridge	Slope	Gully	Valley
Macaranga kilimandscharica	■	■		■	
Faurea saligna	▒	■			
Psychotria mahoni	▒	■	▒		
Rytigynia sp.	▒	■	▒		
Chassalia subochreata	▒	■			
Olea hochstetteri	■		■		
Olinia rachetiana	▒	■	▒		
Allophylus macrobotrys	▒	▒	■		
Syzygium guineense	▒				
Rubiaceae indet.	▒				
Podocarpus milanjianus		■			
Polyscias fulva		■	▒	■	
Maesa lanceolata		■		■	
Rapanea melanophloeos		■			
Drypetes aff. gerrardii		▒	■		
Xymalos monospora		▒		▒	
Ficalhoa laurifolia		▒	▒		
Pittosporum spathicalyx		▒			
cf. Maytenus undata		▒			
Hagenia abyssinica		▒			
Cassipourea ruwensorensis		▒	■	▒	
Chrysophyllum gorungosanum			■		■
Newtonia buchananii			▒		■
Strombosia scheffleri			▒	■	■
Zanthoxylum gilletii			▒		▒
Ritchiea albersii			▒		
Neoboutonia macrocalyx				■	■
Dombeya goetzenii				■	
Croton macrocalyx				■	■
Prunus africana				■	■
Ekebergia capensis				▒	
Alangium chinense				▒	
Vernonia sp.				▒	
Tabernaemontana holstii					▒
Croton megalocarpus					▒
Parinari excelsa					▒
Symphonia globulifera					■

Figure 5.7. The distribution of various tree species near Ruhija, Bwindi Forest, Uganda, after Hamilton (1969). The intensity of shading indicates relative abundance, from abundant (black), through common (dark grey), to present (pale grey). Lack of shading indicates a species is absent.

In a tropical country like Uganda, there are still large variations in temperature, despite the small differences in latitude, because of the presence of mountains. Air temperatures normally vary inversely with altitude. The tops of the Rwenzoris, at over 4000 m altitude, are almost as cold as the Arctic, while the bottom of the Rift Valley around Semliki , at about 600 m, is warm year-round. Vegetation varies greatly as one ascends a mountain in Uganda, largely because of decreasing temperature. Table 5.3 shows how certain characteristics of the vegetation change. Different plant species with different physiologies and appearances will therefore occur at different altitudes, as will different animal species. Figure 5.7 illustrates how these effects determine mountain vegetation types (it also illustrates the effect of rainfall, discussed below). These changes mean that a conservation area situated at, say, 1500 m altitude on a forested mountain will protect a different range of species from another area situated at 2000 m, and different again from one at 1000 m. To ensure adequate protection of all the forest species, a conservation area would have to cover the full altitudinal range of the forest.

Table 5.3.
Changes in rainforest vegetation on tropical African mountains (Deshmukh, 1986)

	Lowland	Lower montane	Upper montane
Ht of taller trees (m)	>30	15-35	<15
Lf area index (cm^2/g)	90-130	80	70
Net wood prodn. (t/ha/yr.)	3-6	1.4	<1.4
Buttresses	Common	Rare	Absent
Predominant leaf size	Large	Large	Small
Conifers	Rare	Common	Common
Vascular epiphytes	Common	Abundant	Common
Non-vascular epiphytes	Rare	Common	Common
Woody climbers	Common	Rare	Rare
Non-woody climbers	Uncommon	Common	Rare

Rainfall varies enormously across the globe, from virtually zero in some deserts to over 5000 mm in some wet montane forests. Even in Uganda, there is great variation, as the map of annual rainfall (Figure 5.8) shows. Parts of Karamoja receive less than 375 mm, most of it falling within a few months of the year, while parts of the Rwenzori mountains may receive over 2500 mm, and possibly much more, falling virtually throughout the year. Furthermore, seasonality of rainfall is also very important in determining what can grow where. Because of this, Kagenda (1975) divided Uganda up into six "rainfall regions" based as much on seasonality as on amount of rainfall

Different plant species tolerate or require different rainfall regimes. In general, closed forest needs more rainfall, and more reliable rainfall, than woodland, which in turn needs more than scrubland or bushland types; most natural grasslands require less still. Most of Uganda's closed forests probably receive about 1200 to 1500 mm of rain per year, in two rainy seasons. Some parts of the country, such as around Gulu, receive sufficient rainfall for forest but none is present, probably because of a long dry season. All Uganda's closed forests lie at the lower end of the range of rainfall regimes under which this vegetation type will grow in the tropics. Tropical closed forest is distributed in Uganda as follows:

- High rainfall belt north-west of Lake Victoria
- High rainfall belt along the eastern side of the Western Rift Valley
- Medium rainfall belt between the first two, where there are some young forests
- Mountains over 1,800 m where sufficient orographic rainfall occurs

5.4.34 Ecological history

What happened in an area in the past will have some bearing on what can grow there now. For example, pine forests are still spreading northwards across Siberia, even though the ice-fields that once stopped them growing there have been gone for hundreds or thousands of years. In Uganda, vegetation belts were about 1000 m lower during the Ice Age peak (21,000-14,000 years ago) than they are now; they are probably still ascending up the mountains. Today, the vegetation zones are not static, and will continue to vary as climates change. Some of the changes in vegetation in tropical Africa over the last two and a half million years are summarised in Box 5.2.

5.4.35 Human activities

One of the biggest factors controlling the distribution of vegetation types and the boundaries of forests these days is the effect of human interference: grazing, burning and cultivation. Although cultivation in Africa's closed tropical forests is generally thought to have begun with the arrival on the continent of suitable crops such as plantains from south-east Asia 2000 years ago, radio-carbon dating suggests that in south-west Uganda, forest clearance may have begun as early as 4,800 years ago (Hamilton, Taylor and Vogel, 1986), although others dispute these dates. Thus the forest-savannah mosaic that covers much of western and southern Uganda is a product not simply of natural processes but of human-induced ones as well, and the same goes for the savannahs and scrublands of other parts of the country. This will be covered more fully in section 5.6.2.

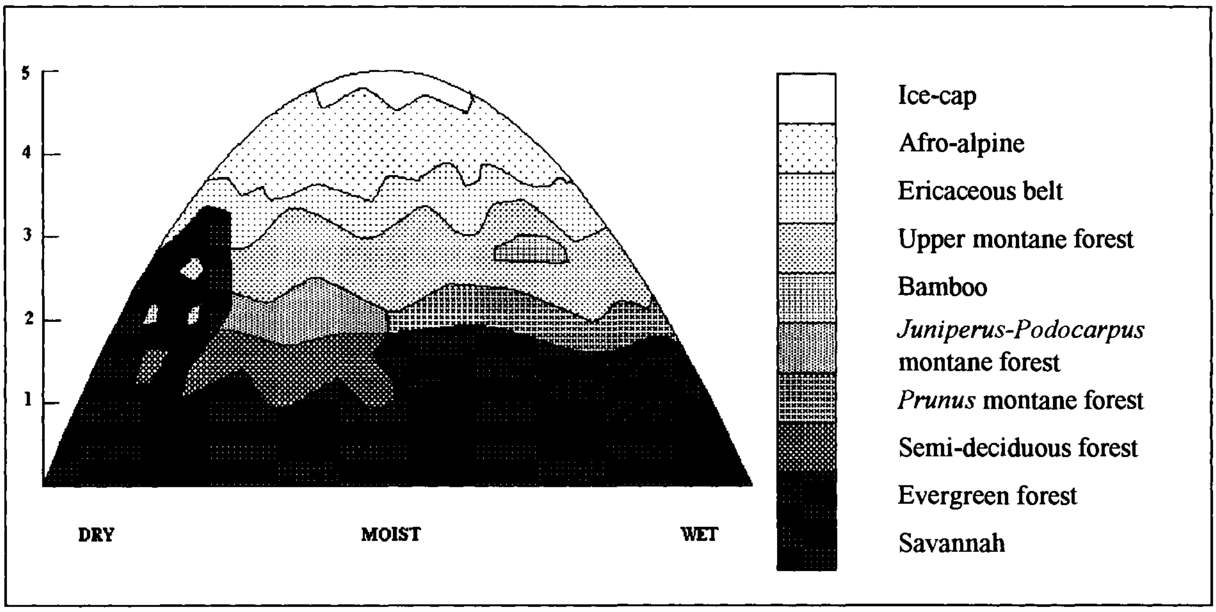


Figure 5.8. Montane and forest vegetation in relation to altitude and moisture in tropical Africa, after Kingdon (1990). This is a generalised diagram; not every mountain may have all zones. In Uganda, ice-caps are restricted to the Rwenzoris. Altitudes are given in thousands of metres.

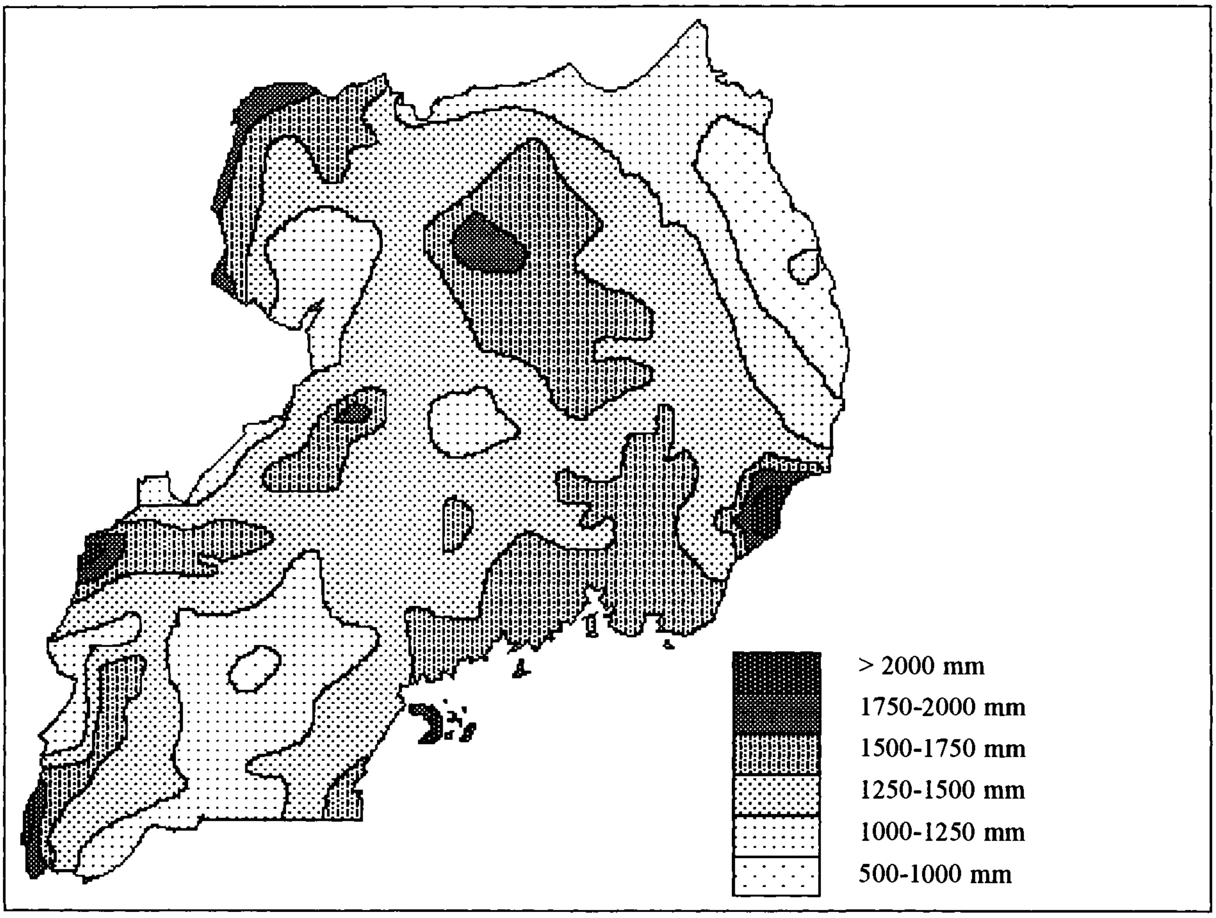


Figure 5.9. Simplified annual rainfall map of Uganda, based on Atlas of Uganda (1967).

Box 5.2
Some of the main changes in climate, and corresponding vegetation changes, in tropical Africa over the last 2.5 million years (After Kingdon, 1990)

- **2,500,000 -1,000,000 Before Present (B.P.)**: 21 "ice ages" leading to cooler and drier conditions alternating with warmer, wetter periods
- **40,000 B.P.**: Oscillating warm to cool to warm; montane forest expanded in cool period
- **33,000 B.P.**: Warm and wet
- **30,000 B.P.**: Cool and dry
- **20,000 B.P.**: Warm and wet
- **13,000 B.P.**: Maximum extent of most recent "ice age", leading to cool, dry conditions and contraction of forest to relatively wet "refugia" (see section 4.3.2)
- **12,000 B.P.**: Rainy seasons wetter; forests begin to expand; Lake Victoria overflows
- **11,000 B.P.**: Wet: forest expansion; warm: ice retreats on Elgon and Rwenzoris
- **10,000 B.P.**: Some evidence for slight forest reduction
- **7,000 B.P.**: Wet - forest at maximum extent
- **5,500 B.P.**: Some moist forests replaced by drier types
- **5,000 B.P.**: First suggestions of forest clearance by humans in Kigezi
- **3,500 B.P.**: Forest decline in West Africa, coinciding with introduction of agriculture
- **1,700 B.P.**: Major forest clearance in East Africa, accompanied by expansion of agriculture and livestock
- **Present**: Most forest cleared from East and West Africa; clearance spreading rapidly in Central Africa

5.5 NICHES AND HABITATS

5.5.1 What is a niche?

A forest or any other ecosystem can only function because all the organisms that go to make up the living part of it (the community) have different roles. Much as within the Forest Department there are staff with widely differing duties, which all help in the day-to-day running of the Department, so too in nature are there organisms with a whole range of roles which all contribute to the functioning of the ecosystem. The role of any organism in the community is called its **niche**. The concept of the niche covers not just what an organism needs to survive, but also how it relates to the rest of its environment. To return to the analogy with the Forest Department, a District Forest Officer needs someone in the Accounts section at Headquarters in order to get a salary processed, but that person in Accounts does not necessarily need that Forest Officer. However, the relationship between the two officers nevertheless contributes to each one's role in the Department. Likewise, in a forest, it may not affect a chimpanzee if there are no dung beetles to consume its dung, since some other scavenger will do the job instead. But it may matter to the dung beetle whether or not there are chimpanzees producing dung for it, and it will also matter to the dung beetle's predators and parasites. So the chimpanzee's niche is not just that of "large arboreal frugivore", it is also that of dung-producer to the forest's dung-beetles.

Let us take the analogy a bit further. Suppose a new DFO was posted to a district that already had a DFO. In the end, one of them would have to move on, or resign, or they would have to divide the job up so that each had a distinct role, as a district cannot support two members of staff with exactly the same job or role. On the other hand, if the new member of staff was a FO in charge of extension, and the district did not already have an extension officer although it did have FOs filling other roles, then there would be no conflict of interest and all staff could remain in post. In a forest, a similar situation exists, in that it is thought that no two species have exactly the same roles or niches. This is called the *theory of competitive exclusion*, because it is predicted that if a new species appears with the same niche as one that already exists in that area, then one of the two species will be completely out-competed in that niche: the forest cannot accommodate both. Either one of the two species will disappear, or one or both of them will shift their roles slightly so that they can both survive.

Niches can be looked upon as an organism's response to environmental variables. Those variables can be the presence or absence of other species (competitors, predators etc.), or non-living things such as climate. Whatever the variable, most species will have some preference for a certain amount of it. For instance, a tree seedling may only germinate over a certain range of temperatures. If it becomes too cold, the seed dies, and if it becomes too hot, it may also expire through heat stress. But this is just one variable. Now consider how that seedling responds under different light conditions. If light levels are too low, it may not germinate, and if light levels are too high, it may germinate but then get killed by intense sunlight. This further limits the range of conditions under which the seedling will survive (Figure 5.10).

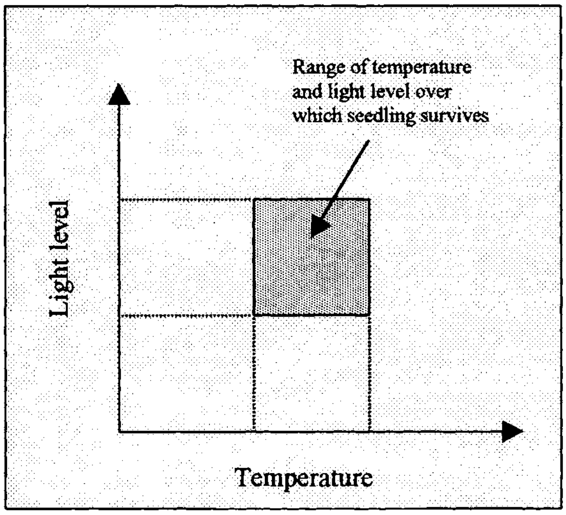


Figure 5.10. Illustration of a niche in two dimensions, using seedling survival under different temperatures and light levels.

Now let us add the effect of different levels of humidity. If the atmosphere is too dry, regardless of temperature or light level, the seedling may desiccate. If it is too wet, it may get killed by mould. We now need a third axis to the graph in Figure 5.9. By considering more and more variables, we would need more and more axes to represent the effect diagrammatically, which is rather difficult to imagine. Nevertheless, we should try to imagine adding hundreds of variables, each one further limiting the range of conditions over which the seedling will survive. Then consider another set of variables for when the seedling has become a sapling, then a mature tree. Because there are so many, the niche has been described as an *n-dimensional hypervolume* (Hutchinson, 1965). Box 5.3 lists just a few of the possible physical variables that may determine the niche of a plant species.

As a further example, this time from an animal, Figure 5.11 illustrates two dimensions in the niche of the tsetse fly. The fly's response to just these two variables means that we can predict roughly where tsetses will survive and where they will not, although we would need to know its response to many more variables to be certain. But even with these two variables, it is clear that certain parts of the country are ruled out completely, as are certain vegetation types. For instance, in closed forest, humidity would be too high, while in shrubless grassland it would sometimes be too low. Hence tsetses tend to occur in bushland where there is some shade which gives the right level of humidity and temperature for their survival. Remember that this is just one species of tsetse fly (*Glossina mortisans*). Other species of *Glossina* may be expected to have slightly different tolerances to these variables, and so may occupy a slightly different environment.

Box 5.3
Some of the physical variables that may determine the niche of a plant species

- Annual temperature
- Temperature in the growing season
- Temperature of coldest month

- Extreme temperature
- Frost frequency
- Frost-free period
- Annual rainfall
- Rainfall in growing season
- Length of dry season
- Rainfall intensity
- Sunshine hours
- Flood frequency
- Relative humidity
- Frequency and severity of wind

- Slope angle
- Aspect
- Exposure index
- Landslide frequency
- Altitude
- Rock type
- Rock chemistry
- Groundwater depth
- Soil salinity
- Effective soil depth
- Evaporation
- Soil structure
- Soil structure
- Soil drainage class
- Soil permeability
- Soil water holding capacity
- Soil nutrient content
- Soil organic matter content
- Soil pH

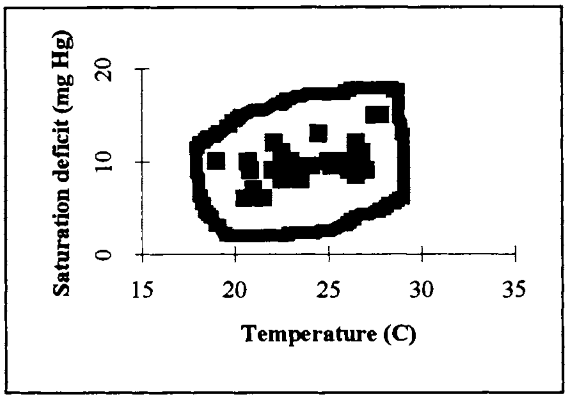


Figure 5.11. Two dimensional representation of the niche of the tsetse fly. Dots indicate combinations of temperature and saturation deficit (a measure of humidity) under which conditions tsetses survive. The dark line encloses an area representing the likely extent of the niche with respect to these two variables. After Rogers (1979).

5.5.2 Fundamental niches, realised niches and resource partitioning

An organism's response to non-living variables determines its maximum possible niche size, or **fundamental niche**, but its **realised niche** (i.e. the niche that is actually occupied) is usually more restricted because of interactions with other species, such as competition and predation. For instance, if there were only one species of squirrel living in a forest, then it might be free to eat nuts, berries, bark and insects. However, if there were several species living in the same forest, they would have to somehow divide up the food resources between them, such that, over the generations, one species became specialised at feeding on nuts and another on insects and so on. This is called **resource partitioning**. It tends to result in species having very specialised niches, and is particularly pronounced in tropical forests where so many species coexist. Table 5.4 illustrates resource partitioning in some African forest squirrel species. Looking at just three characteristics - habitat (see below), food preference and body size, it seems that no two species have the same requirements, even though they all live in the same forest. Tropical forests are, therefore, particularly rich in **specialist** species, and relatively poor in **generalists**, whereas less species-diverse ecosystems, such as deserts and temperate forests, have a higher proportion of generalists. A whole range of variation exists among species of any ecosystem in the gradation of niches from specialist to generalist. Figure 5.12 demonstrates the gradation for some tropical forest species.

Table 5.4.
Resource partitioning in coexisting West African forest squirrels. After Emmons (1980)

Habitat	Food preference	Body size	Species
Canopy of mature and disturbed forest	Bark scrapings	Tiny	*Myosciurus pumilio*
	Insects and other arthropods	Small	*Aethosciurus poensis*
		Medium	*Heliosciurus rufobrachium*
	Nuts	Large	*Protoxerus stangeri*
Ground beneath mature and disturbed forest	Termites	Small	*Funisciurus lemniscatus*
		Medium	*Funisciurus pyrrhopus*
	Hard nuts	Large	*Epizerus ebii*
Dense vegetation	Leaves, insects and other arthropods	Small	*Funisciurus isabella*
Flooded forests	Ants	Medium	*Funisciurus aneryrthrus*

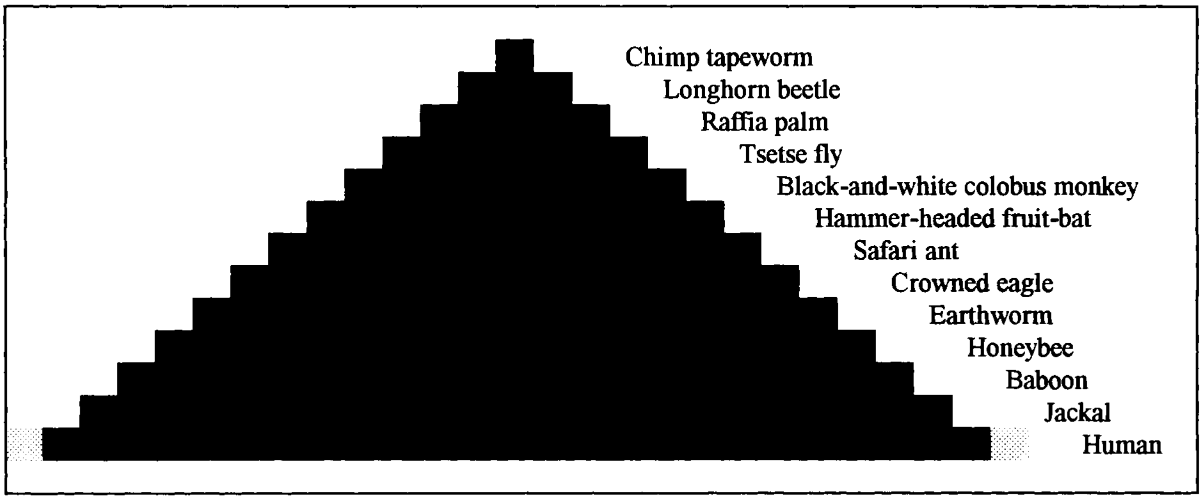


Figure 5.12. Variation in niche-width amongst some African forest organisms. Species with narrow niches (specialists) appear towards the top of the figure, while those with broad niches (generalists) appear towards the bottom. Adapted from Hungerford et al. (1994).

Even within any one group of organisms, there are some species that are more specialised than others. For instance, Bennun et al. (unpubl.) have shown that the forest birds of Uganda and Kenya can be divided fairly readily into three main groups:

- ***forest specialists***: species most characteristic of the interior of undisturbed forest (203 spp.)
- ***forest generalists***: species typical of edges, gaps and secondary forest (167 spp.)
- ***forest visitors***: species which are not dependent upon forest and are usually more common outside it (96 spp.)

As an example of two closely-related birds that fall into different categories, Cassin's spinetail is a bird that is listed as being a forest specialist, since it is only found in large tropical moist forests, while the mottled-throated spinetail is listed as a forest generalist, since it occurs in various woodland and forest types. The authors go on to argue that it is the forest specialists that are most vulnerable to human-induced changes, and therefore merit more conservation attention. For example, the mottled-throated spinetail would probably not suffer much from conversion of dense forest to lighter woodland, whereas Cassin's spinetail would. In general, if we look after the specialists, then the generalists will look after themselves.

5.5.21 Why do we need to know about niches?

It is not necessary, nor would it be possible, to know the precise niche of every species that lives in a forest. However, two things about niches are important:

- The niche of an individual organism belonging to any species confines it to certain conditions, outside of which it cannot survive
- Tropical forests are rich in specialist species with narrowly defined niches

These lead to numerous management implications, and means that altering conditions in a forest will inevitably affect many of its inhabitants. If, for example, we log a natural forest, the humidity and light levels will change so much that we may alter the balance of tree species surviving as seedlings, and ultimately the whole species composition of the forest. This may be desirable or not, depending on the management objectives, but it is certainly worth being aware of. Similarly, if an exotic tree species is introduced into a natural forest that suits it ecologically, it may become invasive, and competitively exclude native species from their own niches (see Section 8.4). If we have an understanding of its niche before we introduce it, we may be able to predict whether it will become invasive and take precautions.

5.5.3 What is a habitat?

A habitat is simply a place where an organism lives. It is made up of a set of conditions which includes other living organisms as well as non-living components. Where an organism is able to live is determined by its niche. To take the example of the tsetse fly (Figure 5.11), its habitat (open bushland) is determined by its preference for certain temperatures and humidity, as well as other components of its niche such as the presence of livestock or game.

5.5.4 Habitats in a tropical forest

There is no theoretical limit to how big or small a habitat may be. Small habitats are often called **microhabitats**, but this just means that they look small to humans. Examples of organisms with small habitats include the mites that live their entire lives in the roots of eyelashes of primates, or the many species of beetle and other insects that complete their life cycles under the bark of old trees, occupying no more than a few cubic centimetres of wood during their lives. In fact, most species in a forest probably occupy habitats in the micro-scale, although our attention tends to be attracted by those few conspicuous species with larger habitats.

5.5.41 Old tree microhabitats

Consider, for instance, an old tree. It may be thought of as just a single organism that is past its prime, and often in forestry it would be considered to be past commercial maturity. But old trees consist of very many distinct microhabitats for a wide range of smaller species, some of them decomposers, others predators and parasites of the decomposers. These are the so-called *saproxylic* organisms, described by Speight (1989) as *species which are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon the presence of other saproxylics.* They include invertebrates and fungi in particular, and are an important group in forests, not only because there are so many species involved (which makes them important for conservation), but also because they help recycle the nutrients in dead wood. Because an old tree is home to so many species, Speight (1989) uses the term "arboreal megalopolis" to draw the comparison with a crowded city. Some microhabitats associated with old trees are listed in Box 5.4. Note that each of the microhabitats listed could be further subdivided according to the microclimate in which each one was found.

Old trees also tend to be rich in **epiphytes**. Epiphytes are plants that use the tree as a substrate or habitat, but do not draw any nourishment from the tree. They get their nutrients either from humus accumulated in crevices in the bark, or from rain, mist, dust or run-off from the tree's bark. Only certain tree species will support epiphytes, but whatever the species, usually the older the tree the more epiphytes it will support. *Cynometra alexandri* and *Parinari excelsa*, both large trees of mature tropical moist forest in Uganda, are particularly important for epiphytes: for instance, Eggeling (1948) recorded nearly 100 species of epiphytes from Budongo Forest, many from mature *Cynometra* trees. Each epiphyte species has its own preferences for microhabitat, which can lead to **zonation** of species along a branch.

Box 5.4
Some microhabitats particularly associated with old, commercially overmature, trees

- Loose bark
- The bark/wood interface
- Heart rots and tree humus
- Rot-holes
- Saproxylic fungi
- Burrows and cavities of saproxylic insects
- Root plates
- Standing dead tree trunks
- Tree stumps
- Fallen twigs
- Underground rotting roots
- Fallen branches and logs, with or without bark

Figure 5.13 shows zonation of 23 species of epiphytes found on a single branch of an old *Parinari* tree. Since about 10% of all vascular plant species are epiphytes (Mabberley, 1992), and most of these live in tropical forests, it is important that we take epiphyte conservation as seriously as tree conservation.

5.5.42 Forest termites

One group of forest organisms that is strongly associated with old trees is the termites. Most species feed on dead wood, although others feed on organic material in the soil, or on leaf litter, or even on living vegetation (much of it derived from the trees anyway). Although to many of us one termite looks much like the next, a single forest may support dozens of species, all with slightly different microhabitats or niches. For example, 32 genera of termites (comprising, therefore, no fewer than 32 species and probably many more) that were found to coexist in a tropical rainforest in Cameroon (Collins, 1989).

5.5.43 Forest bird habitats

Forests offer a large number of possible habitats for plants and animals, which is one reason why they are so rich in species. Part of the reason is to do with their complex three-dimensional structure, for example, the division of the forest into several strata such as canopy, shrub layer and forest floor.

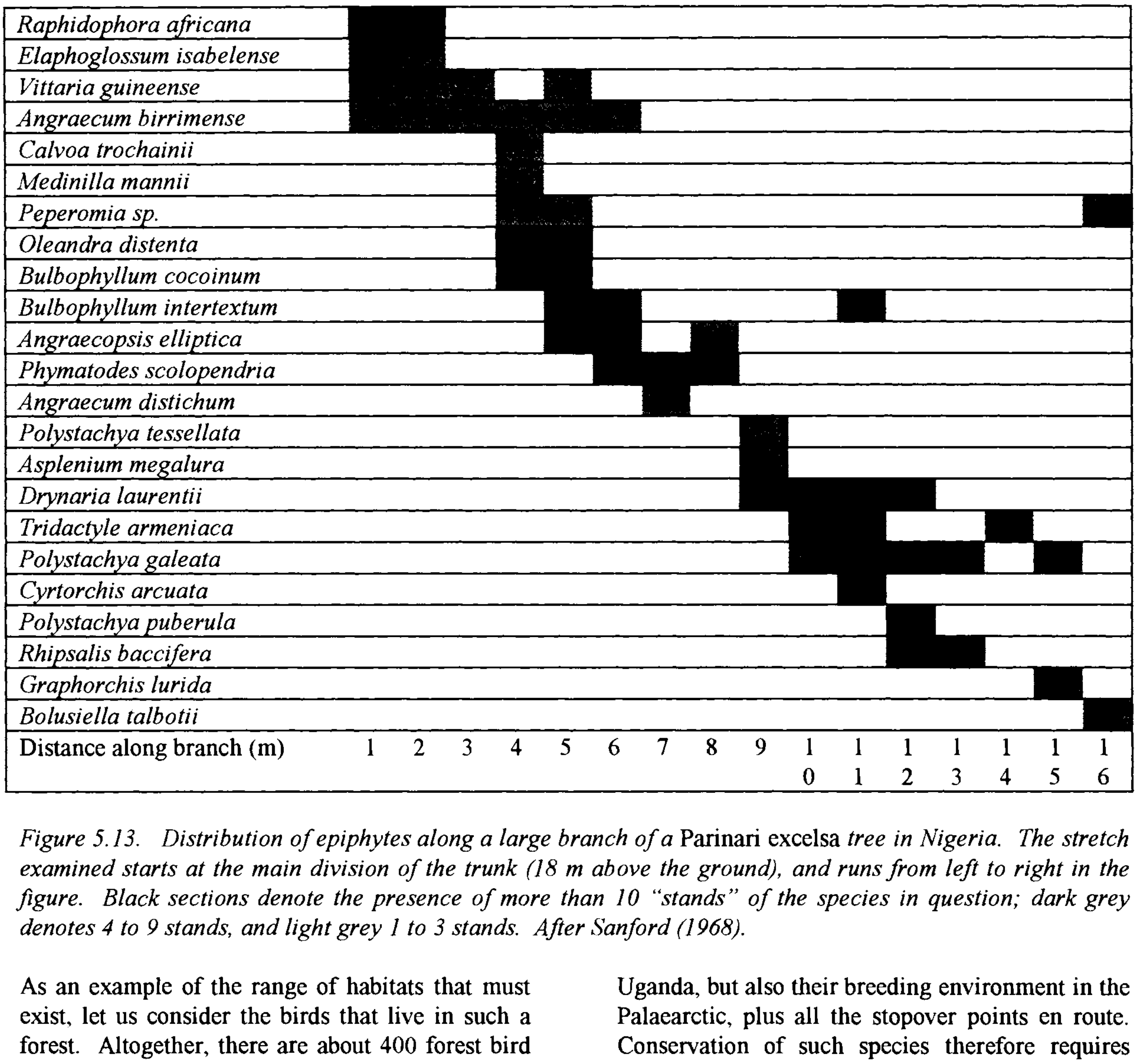
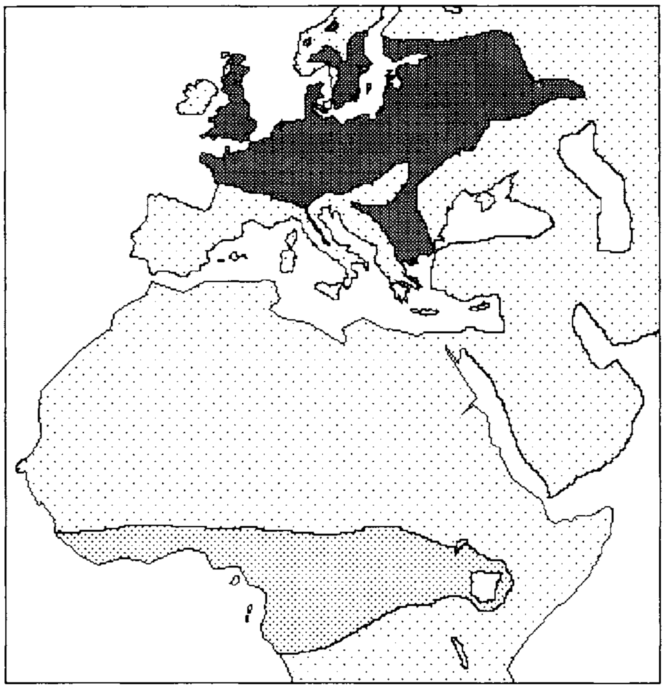


Figure 5.13. Distribution of epiphytes along a large branch of a Parinari excelsa *tree in Nigeria. The stretch examined starts at the main division of the trunk (18 m above the ground), and runs from left to right in the figure. Black sections denote the presence of more than 10 "stands" of the species in question; dark grey denotes 4 to 9 stands, and light grey 1 to 3 stands. After Sanford (1968).*

As an example of the range of habitats that must exist, let us consider the birds that live in such a forest. Altogether, there are about 400 forest bird species in Uganda. As each species exploits the forest in a slightly different way (i.e. each has its own niche), each species has a preference for living and feeding in a certain part of the forest. It is worth noting here that many man-made forests do not have the complex structure of natural forest, so the number of habitats available is much smaller. This is one reason why man-made forests are generally very poor in species (see Section 8.2.2).

5.5.44 The habitats of migrant birds

At the other end of the scale from the microhabitat, some species' habitats can be extremely large. Examples include the many species of bird that migrate annually across continents. About a tenth of all the bird species recorded from Uganda are long-distance migrants that breed in Europe or Asia (the Palaearctic). Their habitats thus include not only their non-breeding environment in Uganda, but also their breeding environment in the Palaearctic, plus all the stopover points en route. Conservation of such species therefore requires international effort. In North America, many migrant species seem to be suffering from tropical deforestation, because the area of Central America where most of these migrants spend the non-breeding season is naturally geographically rather small. The non-breeding range of Palaearctic migrants is fortunately often larger because of the shape of the African continent, so as yet deforestation has not had a noticeable impact. Nevertheless, recent declines in the number of some migrant birds in Europe has been attributed to drought and desertification in Sahelian Africa, through which many migrants must pass twice a year. Although most migrants spend their time in Africa in savannahs and scrubland (Pearson and Lack, 1991), at least 31 species regularly use lowland tropical moist forest, and 32 use tropical montane forest (Curry-Lindahl, 1981). Figure 5.14 shows the breeding and non-breeding range of one species typical of the former.



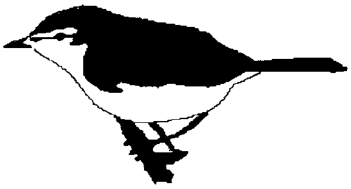


Figure 5.14. Breeding (dark shading) and non-breeding (light shading) range of the wood warbler (above), one of many Palaearctic migrant bird species with such a distribution. Redrawn from Curry-Lindahl (1981).

5.6 SUCCESSION AND TROPICAL FOREST DYNAMICS

Tropical forests, like other ecosystems, are not static. They are constantly changing, in both species composition and extent. Even if we cannot see the change on a human time scale, it is more than likely that change is going on nevertheless, albeit at a pace too slow for us to observe. This means that when we consider management or conservation options for a forest (or other ecosystem) today, we must remember that it may well be different tomorrow. Indeed, the very act of implementing any management may cause change, as we shall see below.

5.6.1 Ecological disturbances

Forests and other ecosystems change of their own accord, but often the event triggering change is some sort of disturbance. Disturbance can be at a variety of scales, from single treefalls to hurricanes or catastrophic fires, and they can be natural or human-induced. Whatever the cause of the disturbance, the event itself initiates an ecological process called **succession**. Succession is defined as *the non-seasonal, directional and continuous pattern of colonisation and extinction on a site*. It results from variation in the ability of species to colonise disturbed areas and from changes in the environment following the establishment of new species. This in turn is a reflection of the ecological niches of the species involved at different stages of the succession. Some species may immediately benefit from a disturbance, and become the first colonisers, while others may only benefit later from the presence of some of those colonisers.

Succession is going on within forests all the time, although normally on a small scale, such as when a tree falls and the subsequent gap is gradually infilled with a succession of colonisers. This is called **gap-phase dynamics**, and will be considered in Section 5.6.3. The local end-point of any succession is a return to the so-called **climax** community. Climax communities are meant to be stable and self-renewing, but often some new disturbance comes along before this state is ever reached. Succession is more obvious when one ecosystem is changing into another, such as when forest colonises savannah, and this is where we will start our examination.

5.6.2 Succession from savannahs to forests

The tropical moist forests of Uganda are mostly outposts of the larger forest block further west in Zaire. Being situated on the fringes of the climatic zone under which tropical moist forest thrives, they are particularly susceptible to slight changes in climate, particularly rainfall. It seems likely that over the millennia and centuries, Uganda's forests have shrunk and expanded according to the prevailing climate - retreating to particularly favourable **refugia** during dry episodes and expanding across the savannahs during wetter episodes (see Sections 4.3 and 5.4.34). For the last few centuries at least (and probably for much longer than this), forests have also had to face disturbance by humans and their livestock. For these reasons the forest boundaries have seldom been static, and even today there are areas in Uganda where we can see that the forest is advancing while in other areas it is retreating. The result of all this change has been the landscape we see in many parts of Uganda today: a **mosaic** of forest and savannah, as shown, for example, in Figure 5.15.

An interesting case of succession is occurring on the western edge of Budongo Forest. Here the forest front has advanced by up to 800 m over the last half century. If all Uganda's forests could expand at this rate without hindrance, then the whole country could be forested within just two thousand years. The reasons for the rapid forest expansion at Budongo probably reflect past human activities rather than any recent change in climate. It is likely that, until this century, burning of the surrounding savannahs for livestock, plus perhaps grazing and browsing pressure from wild game, kept forest expansion in check. This century, with human depopulation following sleeping sickness, and cattle depopulation following trypanosomiasis, plus the enforcement of early burning, and game eradication for tsetse control, the forest was free to expand once again, resuming a trend that some people suggest it might have been following for the last few thousand years (see Paterson, 1991, for details of past management in this area).

It is widely believed that many of the tall-grass savannahs of southern and western Uganda would be quite capable of supporting tropical moist forest if present management were changed. In other words, tall-grass savannah in Uganda is unlikely to be a true **climatic climax**. The same is true of many grasslands throughout the world. Two factors in particular may have lead to the dominance of savannahs at the expense of woodland or forest **fires** and **grazing**.

5.6.21 The influence of fires on forests and savannahs

Fire is a natural feature of grassland ecosystems (through lightning strikes), but seldom has much impact in tropical moist forests. Seasonally dry woodlands may also experience frequent fires. For the last few thousand years, humans have used fire as a tool in managing their environment to suit their own needs, whether to clear land for cultivation or to encourage the spread of grasses suitable for livestock. Because some species of plant (and animal) are better adapted to surviving fires than others, these are the ones that have spread wherever humans have burnt the land. Regular burning over the centuries, possibly every year in the case of many of the tall-grass savannahs in Uganda, has gradually eliminated species that are susceptible to burning and positively encouraged those that thrive on it. Tall grasses such as elephant grass (*Pennisetum purpureum*) and speargrass (*Imperata cylindrica*) burn easily during the dry season, and generate a lot of heat in the process, thereby killing many would-be competitors that may be trying to establish themselves in the grassland. In the following rainy season, these grasses rapidly re-sprout from underground rhizomes, so maintaining their dominance. Such grassland, therefore, is a ***fire-climax*** community.

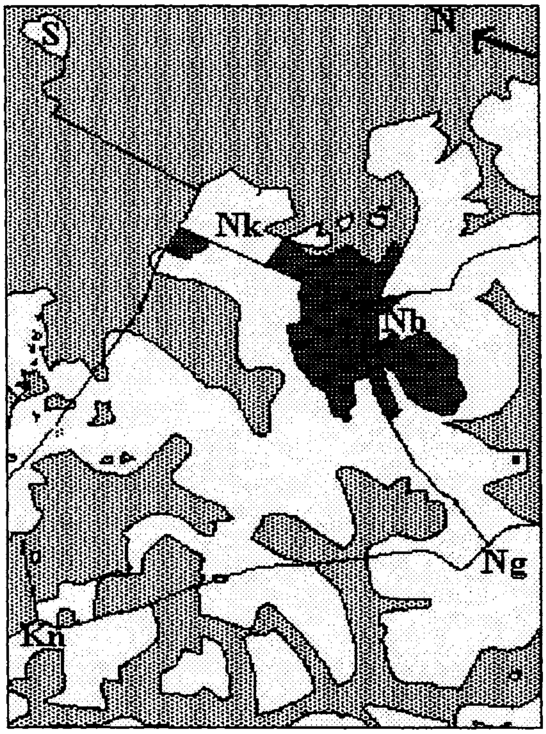


Figure 5.15. Part of the edge of Budongo Forest, Uganda, centred on Nyabyeya, showing a mosaic of natural moist forest (pale shading), savannah (clear) and plantation (dark shading). The mosaic is a result of a mixture of climate, soil, slope, fire, grazing and cultivation, and is now largely "fossilised", as forest expansion is prevented by cultivation of the surrounding savannah. S = Sonso sawmill; Nk = Nyakafunjo; Nb = Nyabyeya; Ng = Nyabugoma, and Kn = Kanyegi. The map represents an area of approximately 50 km^2.

Grasses such as these probably need to be burnt regularly, late in the dry season, to maintain their dominance. They also require full sunlight, so do not prosper under trees. However, if a grassland fire is sufficiently intense, it may spread beyond the grassland into the forest edge, killing some of the fire-sensitive trees in the process. This opens up the ground to colonisation by grasses, which can therefore gradually encroach on the forest. Over the decades and centuries, this could result in forests shrinking to gullies and riverine strips where fires cannot encroach. This process is thought partly to account for the isolation of Rabongo Forest in Murchison Falls National Park (Buechner and Dawkins, 1961).

But what happens if fires are? Early this century in Uganda, a policy of early burning was introduced. Burning early in the dry season means that the resultant fires are less intense because the grass is still moist. This means that some of the more fire-resistant shrubs that are attempting to establish themselves in the grassland will not be killed off, so gradually an open woodland may develop. Meanwhile, the forest edge will not be exposed to such severe fires, and a band of woodland may develop there too, effectively buffering it from grassland beyond, and stopping the forest from shrinking further. In many parts of Uganda this century, grassland has turned to woodland, partly as a result of this policy. For instance, such a trend was reported in *Combretum* woodland in Bunyoro (Turner, 1967), where a policy of late burning from 1914-1924 resulted in “lightly bushed” country, which subsequently progressed to “dense bush” following the introduction of an early burning policy in 1924.

If fire is completely prevented, the build-up of grass litter may eventually reduce the vigour of grass, and may encourage trees and shrubs to establish themselves. Once a few trees are established, conditions become more favourable for other tree species that require shady or moist conditions to germinate or survive as seedlings. Gradually, a forest may grow where once only grass survived. What species colonise depends partly on what seed-sources are around. A tropical moist forest will only develop on the site if there is an area of established moist forest nearby.

Figure 5.16 illustrates the results of a 28-year long experiment on the effects of fire in fire-climax savannah in a forest reserve in Nigeria, which commenced in 1929. As expected, continuing with a late burn regime for 28 years results in a savannah with few trees, all of which are fire-resistant. Early burning results in an increase in trees generally, although very few are fire-sensitive. Complete protection results in a vast increase in the number of trees, including many fire-sensitive ones. Hopkins (1974) reported that after just six years of protection, 35% of the trees in the plot belonged to forest species, while after 28 years the proportion had risen to 64%, at which time only one species of savannah grass was still present. If the experiment had been continued to the present day, the proportion of fire-sensitive trees in the plot completely protected from fire would probably have risen to something like that which exists in tropical moist forest nearby.

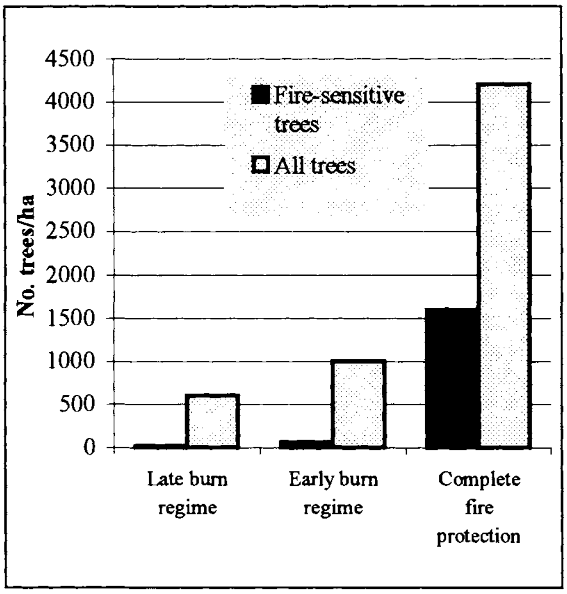


Figure 5.16. The effects of 28 years of management on cleared fire-climax savannah in Olomeji Forest Reserve, Nigeria. After Hopkins (1974) and Charter and Keay (1960).

5.6.22 The influence of grazing on forests and savannahs

Many woodlands and grasslands can make good grazing land for cattle, and humans have used them for this purpose for centuries. Wild game are also important grazers in some areas. Both game and cattle can have a big impact on vegetation structure, and can sometimes shift the balance between woodland and grassland. **Elephants** are particularly important in this respect. In Uganda, elephants were once widespread, but during the twentieth century they were pushed back into smaller and smaller areas, restricting their migrations and forcing them to put more pressure on less land. They also came into increasing conflict with humans. Budongo Forest lies in the path of a traditional elephant migration route down the western side of Uganda.

At times, up to 5000 elephants were thought to be in the forest (Swynnerton, 1924), causing serious problems for silviculture in that they liked to browse regenerating mahoganies in any clearings created by logging ((Langdale-Brown et al., 1964), so much so that there were soon calls for their elimination from the forest (Laws et al., 1975). There are now none left, which may be good for silviculture but this may also be expected to have long-term consequences on forest composition. [By comparison, in western Ghana forest elephants have been recorded browsing on 138 different plant species (Mabberley, 1992)].

Meanwhile, in the southern part of Murchison Falls National Park, elephant densities were rising as they became more and more confined to the park. By 1967, densities in this part of Bunyoro were 2.7 elephants per km^2 (Laws et al., 1975). Even by the early 1960s, there was great concern that the elephants here were destroying large areas of *Terminalia - Combretum* woodland, converting it to grassland (Buechner and Dawkins, 1961), and it was felt that something would have to be done to reduce the problem. The problem went away during Uganda's war years, as nearly all the elephants were shot. The grassland is now rapidly reverting to woodland again, but a legacy of those years is the rarity of elephant-resistant trees in Rabongo Forest, a small tropical moist forest in the middle of the park.

5.6.23 The forest succession sequence

Let us now return to how disturbance such as fire or grazing can trigger a process of succession. We have already seen that if fire or grazing is stopped, then forest can spread. The same thing can happen if cultivation ceases. Whatever the initial disturbance, it is thought that there will usually only be one sort of climatic climax community that will eventually re-establish itself. Figure 5.16 shows various routes to a climax community of moist semi-deciduous tropical moist forest that may exist in western Uganda.

Succession does not stop once forest cover has been restored. The forest may continue to change in species composition for several hundred years. Eggeling's (1947) work on the ecology of Budongo Forest, for example, suggested that in Budongo, the forest succession consists of four distinct forest types, which he called Colonising (Woodland) Forest and Colonising (*Maesopsis*) Forest (both early on in the succession, the former on poorer sites than the latter); followed by Mixed Forest, and finally the climax Ironwood (or *Cynometra*) Forest. Table 5.5 shows the relative abundance of the main tree species in each forest type and in the **ecotones** (intermediate successional stages) between them.

Table 5.5.
Succession of tree species in Budongo Forest, Uganda. Figures refer to total number of individuals which were represented on three or more sample plots by four or more trees exceeding 20 cm dbh. The sequence is from left to right, but the first two types are complementary. From Eggeling (1947)

Species	Woodland Forest	*Maesopsis* Forest	Ecotone	Mixed Forest	Ecotone	Ironwood Forest
Maesopsis eminii	-	74	27	-	-	-
Olea welwitschii	48	54	31	-	-	-
Spathodea campanulata	23	10	4	-	-	-
Sapium ellipticum	14	12	8	-	-	-
Caloncoba schweinfurthii	131	164	6	-	1	-
Phyllanthus discoideus	19	32	32	1	1	-
Erythrophleum suaveolens	15	15	5	2	1	-
Funtumia spp.	1	32	104	20	23	-
Trichilia prieuriana	-	-	2	20	2	-
Alstonia boonei	-	4	2	10	8	1
Mahogany spp.	-	-	2	15	7	1
Chrysophyllum spp.	1	8	6	71	11	1
Celtis spp.	23	61	90	319	141	72
Rinorea ardisiaeflora	-	-	5	13	70	27
Cynometra alexandri	-	-	-	36	55	119
Lasiodiscus mildbraedii	-	-	-	-	118	258

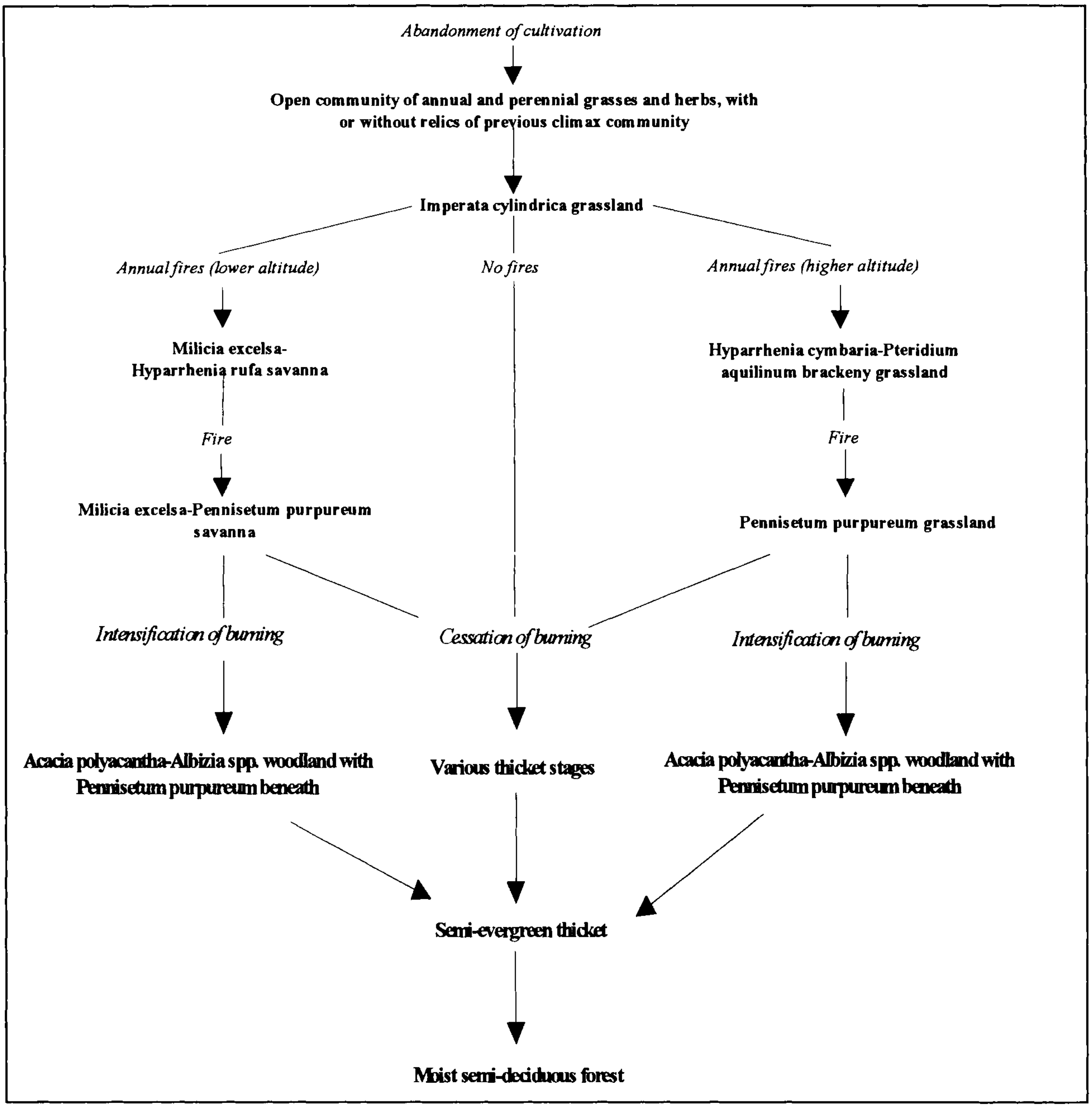


Figure 5.17. Successional routes leading to moist semi-deciduous tropical forest in western Uganda. After Langdale-Brown (1960).

We should remember that succession is not just something that happens to plants. Animals, too, respond to disturbance and to change. So for any succession of plants, there is a corresponding succession in animal species too. Figure 5.18 shows how certain bird species may succeed one another as grassland develops towards forest.

In general, the total number of species living in a given area seems to increase as the succession continues towards the climax. There are exceptions to this, and it is possible that Budongo Forest forms one such exception in that the mixed forest seems, according to some analyses, to be richer in tree species than the ironwood forest. This will be discussed again in Section 6.4.2. But looking at Figure 5.19, which shows the change in number of species of vascular epiphytes along the succession in Budongo, ironwood forest seems to be richer than mixed forest which in turn is richer than either of the colonising types. A further study, this time from Amazonian flood plain forest (Figure 5.20), shows a strong increase in bird, tree and primate richness along the succession towards the climax.

Species	Recently burnt	Tall grassland	Wooded savannah	Colonising forest	Mature forest
Senegal plover	■				
Pin-tailed wydah	■	■	■		
Ground hornbill	■	■	■		
Bronze mannikin	■	■	■		
Black-shouldered kite	■	■	■		
Black bishop		■	■		
Crested guinea fowl		■	■	■	
Grey hornbill			■		
Green wood-hoopoe			■	■	
Woodland kingfisher		■	■	■	
Common bulbul		■	■	■	
Golden-rumped tinkerbird			■	■	■
Little greenbul				■	■
Crowned eagle			■	■	■
Black-and-white casqued hornbill				■	■
Blue-breasted kingfisher				■	■
Forest francolin					■

Figure 5.18. Examples of some of the many bird species associated with various stages of forest succession in western Uganda. Black indicates preferred habitat, grey indicates that the species may also be present.

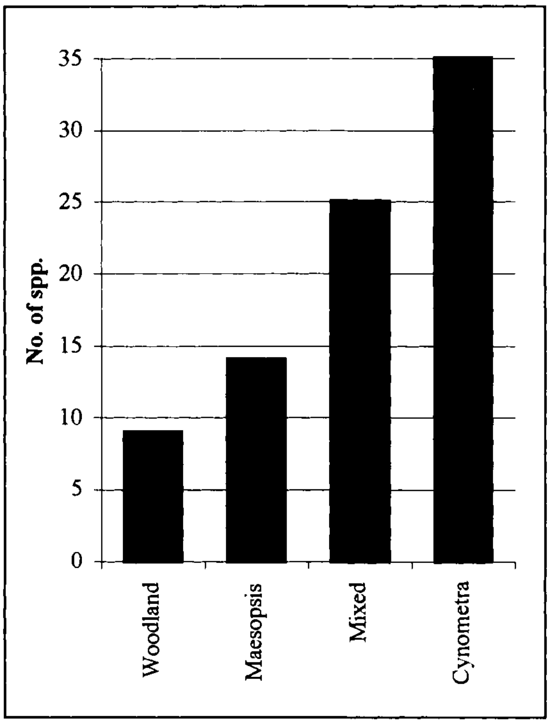


Figure 5.19. The number of species of vascular epiphytes in plots of different forest types in Budongo Forest, Uganda. After Eggeling (1948).

5.6.3 Succession within forests: gap phase dynamics

A forest can be viewed as a mosaic or patchwork of different-aged stands of trees. Some of these stands may cover many hectares, but most are much smaller than this. The reason for this mosaic lies in the way a forest regenerates itself: the so-called forest cycle (Whitmore, 1978). Figure 5.21 shows the four main phases of the forest cycle.

Whenever a tree falls in a forest, whether through old age, a natural disturbance or some human activity, a succession is initiated as plants colonise the gap thereby created. Which tree species are involved in the succession will determine the structure of the future forest for many decades, even centuries. This is why **gap phase dynamics** is considered to be so important in forest ecology, and why it is important for foresters to be aware of it too. The scale of the patchwork is determined by the main gap sizes in a forest, which in turn are determined by what disturbances the forest experiences. Some forests regularly experience severe disturbance, for instance forests on oceanic islands in the path of hurricanes, or forests on steep and unstable slopes prone to landslides, where whole forests may be felled in a single disturbance event. Other forests, probably including most of those in Uganda, naturally experience less severe disturbance. In such forests, most gaps are rather small. Table 5.6 shows a breakdown of gaps and their causes in MPassa Forest in Gabon; a similar breakdown probably applies to many Ugandan forests.

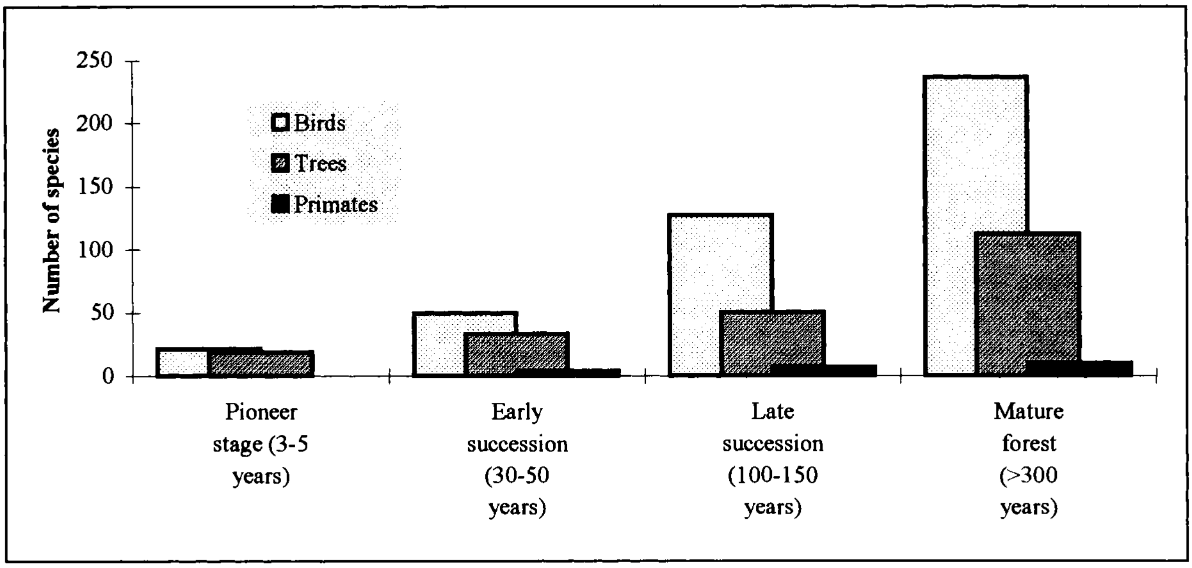


Figure 5.20. The number of species of birds, trees and primates at various stages of primary forest succession in Amazonian flood plain forest. Numbers of trees are >10 cm dbh, in 0.5 ha sample plots. After Terborgh (1986).

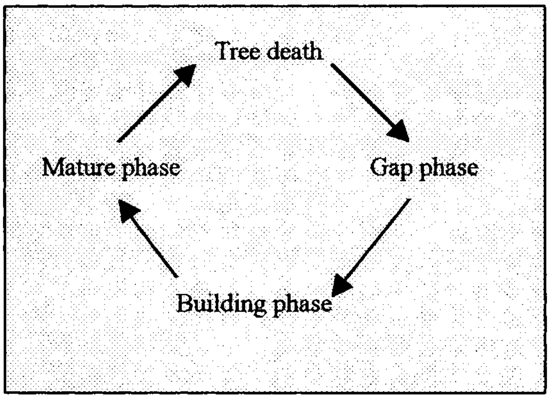


Figure 5.21. The four phases of the forest cycle, according to Whitmore (1978).

But even for a forest that does not naturally experience large-scale disturbance, there may be occasional freak events which have a big impact on the forest. In 1962, for instance, a freak storm hit the northern shore of Lake Victoria, felling many square kilometres of mixed forest in southern Uganda, and initiating succession anew (Mabberley, 1992). Such storms may be regular events to which the forest is adapted, even if they seem very irregular on a human time scale. Just because we may only live for a few decades, many trees live for hundreds of years, and a large natural disturbance once every 300 years may be the main factor in determining the forest's structure and species composition. We should thus be cautious in our conclusions about successional processes based on observations spanning only a few years.

Table 5.6.
Gaps and their causes in MPassa Forest, Gabon (Pickett and White, 1985).

Gap creation process	**% of gaps in forest**	**% of total gap area in forest**
Falling tree parts	23	10
Single falling trees	51	38
"Domino" treefalls	14	16
Overlapping or abutting treefalls	13	36

For example, was Eggeling justified in calling Ironwood forest a climax vegetation type in Budongo, or if we waited a few hundred years might we see it swing back to mixed forest or to some other type? As Pickett and White (1985) point out, "*primeval tropical rainforest, undisturbed and stable since the dawn of time, is a myth. Instability of varying extents occurs on several time-scales. The recovery to a steady-state is likely to take several centuries and is perhaps never achieved in many places*". This is one reason why **permanent sample plots** are so valuable, as long as the records are maintained.

In Uganda, the first Forest Department research plots in natural forest were established in 1933; by 1960 there were 267 (Hamilton, 1984). Unfortunately, many of these have since been lost, but those that survive are likely to tell us much about the ecological processes at work in Uganda's forests, and the effects of management on them.

5.6.31 Pioneer and climax tree species

Not all tree species are equally adept at colonising gaps. Indeed, a gap itself is far from uniform, and different tree species will perform differently in different parts of it. Trees are adapted for exploiting different sized gaps, and different stages in the succession. Broadly, they can be divided into **pioneer species** and **climax species**. The main characteristics of these two groups, and how they differ, are shown in Table 5.7.

Some examples of the two groups are given in Box 5.5. The mahoganies are not included because they are somewhat intermediate, in that they can germinate in the shade, but will only survive if there is a canopy opening within a year or two of germination (Synnott, 1975).

Recognising this problem in defining some of the key timber trees, Hawthorne (1993), working in the tropical moist forests of Ghana, identified four main groups or **guilds** of forest trees:

- **Non-cryptic pioneers:** require gaps for germination and only prosper in high light levels
- **Cryptic pioneers:** require gaps for germination, but can prosper later as understorey species in closed forest
- **Non-pioneer light-demanders:** germinate in shade, but require gaps for further development
- **Non-pioneer shade-bearers:** germinate in shade, and can prosper in the absence of gaps

Because of the differences in niches amongst the various tree species, and particularly in their response to light and humidity levels and their dispersal mechanisms, different species will dominate at different stages following gap creation. Broadly speaking, the gap will first become dominated by pioneer species, and later by climax species.

Table 5.7.
The main characteristics of pioneer and climax tree species. After Whitmore (1990)

Characteristic	**Pioneer species**	**Climax species**
Synonyms	Shade-intolerants Light-demanders Secondary species	Shade-tolerants Shade-bearers Primary species
Definition	Species whose seeds can only germinate in gaps in which full sunlight impinges at ground level for at least part of the day	Species whose seeds can germinate under forest shade and whose seedlings can establish and survive in shade for at least a year or two
Seed production	Copious, small, produced continually or frequently	Less copious, large, produced annually or less than annually
Dispersal	Wind or animals, often over long distances	Various, including gravity, sometimes only over short distances
Seed dormancy	Normally present; seeds never recalcitrant	Often absent; seeds often recalcitrant
Soil seed-bank	Present	Absent
Growth	Indeterminate, no resting buds	Determinate, with resting buds
Height growth	Fast	Slower
Forking	High	Low
Leaves	Short-lived; high turnover rate	Long-lived; low turnover rate
Roots	Superficial	Some deep
Root/shoot ratio	Low	High
Wood	Usually pale, low density, not siliceous	Often dark, high density, sometimes siliceous
Photosynthesis rate	High	Low
Toxicity of leaves	Low	High
Susceptibility to herbivore damage	High	Low
Geographical range	Wide	Often narrow

Box 5.5

Some examples of pioneer and climax tree species in Ugandan forests

Pioneer species

- *Albizia zygia*
- *Caloncoba schweinfurthii*
- *Chrysophyllum albidum*
- *Croton macrostachyus*
- *Dombeya mukole*
- *Ficus exasperata*
- *Macaranga schweinfurthii*
- *Maesopsis eminii*
- *Milicia excelsa*
- *Musanga cecropioides*
- *Musanga leo-errerae*
- *Pericopsis elata*
- *Rauvolfia vomitoria*
- *Ricinodendron heudelotii*
- *Solanum giganteum*
- *Trema orientalis*
- *Vernonia conferta*

Climax species

- *Celtis durandii*
- *Cynometra alexandri*
- *Funtumia elastica*
- *Lasiodiscus mildbraedii*
- *Microdesmis puberula*
- *Parinari excelsa*
- *Rinorea beniensis*
- *Turraeanthus africanus*
- *Uvariopsis congensis*

5.6.32 Seed dispersal in forest trees

So far we have been talking about plants colonising areas, but we have not yet considered how they get there. All plants need to disperse their seeds somehow, so that their offspring stand a chance of finding conditions suitable for germination and growth. Method of seed dispersal is an important aspect of a species' niche, and we find different species employing different dispersal mechanisms. For each mechanism, some are specialists, others generalists. Three main categories of dispersal mechanism occur (Bawa and Hadley, 1990):

- **Self-dispersal** mechanisms include the simple use of gravity and more complex techniques involving "explosive" seed-pods. Both mechanisms only result in short-distance dispersal from the parent tree, so species which use them are usually slow to spread. *Acacia* and *Albizia* species are good examples, as are many tropical forest trees.

- **Wind dispersal** is commonest amongst tree species growing under fairly exposed conditions, whether this be as isolated trees in savannah (such as many species of *Combretum* and *Terminalia*) or as emergent trees in tropical moist forest (such as *Cynometra, Alstonia* and the mahoganies). These trees can use the wind to disperse their seeds over relatively long distances from the parent tree.

- **Animal dispersal** is very widespread in tropical trees. The technique enables trees to disperse their seeds over very long distances from the parent tree, helping them to colonise new areas and encouraging out-breeding. The seeds normally have to be packaged in some way to attract an animal, for instance by being embedded in a tasty fruit or being brightly coloured. Different "packaging" attracts different species of animal.

- A fourth category, **water dispersal,** is also important in some forest types such as riverine forest.

Figure 5.22 shows how the relative proportions of plant species using each mechanism vary according to forest type, from a study in Zaire. Some examples of Ugandan trees that use the three main mechanisms are given in Box 5.6. Although the list is not exhaustive, it gives a fair representation of the proportion of tree species that fall into each category.

It seems, therefore, that most tropical trees use animals to disperse their seeds. In tropical moist forest in Nigeria, 46%-80% of all tree species have fleshy fruit, designed for animal dispersal, whereas only about 10%-25% of temperate American tree species have fleshy fruit (Jones, 1956, Howe and Smallwood, 1982). Interestingly, animals are also the main pollination agents in tropical forests, accounting (in South and Central America) for nearly 100% of lowland tropical forest trees, as opposed to 50% of tree species at a latitude of 20 degrees North, and only 20% at 60 degrees North (Regal, 1982).

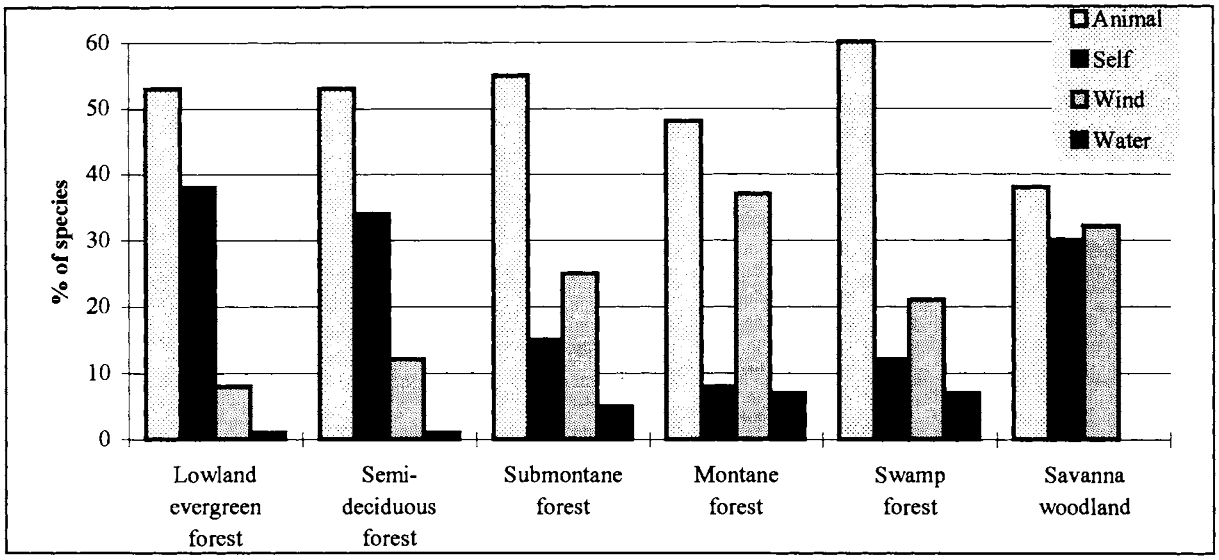


Figure 5.22. Seed dispersal mechanisms amongst Zairean forest plants. After Malaise (1978).

Box 5.6
Examples of Ugandan tree genera using the three main mechanisms of seed dispersal

Self-dispersed trees

- *Acacia*
- *Afzelia*
- *Albizia*
- *Baikiaea*
- *Cassia*
- *Dalbergia*
- *Entada*
- *Erythrina*
- *Erythrophleum*
- *Isoberlinia*
- *Securidaca*

Wind-dispersed trees

- *Alstonia*
- *Bombax*
- *Combretum*
- *Entandrophragma*
- *Funtumia*
- *Hallea*
- *Holoptelea*
- *Khaya*
- *Lovoa*
- *Markhamia*
- *Piptadeniastrum*
- *Pterygota*
- *Salix*
- *Senecio*
- *Spathodea*
- *Terminalia*
- *Vernonia*

Animal-dispersed trees

- *Alangium*
- *Alchornea*
- *Antiaris*
- *Antidesma*
- *Balanites*
- *Beilschmiedia*
- *Blighia*
- *Borassus*
- *Caloncoba*
- *Canarium*
- *Celtis*
- *Chrysophyllum*
- *Coffea*
- *Cola*
- *Cordia*
- *Croton*
- *Desplatzia*
- *Discoglypremna*
- *Dracaena*
- *Drypetes*
- *Elaeis*
- *Erythroxylum*
- *Ficus*
- *Grewia*
- *Guarea*
- *Ilex*
- *Isolona*
- *Juniperus*
- *Kigelia*
- *Klainedoxa*
- *Lindackeria*
- *Macaranga*
- *Maesopsis*
- *Mammea*
- *Microdesmis*
- *Milbraediodendron*
- *Milicia*
- *Musanga*
- *Myrianthus*
- *Nauclea*
- *Olea*
- *Parinari*
- *Parkia*
- *Phoenix*
- *Phyllanthus*
- *Podocarpus*
- *Prunus*
- *Pseudospondias*
- *Rauvolfia*
- *Ricinodendron*
- *Salvadora*
- *Solanum*
- *Sterculia*
- *Strombosia*
- *Strychnos*
- *Symphonia*
- *Mabernaemontana*
- *Tapura*
- *Tetrapleura*
- *Treculia*
- *Trema*
- *Trichilia*
- *Turraeanthus*
- *Uvariopsis*

Animals act as dispersal agents either as a by-product of their own feeding behaviour, or, less frequently, through picking up seeds that get tangled in their fur or feathers. Different animals have preferences for different sorts of fruit and seeds; for instance some specialise in certain size-classes of fruit or seed. Many hornbills prefer small fruit, or fruit with small seeds, or seeds with red or purple arils, whereas many monkeys prefer fruit with a succulent pulp, containing many seeds, or that are orange, while duikers prefer fruit with succulent fibrous pulp, or nuts with a kernel, or large fruit generally (Gautier-Hion, 1990). This means that some animals are responsible for dispersing the seeds of many trees, while others are only important for one or a few species. Figure 5.23 shows the relative importance of different animals for dispersal of forest plants in Gabon.

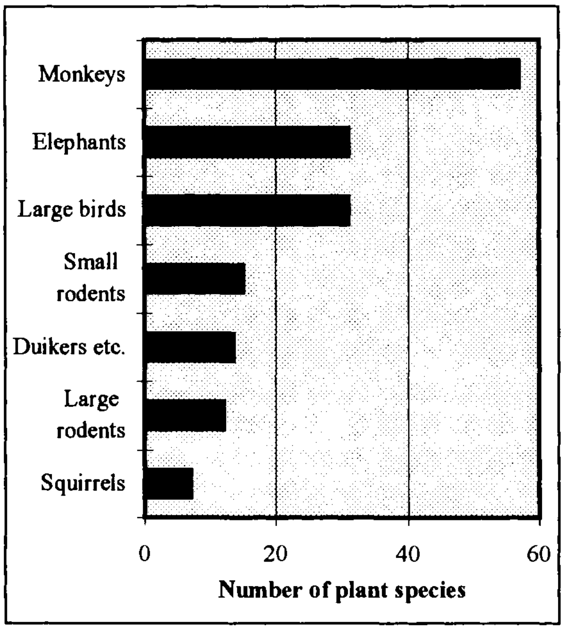


Figure 5.23. The relative importance of different animals for dispersal of forest plants, from a study in Gabon (Gautier-Hion, 1990).

Primates, large birds and elephants seem to be the most important dispersers of tree seeds. Elephants seem to be particularly important, because, of the tree species whose seeds they disperse, they are often the only animal large enough to eat the seeds and thereby disperse them. For example, in a study in Côte d'Ivoire, seeds from one year's worth of elephant droppings were found to have come from 37 tree species, only 7 of which are known to be dispersed by monkeys or birds as well as elephants (Alexandre, 1978). This has important implications for conservation and forest management, because it indicates that it is not enough to protect just the trees themselves. Without the dispersers, many of the trees would not be able to survive in the long term. Thus the long-term future in Uganda for elephant-dispersed trees such as *Balanites wilsoniana, Warburgia ugandensis,* and even *Borassus aethiopum* is now in doubt, even though adult trees are still common in many areas. Likewise, the animals would not be able to survive without the range of trees producing fruits and seeds. For example, in Gabon, fruits and seeds make up the staple diet of 45% of all the mammal species found in the tropical forest there (Gautier-Hion, 1990).

Dispersal of tree seeds by primates has been investigated in Budongo Forest by Plumptre et al. (1994). Table 5.8 lists the species that have been found as intact seeds in the faeces of primates. Many important timber trees are included in the list, although the authors point out that more research would be necessary to determine just how important these primates are for the survival of these trees. Note, too, that some exotics are also on the list.

Table 5.8.
Tree species in Budongo Forest, Uganda, for which intact seeds have been found in the faeces of primates. After Plumptre et al. (1994).

Tree species	Blue mon-key	Chim pan-zee
Broussonetia papyrifera		✓
Caloncoba schweinfurthii		✓
Celtis durandii	✓	✓
Celtis mildbraedii		✓
Celtis zenkeri	✓	✓
Chrysophyllum albidum	✓	✓
Cleistopholis patens		✓
Cordia milleni		✓
Ficus spp.	✓	✓
Klainedoxa gabonensis		✓
Maesopsis eminii	✓	✓
Margaritaria discoidea	✓	
Mildbraediodendron excelsum		✓
Milicia excelsa		✓
Morus lactea	✓	✓
Myrianthus arboreus	✓	✓
Pseudospondias microcarpa		✓
Psidium guajava		✓
Ricinodendron heudelotii		✓
Uvariopsis congensis		✓

5.7 SUMMARY

This chapter has been particularly detailed and wide-ranging, to emphasise that ecology touches so many areas of forest management and conservation. Nevertheless, it has not really been possible to do the subject full justice here, and anyone wanting to take their reading further should look at the reading list below.

Particularly valuable lessons from ecology are that:

- Different areas support different communities, partly because of differences in the physical environment.
- Species interact in often complex ways which result in communities of species living together and depending to varying degrees on each other. Interspecific relationships are at their most complex in tropical forests.
- Changes that affect one species will almost certainly affect the network of other species living in the same area. The more species-rich an area, the more such species will potentially be affected.
- Some species are very susceptible to change, while others thrive on it.
- Some species have very precise requirements for life (specialists) while others are more tolerant of a range of conditions (generalists). Tropical forests are particularly rich in specialist species.
- Communities are often naturally dynamic in their species composition, and are prone to change over a variety of time-scales and distances.

5.8 FURTHER READING

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