Part I Introduction

Chapter 2

Flooded and Riparian Habitats in the Tropics

Community Definitions and Ecological Summaries

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Introduction

Wetlands occupy the interface between fully terrestrial and aquatic ecosystems, making them inherently different from both systems yet dependent on both (Mitsch & Gosselink 2007). A number of distinct types of flooded and riparian wetland habitats occur in the tropics, including those with seasonal or permanent inundation (Kalliola *et al.* 1991), with or without the influence of salt. Riverine margins and river deltas can also contain flooded habitats. For example, seasonal floods can submerge riparian forests alongside rivers, sometimes extending several kilometres from the riverbank, with permanent and seasonal wetlands connected to the floodwater (Gautier-Hion & Brugière 2005).

Vascular plant species evolved and diversified in terrestrial ecosystems and, in general, die more readily in response to flooding than to desiccation (Larcher 1994). In tropical wetlands, the constraints imposed by flooding are even more pronounced as high ambient temperatures result in high rates of plant metabolism. Inundation causes drastic changes in the bioavailability of nutrients, oxygen levels, and concentrations of phytotoxins (Parolin *et al.* 2004), with oxygen rapidly consumed by respiring roots and microorganisms and soils becoming hypoxic or anoxic within a few hours of flooding (Visser *et al.* 2003). Oxygen depletion is accompanied by increased levels of carbon dioxide, anaerobic decomposition of organic matter, increased solubility of mineral substances and reduction of the soil redox potential (Vartapetian *et al.* 2003), followed by the accumulation of potentially toxic compounds (Ponnamperuma 1984). Only those plant species adapted to these conditions persist in these habitats (De Oliveira *et al.* 2014).

Tropical wetlands have characteristic vegetation zones, with the most tolerant species growing in areas subject to longer and deeper flooding. In the Amazon, flood waters can be 15 m deep and remain for up to 9 months, but trees survive and remain rooted in the soil (Junk *et al.* 1989). A regular periodicity of flooding is important to allow plants to evolve and adapt (the 'Flood Pulse Concept': Junk *et al.* 1989; Junk & Wantzen 2004), so in wetlands with unpredictable flooding, such adaptations are rare and plant diversity is lower.

Species richness and the number of endemic plant species in most tropical wetlands is low, with two exceptions: the Everglades and Amazonia (Junk *et al.* 2006; Slik *et al.* 2015; Wittmann *et al.* 2013).

Various kinds of tropical flooded and riparian wetland habitats are inhabited by members of the Primate order (the topic of this volume), but many primate studies have used inconsistent terms for flooded habitat types. Here, we summarize the ecology of flooded and riparian habitats in South and Central America, Africa and Asia and define habitats used by primates and employed throughout this volume. Habitats include lowland tropical floodplain forest, riverine and gallery forest, river delta, swamp forest(s), mangroves, oxbow lakes, reedbed/papyrus, seasonally flooded grassland and intertidal zones.

Definition of Habitats

In the following sections, we describe the major tropical wetland habitats of importance to primates.

Lowland Tropical Floodplain Forest

Definition

Floodplains are highly dynamic, where the aquatic and terrestrial transition zone (the whole floodplain area) alternates between wet and dry, with a moving littoral region (Junk *et al.* 1989). The natural disturbance caused (Leyer 2006), and materials deposited (Maddock 1976), by flooding produce diverse floodplain structures. Forests growing on floodplains often include three layers of vegetation: a canopy layer of mature trees, saplings and shrubs in the understory and herbaceous plants and tree seedlings covering the ground (Yin 1998).

Neotropics

Several extensive freshwater floodplains occur in tropical America: the Amazon (Toivonen *et al.* 2007), Orinoco (Rosales *et al.* 2002), Pantanal (Junk & Nunes da Cunha 2005) and Paraguay/Paraná (Galán de Mera & Perea 2008). The Amazon floodplain is mostly forested, whereas the Orinoco, Pantanal and Paraguay/Paraná are dominated by grasslands. The largest floodplain forests of the Amazon are characterized by immense cyclic water-level fluctuations; a flood pulse produces water depths up to 12–15 m and flood durations between 50 and 210 days per year (Junk *et al.* 1989). As a result, ecological processes, including plant reproductive cycles (e.g. flowering, fruiting) and animals' seasonal movements and migrations are synchronized with the flooding period (Schöngart *et al.* 2002).

In contrast, flood tolerance and responses to inundation cycles varies greatly between species (Parolin 2001), resulting in a mosaic of habitats within and between floodplain ecosystems (Wittmann *et al.* 2013).

Two types of floodplain forest exist in the Amazon, determined by the water quality of the flooding rivers (Prance 1979). Várzeas form along the banks of whitewater rivers, which are nutrient rich, originate in the Andes and have a high sediment load. *Igapós* form along the banks of blackwater and clearwater rivers, both with low sediment loads; their flooded soils have low nutrient contents (Furch 1997). Seven per cent of the Brazilian Amazon (400 000 km^2) can be categorized as floodplain forest, with approximately 300 000 km^2 covered by *várzea* and 100 000 km^2 covered by *igapó*. The Amazonian *várzea* is the most species-diverse floodplain forest in the world (Wittmann *et al.* 2006). Characteristic plant genera of both habitats include *Aldina* (Fabaceae: Papilionoidae), *Amanoa* (Euphorbiaceae), *Buchenavea* (Combretaceae), *Elaeoluma* (Sapotaceae), *Eschweilera* (Lecythidaceae), *Hevea* (Euphorbiaceae), *Hydrochorea* (Fabaceae: Mimoidoidae), *Mabea* (Euphorbiaceae), *Macrolobium* (Fabaceae: Caesalpinoidae) and *Pouteria* (Sapotaceae). Research on primates in these habitats includes studies of white uacaris (*Cacajao calvus calvus:* de Alecântara Cardoso *et al.* 2014), red uacaris (*Cacajao c. ucayalii*: Bowler & Bodmer 2011; Bowler *et al.* 2012), golden-backed uacaris (*Cacajao ouakary*: Barnett *et al.* 2005, 2012c; Bezerra *et al.* 2011; Defler 2001), squirrel monkeys (*Saimiri vanzolinii, S. sciureus*: Paim *et al.* 2013) and assemblage-level studies of *Alouatta, Ateles, Cebus, Pithecia, Saimiri, Saguinus* and *Sapajus* (e.g. Haugaasen & Peres 2005a, 2009).

Africa

In the Congo Basin, forested floodplains extend along the Congo River and its tributaries. A geographical depression, the *cuvette centrale congolaise*, located at the centre of the Congo Basin, supports swamps and wetlands intermixed with lowland rainforest. In the more permanently flooded areas, the canopy is 30–35 m and trees often have stilt roots. The upper floodplain is well drained in periods of low water, but is flooded once or twice a year. Its forest canopy reaches 20–25 m with a relatively low tree density, but many lianas. Species include *Didelotia unifoliata* (Fabaceae: Caesalpinioideae), *Diospyros* spp. (Ebenaceae), *Uapaca* spp. (Phyllanthaceae), *Guibouria demeusei* (Fabaceae: Caesalpinioideae), *Mitragyna stipulosa* (Rubiaceae) and *Oubanguia africana* (Lecythidaceae). Soil of the upper floodplain is sandy, while the lower floodplain has peat soils, often of considerable depth.

The Congo Basin supports one of the highest diversities of primates in the world, including some found nowhere else: the bonobo (*Pan paniscus*), found only south of the Congo River, and Allen's swamp monkey (*Allenopithecus nigrovirdis*; Maisels *et al.* 2006), Africa's only primate swamp specialist (Chapter 43).

Asia

In the absence of human impact, forest would form the natural vegetation of most wetland areas in Southeast Asia (Corlett 2009), although much has now been converted to oil palm (Abram *et al.* 2014; Runting *et al.* 2015). In south central Cambodia, the Mekong and Tonle Sap rivers join forming the lower Mekong floodplain (70 000 km^2) (Rainboth 1996). The Tonle Sap is highly seasonal and flooding in the wet season can inundate ten times the area of the dry season (Arias *et al.* 2013, 2014a). On the edge of the permanent Tonle Sap lake is a tall strip of forest which acts as a physical barrier between the open lake and the floodplain (Arias *et al.* 2014b; Kummu & Sarkkula 2008).

The forests of Borneo, are one of the most species-rich habitats on earth (Whitten *et al.* 2004), with 60% higher biomass than the Amazon (Slik *et al.* 2010). The Kinabatangan River, 560 km long, is the longest river in Sabah and is made up of a patchwork of different habitat types, i.e. riverine forest, seasonally flooded forest, swamp forest, dry dipterocarp forest and mangrove (Boonratana 2000a; Sha *et al.* 2011; Chapter 4). This area sustains one of the world's richest primate ecosystems inhabited by ten species; five of these endemic to Borneo: the Bornean orangutan (*Pongo pygmaeus*), Bornean gibbon (*Hylobates muelleri*), proboscis monkey (*Nasalis larvatus*), red leaf monkey (*Presbytis rubicunda*) and Hose's langur (*Presbytis hosei*) (see Chapter 29).

Riverine and Gallery Forest

Definition

The terms 'riverine' and 'gallery' forest are often used interchangeably as both form forested riparian corridors in otherwise grass-dominated or savanna-woodland ecosystems. However, these two habitat types can be distinguished (Kingdon *et al.* 2013). Riverine forests grow along the banks of rivers or streams where the soil is moister than the surrounding area. Immediately next to the river, the soils are fertile, the understory is green and moist with little grass, and hence these areas rarely burn. These factors are more important in determining the vegetation of the riverine edge than the surrounding climate (Emmerich 1990). Riverine forest strips are periodically flooded when the river bursts its banks; which can occur annually, more than once a year or every few years (Chapter 33).

Gallery forest is a type of forest outlier in a grassland region where the soils are moist enough and the conditions humid enough to support evergreen or semi-evergreen trees (Rosevear 1953a). Typically, gallery forest is found in narrow sheltered valleys and ravines on hillsides.

Neotropics

In the *cerrado* (tropical savanna of Brazil), gallery forest occurs where the water table is close to the surface. These forests can be dense and stratified, composed of evergreen trees and a sparse understory. These forests make up < 10% of the *cerrado*, but are found throughout the region (Redford & Fonseca 1986). There is a sharp and distinct boundary between gallery forest and xeromorphic *cerrado* vegetation (Mares *et al.* 1989). These forests can be important for local primates (Chapter 31).

Riverine forests of this region contain many species that are also found in Amazonian rainforest and along the Atlantic

coast of Brazil (Oliveira-Filho & Ratter 1995). In the transition zone between gallery forest and *cerrado*, the waterlogging of the wet season excludes woody *cerrado* species, while desiccation of the soils in the dry season excludes gallery forest species (Pennington *et al.* 2000).

As an example, the Miranda riverine forest in the Pantanal is 50–200 m wide with an 8–13 m canopy (emergents up to 17 m). Inundation pulses occur from January to March and the water level in the gallery forest may reach 1.5 m. Many trees are deciduous, dropping their leaves from July to September, but evergreen species are also abundant including *Inga vera* (Fabaceae: Mimoisoideae), *Ocotea diospyrifolia* (Lauraceae) and *Vitex cymosa* (Lamiaceae). Fruiting has two peaks annually, one in the middle of the wet season and the other in the transition from wet to dry (Ragusa-Netto 2004).

Africa

Riverine forests are found along many of the continent's rivers. Within the rainforest zone, riverine forest can be distinguished from rainforest by a different species composition. In East Africa, riverine forests of the Tana floodplain are restricted to small stands that depend on the ground water from the river (Hughes 1985; Chapter 30). In savanna habitats of Africa, strips of riverine forest extend far into these drier regions.

Riverine forest strips provide movement corridors for forest animals, including many species of primates, and refuges for forest plants. They provide sources for forest expansion if the climate becomes wetter, or areas to retreat to if it becomes drier, which has happened cyclically in parts of tropical Africa over millions of years. For example, the rivers draining the Congo Basin often support riverine forest strips far outside the current rainforest zone. In wetter climatic periods, these forests could expand to form an expanded rainforest zone.

Asia

There are many seasonally flooded riverine forests in South Asia (e.g. Dudgeon 1992, 2000a, b; Chapter 44). Some of the most extensive are in Bangladesh and are situated in the natural levees of rivers subject to overflow during the monsoon.

The spatial extent of the riparian zone generally encompasses the terrestrial landscape between low- and high-water marks (Naiman *et al.* 1993, 2000; Naiman & Décamps 1997; Vellidis & Lowrance 2004). Riparian deforestation and pollution is common in many Asian rivers, especially in Southeast Asia, hence these forests are in decline (Dudgeon 2000a; Iwata *et al.* 2003).

River Delta

Definition

River deltas can support both forest and non-forest habitats. They are formed by the deposition of sediment carried by the river as it enters the sea, with deltas classified according to the main control of this deposition; river, wave or tide. The sediment deposition shapes the resulting delta and its vegetation with drier remnants of levees being more diverse than waterlogged areas. Species composition is also linked to the adjacent fringing vegetation, e.g. mangroves or upland forest.

Neotropics

The Amazon and Orinoco Delta swamp forests occur within a diverse matrix of coastal vegetation types and are characterized by permanent inundation and abundant waterways and canals (IUCN 1996), with the core a 'tropical ombrophilous swamp forest' (UNESCO 1981). These deltas support a number of endemic plant species (Dinerstein *et al.* 1995). Primates of the Orinoco Delta have recently been surveyed by Bernardo Urbani (unpublished data). The primates of the islands in the Amazon delta are also poorly known, with the few published surveys focusing on the larger islands (e.g. Marajó) (Fernandez *et al.* 1995; Peres 1989; Chapter 45).

Africa

The Niger Delta in southern Nigeria contains a diverse mix of swamps in a 'mosaic of edaphic grassland and aquatic vegetation' (White 1983) separated from the Atlantic Ocean by mangroves (Welcomme 1986; Chapter 40). Average tree height is relatively low (20–25 m) and the forests are dominated by *Hallea ledermannii* (Rubiaceae), *Ctenolophon englerianus* (Ctenolophonaceae), *Klaineanthus gaboniae* (Euphorbiaceae), *Hexalobus crispiflorus* (Euphorbiaceae), *Symphonia globulifera* (Clusiaceae) and *Pycnanthus marchalianus* (Myristicaceae) (Werre 2001b). Emergents vary with soil water content; in drier sections, red ironwood *Lophira alata* (Ochnaceae), *Sacoglottis gabonensis* (Humiriaceae) and *Irvingia gabonensis* (Irvingiaceae), are most common, while in the wetter sections it is *Alstonia boonei* (Apocynaceae). Oil palm (*Elaeis guineensis*) is common and the understory is often dominated by rattan palms (e.g. *Calamus deerratus, Raphia* spp.). Further detail on the Niger delta is provided in Chapters 30 and 40 of this volume.

The Tana Delta is the name loosely given to the flood plain ecosystem of the lower Tana River, a vast wetland complex on the Kenyan coast. The delta is roughly triangular in shape, with its apex at Lake Bilisa (north of Garsen) and its base a 50 km stretch of beach along Ungwana (or Formosa) Bay, stretching from Kipini in the northeast to Mto Kilifi in the southwest. Habitats include fresh and brackish lakes, freshwater and saline grasslands, and successional stages of forest and woodland on the riverbanks and the dune ridges parallel to the shore (see Chapter 30).

Asia

The Mekong River, one of the largest rivers in Southeast Asia, flows southward from the Tibetan Plateau to the South China Sea through the Indochina Peninsula and forms a wide delta plain at its mouth containing one of the largest deltas in the world. In the past, the pileated gibbon *Hylobates pileatus* may have occurred in Vietnamese territory to the west of the Mekong Delta, though east of the Mekong only the primate genus *Nomascus* occurs (Groves 2007a). The primates of the Sunderbans (the combined deltas of the Ganges, Brahmaputra and Meghna rivers) are covered by Mallick (Chapter 16).

Swamp Forest

A swamp forest is a forested waterlogged area where the physiognomy of the vegetation is clearly different from well-drained forest vegetation (Kalliola *et al.* 1991). Forested swamp types can often be distinguished by vegetation; palm swamp and forest swamp, while peat swamp and backswamp are usually defined by soil type.

Palm Swamp

Definition

Palm swamp is found mainly on alluvial soils subject to flooding and anaerobic conditions. Their defining feature is a high concentration or dominance of palms of various types.

Neotropics

South American palm swamp forests are dominated by *Mauritia flexuosa* (known by many names: South American moriche palm, *ite palm, ita, buruti, canangucho, aguaje*). Producing nearly monospecific stands (Penn 1999), *M. flexuosa* can reach up to 35 m at high densities. Many animal species – including primates (Bennett *et al.* 2001; Bowler & Bodmer 2011; Pontes 1999) – depend on the *M. flexuosa* fruit, which has high vitamin C content and fruits when many other trees don't (Chapters 27 and 31).

The permanently waterlogged palm swamp of the Pastaza–Maranon basin in the northern Peruvian Amazon (Roucoux 2013) is a closed-canopy forest dominated by *M. flexuosa* (most abundant species by basal area), *Mauritiella armata* and *Tabebuia insignis* (Bignoniaceae) (Atrium 2012).

Africa

Forest swamps cover huge areas of the central Congo Basin (Burgess *et al.* 2004; Thieme *et al.* 2005), where they are dominated by *Raphia* palm (Kingdon 1997; White 1993). These *Raphia* swamp forests support high densities of western lowland gorilla (*Gorilla gorilla gorilla*) (Rainey *et al.* 2010; Chapter 43). In Budongo forest, Uganda, chimpanzees compete for the pith of *Raphia farinifera*, which provides them with sodium (Reynolds *et al.* 2009).

Asia

Nipa palm (*Nypa fruticans*) is commonly found in the tidal wetlands of Southeast Asia, forming monodominant or mixed stands along the tidal section of rivers, as well as covering extensive low-lying areas in estuaries (Chapter 4). At the mouths of large rivers with a high freshwater discharge, mangroves are often replaced by nipa palm stands that perform the same ecological function, trapping sediments (Fong 1992). In Southeast Asia, Nibong palm (*Oncosperma tigillarium*) is also commonly found along the tidal section of rivers (near mangroves).

Forest Swamp

Definition

Freshwater swamp forests grow on fertile alluvial soils in areas of low relief. In contrast to palm swamp, they support a higher diversity of trees and not monospecific stands of palms.

Neotropics

Wallaba is the local name for *Eperupa falcata* (Fabaceae: Caesalpinioideae) which dominates Guyanese swamp forests (J. Chave, pers. comm., 2013). Wallaba swamp is both structurally and floristically distinct from lowland rainforest (Davis & Richards 1934). Three features produce its characteristic appearance: an extraordinary number of trees per unit area, a scarcity of very large trees and an almost complete absence of buttressed trees. Usually wallaba forests are adjacent to areas of white sand and there is a sharp boundary between the white sand and the brown wallaba soil. The use of these forests by primates in Guyana is described by Shaffer *et al.* (Chapter 28). In French Guiana, *E. falcata*-dominated swamp forests are called *wapa*. Though *E. falcata* is overwhelmingly dominant, there are sometimes tree species of Myristicaceae and Sapotaceae within these forest stands.

Africa

In southern Nigeria, forest swamps are the product of both fluviatile and marine sediment build up (Grubb 1990). Species include: *Lophira alta, Ricinodendron heudelotii, Sacoglottis gabonensis, Uapaca* spp., *Hallea ledermanii* (Rubiaceae) and *Ficus vogeliana* (Moraceae) (Werre 2001b).

Southeast Asia

Forests subject to flooding by freshwater are extremely floristically varied within the region and are lumped together into one category purely for convenience (Corlett 2005). In Sumatra, the dominant tree is *Adina polycephala* (Rubiaceae) but *Malaleuca leucadendron* (Myrtaceae) also covers extensive areas (FAO 1981). Swamp forests can range from species-poor stands dominated by the genus *Malotus* to floristically diverse forests similar to the surrounding lowland rainforest. The tall legumes *Koompassia, Callophyllum* and *Melanorrhoea* and *Metrixylon sagu* thrive in this habitat (MacKinnon 1987).

Peat Swamp

Peat swamp soils are made up primarily of organic matter (Driessen 1978), nutrient poor, often acidic (pH < 4) and hygromorphic, being almost permanently flooded or waterlogged. Peat swamp forests are species poor and support few endemic species (IUCN 1991). Despite extreme conditions, trees can grow above 70 m high, reliant upon nutrient inputs from rainfall, dust and marine aerosols (Yule 2010).

Africa

Recently, a huge bog (over 145 500 km^2) was discovered in the centre of the Congo Basin. The swamp found in Congo Brazzaville is up to 7 m thick and thought to contain billions of tonnes of peat (Dargie *et al.* 2017).

Asia

The edges of swamp forests in Malaysia are characterized by strangler figs, an important food for mammals (Payne & Andau 1994), and more than 30 palm species are found in the peat swamp forest, also providing food. On Sumatra, peat deposits are at least 50 cm thick (but up to 20 m); fires are common and prevent natural succession, promoting the

development of extensive nearly monospecific stands of paperbark (*Melaleuca cajupiti*, Myrtaceae) (Whitten *et al.* 2000). The Tonle Sap–Mekong peat swamp forests of southern Vietnam and Cambodia are also dominated by *Melaleuca* (though it is *M. leucadendron*); they are low in plant diversity, but significant in maintaining ecosystem function, reducing water flow in the wet season and minimizing flooding, storing freshwater and reducing soil acidification.

Backswamp

Definition

Geologically, a backswamp is the section of a floodplain where deposits of fine silts and clays settle after a flood, usually behind the natural levee of the main river or one of the distributary rivers. Backswamp areas tend to have saturated soils throughout the dry season (Hamilton *et al.* 2007). These forests are less diverse than riverine forest; trees must grow in saturated soils that lack oxygen all year.

Neotropics

In the Peruvian part of the watershed of the Madre de Dios river, backswamp forest is particularly common on the left river bank. Forests are dominated by *aguaje* palms (*Mauritia flexuosa*, forming palm swamp forests known as *aguajales*) but other species, especially figs (*Ficus* spp.) – keystone species and important resources for primates – can also be abundant.

Africa

Backswamp areas in the Niger delta of Nigeria are relatively stable, consisting of constantly waterlogged heavy clay covered by peat (NEDECO 1961). The waterlogged backswamps are not as diverse in species as the drier areas of the swamp (Werre 2000). Forests of backswamps include members of the Euphorbiaceae (*Uapaca* spp., *Klaineanthus gaboniae, Macaranga* spp.), Clusiaceae (*Symphonia globulifera*) and Rubiaceae (*Hallea ledermannii, Rothmannia* spp.) families.

Asia

Many of the former backswamp areas in Asia were converted to agriculture centuries ago as they are fertile and amenable to irrigated agriculture – especially rice. Bowl-shaped depressions between the natural levees of rivers in Bangladesh are known as *haors* and, in eastern Bangladesh, they cover 2.5 million hectares (Poffenberger 2000). Forests in this area are dominated by tree species that can withstand inundation, including *Barringtonia acutangula* (Lecythidaceae), *Pongamia* (=*Millettia*) *pinnata* (Fabaceae: Papilionoideae) and *Crataeva nurvala* (Capparaceae).

Mangroves

Definition

Mangroves are largely restricted to the tropics and a few warm temperate regions (Chapter 7). Adapted to the intertidal zone, the physical environment of mangroves is defined by regular inundation of the soil and variable salinities, and although the soils range in type, most are anaerobic within a few millimetres of the soil surface. Mangrove trees are specifically adapted to this saline, low oxygen environment and are rarely found elsewhere. Characteristic physiological and morphological adaptations include active extrusion of salt from xylem (via deposits in bark, senescence in leaves, salt glands on leaves), and a number of secondary root adaptations: pneumatophores (upward extensions from subsurface roots into the air), knee roots (rounded knob-like extrusions) and buttress roots (important for structural support).

Mangroves can form extensive forests with canopy heights above 30 m, but in more arid or saline conditions they form dwarf or scrub communities. The most extensive mangrove forests occur in river deltas, but mangroves are also common along coastlines where wave energy is low. The coasts of Central America and Central Africa have hundreds of kilometres of almost continuous mangrove systems, which can extend into deltaic or estuarine systems, often far inland.

Mangroves have a vital role in coastal protection. They are also important for the breeding, passage and wintering of water birds. Sea turtles feed in mangrove ecosystems, which are important breeding and nursery grounds for fish and invertebrates while regulating water and nutrient flows to adjacent ecosystems.

Neotropics

Over 80% of mangroves are found in complex deltaic systems. In Brazil, the coastal region (Pará) is dominated by three mangrove species (Krause *et al.* 2001); *Rhizophora mangle* (Rhizophoraceae: the red mangrove), *Avicennia germinans* (Acanthaceae: the black mangrove, referring to the colour of the trunk and the heartwood) and *Laguncularia racemosa* (Combretaceae: the white mangrove, as bark appears white). Red mangroves grow closest to the sea, tolerating the deepest water, while white mangroves grow furthest inland. The primates of Neotropical mangroves are described by Santos and Bridgeman (Chapter 8).

Africa

Mangrove swamps in West Africa are becoming increasingly important refuges for large mammals, including primates, as human populations expand (Bi *et al.* 2009; Galat-Luong & Galat 2007). Nigeria has the largest extent of mangroves in Africa, mainly within the Niger delta, which extend up to 50 km inland (Chapter 40). In East Africa, the most extensive mangrove stands are in the Rufiji and Zambezi river deltas, and in Zanzibar, stands of *Rhizophora mucronata* are common, productive and aseasonal with continuous leafing, flowering and fruiting of trees providing food for endemic red colobus monkeys (*Procolobus kirkii*) and also Sykes monkeys (*Cercopithecus mitis albogularis*) (Nowak 2008). Primates of African mangroves are summarized by Head *et al.* (Chapter 12).

Asia

This region has the highest mangrove diversity in the world, with extensive mangrove stands in many countries (Spalding *et al.* 2007). Compared with other forest types in the region,

mangroves have simpler structure and species composition (Corlett 2005). The Sundarbans in Bangladesh and India form the world's largest mangrove area, covering 20 400 km^2, deriving their name from the dominant mangrove species *Heritiera fomes* (Malvaceae), known locally as *sundri* or *sundari*. In coastal India and Pakistan, the Indus Delta mangrove habitat is adapted to extreme temperatures and salinity. There are also large stands of mangrove in the Mekong Delta, although they declined from 21 221 ha in 1965 to 12 797 ha in 2001 (Thu & Populus 2007), and have declined further since then.

The proboscis monkey is a known mangrove specialist, using the mangroves for sleeping (Bernard *et al.* 2011*a*), and also other activities (Bennett & Sebastian 1988; Boonratana 1993; Salter *et al.* 1985). In this volume, the ecology of primates in Asian mangroves are described by Bernard *et al.* (Chapter 13), Nijman (Chapter 14), Shekell *et al.* (Chapter 15) and Mallick (Chapter 16).

Oxbow Lakes

Definition

Oxbows are crescent-shaped lakes alongside meandering, braiding or reconnecting rivers. The erosion and deposition of sediments may alter the course of a river as hydraulic action, abrasion and corrosion can increase the curve of a meander, narrowing the neck until the river cuts the meander at the time of flooding (Hickin 2003). Many oxbow lakes can become reconnected to the main river channel in times of high water and hence are considered 'semi-open' ecosystems (Davenport 2008; Junk 1997) with fish, nutrients and floating macrophytes able to enter and exit the lake through a temporary connective channel (Osorio *et al.* 2011).

Neotropics

In the Neotropics, oxbow lakes are frequent in Amazonia, where the low relief and high sedimentation rate means that river systems are highly dynamic forming meanders and regularly changing their course (Toivonen *et al.* 2007). In the Manú Biosphere Reserve in Peru, the watershed of the Rio Manú, oxbow lakes are called *cochas* and vary notably in physical, chemical and biological properties (Davenport 2008). Some oxbow lakes quickly form low-lying *renacals* or swamp forests dominated by *Ficus trigona* (Moraceae) and others may temporarily become filled with grasses and tree seedlings, ultimately succeeding to other forest types (Gentry & Terborgh 1990). Some primate studies have been conducted along oxbow lakes, such as on the black-faced black spider monkey (*Ateles chamek*) at Lago Caiman, Noel Kempff Mercado National Park, Department Santa Cruz, Bolivia (Wallace 2006), and white uacari (*Cacajao calvus calvus*) at Lake Teiu, Brazil (Walker & Ayres 1996).

Africa

In Kenya, oxbow lakes have been created along the Tana River; these lakes influence forest dynamics (Hughes 1990) and are occupied by primates such as the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and red colobus *Procolobus rufomitratus* (Chapter 30). In Madagascar, two gallery forests in the Berenty Reserve, the main Berenty forest (200 ha) and Bealoka (100 ha), are threatened forested islands formed by ancient oxbow lakes (Chapter 5). These forests are characterized by tamarind trees, *Tamarindus indica*. These unusual gallery forests, and the spiny forest that lies beyond the steep river banks, are used by lemurs, including *Lemur catta* (Jolly *et al.* 2006).

Asia

In Asia, oxbow lakes are found in various regions including in the Ganges river in India (local name: *baors*) (Hasan *et al.* 2001). In the dry season, most of these oxbow lakes become fully isolated from the main river leading to changes in water chemistry, aquatic plants and animals. Approximately 600 oxbow lakes are found in southwestern Bangladesh, covering around 5488 ha. There are also oxbow lakes in many floodplains of large rivers, e.g. the Kinabatangan, Sugut and Padas rivers, in Sabah, Malaysia (e.g. Azmi 2007; Jawan & Sumin 2012). Stretches of the Kinabatangan River contain *c.* 30 oxbow lakes with various stages of infilling (Boonratana & Sharma 1997; Davison 2002: noted as cited in Salgado-Lynn 2010).

Reedbed/Papyrus

Definition

Largely confined to Africa, papyrus swamp is named for its dominant species *Cyperus papyrus* (papyrus sedge, paper reed, Indian matting plant, Nile grass). An aquatic, herbaceous perennial sedge, it forms tall monoculture stands in shallow water (Thompson 1976). Papyrus swamps have a high growth rate (C4 photosynthesis; Jones 1988) and the ability to recycle nutrients. They provide structural refugia and habitats for several endangered wildlife species (Chapman *et al.* 1996; Maclean *et al.* 2006). *Cyperus papyrus* occupies two major habitats: the edges of freshwater lakes (a floating mat attached at its perimeter) and river valleys where flow is slow (spreads across the frequently flooded valley floor).

The natural distribution of *C. papyrus* is within a belt across equatorial Central Africa (17°N–29°S), with the most extensive swamps in Lake Victoria and the Nile basins (Thompson 1976). *Papyrus* sedge also dominates areas of the Okavango inland delta in Botswana.

One primate species on Madagascar, the Lac Alaotra bamboo lemur (*Hapalemur alaotrensis*), feeds almost exclusively on papyrus and reeds in marshland, the only primate adapted to marsh habitat (Chapter 34).

Seasonally Flooded Grassland

Definition

Flooding is an important ecological phenomenon of riverine systems as floodwaters regenerate the floodplain with nutrients and facilitate the development of a mosaic of aquatic plants, flooded grassland, riparian forest, savanna, woodland and dry forest (Pott *et al.* 2011).

Neotropics

The most extensive seasonally flooded grassland in South America is the Pantanal, a savanna wetland inundated by tributaries of the upper Paraguay River. Characterized by an indistinct and ever-changing boundary between water and land, seasonal hydrology patterns drive the productivity of this system (Junk 1993; Vinson & Hawkins 1998; Wantzen & Junk 2000). The flood discharge carries nutrients, sediment and inorganic and organic material which enriches the floodplain allowing the proliferation of microorganisms, invertebrates, fish, amphibians, reptiles, birds and mammals (Mamede & Alho 2006). The flooded Pampa grasslands in Argentina are inundated entirely by rainfall (Perelman *et al.* 2001).

Africa

A number of large, seasonally inundated wetlands exist in Africa, scattered throughout the seasonally wet and dry areas of the Sahel zone of western Africa, and also in eastern and southern Africa (Burgess *et al.* 2004). As an example, on the southern edge of the Sahara, the Lake Chad savanna is flooded when the lake expands in the wet season. Despite high evaporation the lake retains low salinity because inputs are riverine and saline waters sink, leaving the lake through subterranean conduits. Floating Nile lettuce (*Pistia stratiotes*, Araceae) is present alongside *Cyperus papyrus* and *Phragmites* spp. (Poaceae) with *yaere* grassland on the southern lakeshore, where flooding is prolonged and water depth reaches 1–2 m.

The inner Niger delta (Mali) and the Hadejia-Nguru wetlands (Nigeria) in the Sahelian belt are also large, seasonally flooded, wetlands that support extensive grassy wetland vegetation that expands and contracts in line with the flooding cycles (Thieme *et al.* 2005).

Further to the east in Africa, the nutrient-rich White Nile overflows in southern Sudan to form the extensive Sudd swamps (Seymour 2013). Within the Sudd swamps, there are a series of ecological zones from open water to submerged vegetation, including flooded grassland (Hickley & Bailey 1987), and it has been estimated that only 11% of the total flooded area is permanent water (Welcomme 1979).

The seasonally flooded grassland of the Okavango, Botswana is inundated to a variable extent every year when floodwaters from the Angolan highlands arrive between February and May (Gumbricht *et al.* 2004). The main species of grass are *Miscanthus junceus, Phragmites communis, Cyperus articulates* and *Schoenoplectus corymbosus* (all Cyperaceae). The Okavango supports some of the largest concentrations of wildlife in Africa (Thieme *et al.* 2005), including chacma baboons (*Papio ursinus*) behaviourally adapted to flooding in this region.

Asia

In Southeast Asia, natural, non-forest wetlands seem to be confined, in the lowlands, to areas with seasonal rainfall. In these climates, swamp grasses, sedges and ferns dominate the system (Corlett 2005).

Intertidal Zones

Definition

Tidal flats are a transitional zone between aquatic and terrestrial ecosystems. Marine and freshwater tidal zones differ; marine are often subject to high wave energy and may have large tides, while tidal effects in freshwater ecosystems tend to be smaller. Intertidal zones are often dispersal corridors for plants and animals that float as seeds, propagules or rafts of debris (Nilson & Svedmark 2002; Renofalt *et al.* 2005). These zones can provide rich foraging grounds, including for primates like the Burmese long-tailed macaque (*Macaca fascicularis aurea*) (Chapter 19), Japanese macaque (*M. fuscata*) (Chapter 18) and chacma baboon (*Papio ursinus*) (Chapter 20).

'Beach forest', not to be confused with mangroves, completely roots in freshwater and is almost never inundated by seawater. Beach forest tends to exist above the high-tide line, but is tricky to identify as similar species composition is found in the transition zone from mangroves to upland forest. Beach forests provide suitable habitat for primates especially in Southeast Asia where beach forests are called '*Barringtonia* formations'.

Neotropics

Neotropical beach vegetation consists of coastal forest on sandy soils. Called *restinga* in Brazil, they vary from being dominated by trees, shrubs or creeping vines. Salt marshes are also present (da Silva *et al.* 2010; Pimental *et al.* 2007). Important tree species include *Humiria balsamifera* (Humiriaceae), *Pouteria ramiflora* (Sapotaceae), *Anacardium occidentale* (Anacardiaceae), *Byrsonima crassifolia* (Malpighiaceae) and *Tapirira guianensis* (Anacardiaceae), while *Sesuvium portulacastrum, Ipomoea pes-caprae* (Convolvulaceae), *Sporobolus virginicus* (Poaceae) and *Blutaparon portulacoides* (Amaranthaceae) are important herbs and vines, serving to stabilize the sand (da Silva *et al.* 2010). Though several Neotropical primates regularly use mangroves (Chapter 8), there seem to be no published records of habitual beach use as in Africa (Chapter 20) or Asia (Chapters 18 and 19). In Costa Rica, white-headed capuchins (*Cebus capucinus*) visit beaches, but only to steal food from tourists (Edilton Rodrigues Santos and Stephen Ferrari, unpublished data; see Santos 2013). In South America, blond capuchins (*Sapajus flavius*) feed on the fruits of introduced oil palm (*Elaeis guineensis*) in forest fragments by Porto de Galinhas beach, Permanbuco state, northern Brazil. In addition, a group of common marmosets (*Callithrix jacchus*) regularly feed on fruit/gum/insects at the border between the Atlantic forest and the sandy beaches at Porto de Galinhas and São José da Coroa Grande (Antonio Mendes Pontes, unpublished data). In coastal Paraíba state, northern Brazil, *S. flavius* forage in vegetation and their footprints have been recorded on sand dunes (Monique Bastos and Bruna Bezerra, unpublished data). In Sao Paulo state, southern Brazil, the Superagui island population of the Critically Endangered black-faced lion tamarin (*Leontopithecus*

caissara) uses arboreal restinga (coastal forest on sandy soils) as a primary habitat (Nascimento & Schmidlin 2011). Surprisingly, primates are not known predators of sea turtle eggs (Engeman *et al.* 2003; Stancyk *et al.* 1982), even though a number of other opportunistic mammalian foragers (e.g. raccoons, *Procyon* spp.) feed on them (Garmestani & Percival 2005), and capuchins may predate river turtle eggs (Barnett *et al.* 2005; Batistella & Vogt 2009).

Africa

The Jozani beach forest of Zanzibar is dominated by a species of *Eugenia* (Myrtaceae) and *Vitex doniana* (Robins 1976), but composition is not uniform with species distribution dependent upon water availability. Beach forest on Uzi Island, Zanzibar, has *Vitex trifolia, Hibiscus tiliaceus* (Malvaceae), *Terminalia boivinii* (Combretaceae), and *Rhus natalensis* (Anacardiaceae), all consumed by red colobus monkeys, which also use the adjacent habitats: mangroves and coral rag forest (Nowak 2007).

Asia

On accreting sandy beaches, a low community of creeping herbs, grasses and sedges occupies the zone between the sea and firm land (Corlett 2005). Here, beach forest is known as '*Barringtonia* formation' or *Barringtonia asiatica–Terminalia catappa* vegetation after the dominant tree species *Barringtonia asiatica* (though *B. asiatica* itself is not always present in the formation) (Whitten *et al.* 1997). *Barringtonia* formation is tolerant of salt spray, nutrient deficient soil and seasonal drought and merges with lowland rainforest inland. *Calophyllum inophyllum* (Sapotaceae) is also present and some of the plants found in this type of beach vegetation are typical of sandy shores throughout the tropics.

Conclusion

The range of flooded habitats across the tropics has undoubtedly influenced the evolution and persistence of non-human primates. The diversity of wetland habitats is mirrored by highly biodiverse inhabitants, including primates which may use flooded areas for refuge given these are not easily accessible to humans. When surrounding *terra firma* forest has been cleared, often much of the original floodplain forest remains standing because wet areas are not as ideal for agriculture and habitation. As a consequence, despite large-scale land-use change and habitat degradation, flooded habitats still host a large number of primates and other mammals that may otherwise be rare or even extinct.