Aquatic Habitats in Forest Ecosystems

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Introduction

There is a wide variety of aquatic habitats found in forested areas ranging from water-filled tree holes through to large rivers, lakes, and inundated forests. This article initially reviews the classification of aquatic habitats and some of their important geomorphological, physicochemical, and biological parameters. Following this, different classes of aquatic habitats in forests are presented in outline with consideration of their global distributions, defining abiotic characteristics and aquatic biota. A broad distinction has been made between aquatic habitats where the forest itself forms part of the habitat matrix (forested wetlands) and those where the forest is only on the periphery (water bodies in forests). Four subdivisions of forested wetlands are discussed: (1) peat bog forests, (2) swamp forests, (3) floodplain forests, and (4) mangrove forests, and three types of water bodies in forests: (1) container habitats (phytotelmata), (2) ponds and lakes, and (3) streams and rivers. For the latter groups, emphasis has been placed on the differences in characteristics when compared to nonforested ecosystems. Finally human interactions with aquatic systems are discussed, including both dependency on aquatic resources and anthropogenic threats.

There have been many attempts to classify aquatic habitat types based on combinations of geomorphological, physical, chemical, or biological characteristics. Some of the most important and frequently used classification variables are given in **Table 1**. Whilst providing an excellent framework for rationalizing our understanding of aquatic systems, there are inevitably exceptions to all classifications. Usually, this is because the habitat characteristics exist as continuous variables rather than distinct states and thus the criteria for inclusion in a particular category will be, to some extent, subjective. For example, some rivers will dry up to a series of pools, thus transforming a flowing water (lotic) habitat into a still water (lentic) one. Similarly, many of the habitat variables covary – nutrient levels are generally strongly correlated with organic production, for example. Despite these caveats, it is possible to identify a number of types of aquatic habitat in forested ecosystems.

At the highest hierarchical level, there is a broad distinction between aquatic habitats where the forest itself is an integral part of the habitat and those where the forest is only on the edges of the water body. There is no standard terminology for either group and there are a huge variety of local names for subdivisions within each. In this article, 'forested wetlands' is used for aquatic habitats where there are inundated live trees found throughout the water mass whereas 'water bodies in forests' is used where live trees surround or line the water and do not extend throughout the habitat.

Table 1 Some common continuous variables used to classify aquatic habitats

Type of variable[a]	*Example variables*	*End points of continuum*	
Geographical or geomorphological	Size of water body	Small	Large
	Depth of water	Shallow	Deep
	Permanence of water (hydroperiod)	Ephemeral	Permanent
	Stability	Fluctuating	Stable
	Degree of water flow	Lentic	Lotic
	Gradient	Steep	Shallow
	Latitude	Tropical	Temperate
Physicochemical	Temperature	Low	High
	Light	Fully shaded	Open
	Degree of mixing	Amictic	Polymictic
	pH	Acid	Alkaline
	Oxygen levels	Anoxic	Oxygenated
	Nutrient levels (N, P)	Low	High
	Suspended sediment	Clear	Turbid
Biological	Organic production	Oligotrophic	Eutrophic
	Source of production	Autochthonous	Allochthonous
	Organic debris	None	Plentiful
	Dominant trophic group	Shredders	Filter-feeders

[a] Some variables will only apply to a subset of aquatic habitats discussed in the text; for example, degree of mixing is generally only used for standing water bodies.

Forested Wetlands

The total extent of forested wetlands in the world has been estimated at 3.4 million km^2 but there are considerable uncertainties in this figure. Furthermore, there are very large variations in degree and period of inundation and thus the actual extent of forested wetlands at any point in time is difficult to determine. The local hydrological balance between inputs (rainfall, surface runoff, and groundwater seepage), storage, and outputs (evapotranspiration, infiltration, and runoff) determines the formation, maintenance, and hydroperiod (the amount of time that the forest is inundated) of forested wetlands.

Important characteristics shared by all forested wetlands are submerged physical habitat structure (tree trunks and branches) and wide distribution of terrestrially derived organic input over the entire water surface. Tree trunks and branches play a very important role in modifying hydrological parameters, including slowing of water flow and precipitation of suspended material. Furthermore, they provide surfaces for colonization by aquatic biota. Terrestrial input of material may be from the trees themselves (leaves, fruit, and seeds) or plants or animals living on the trees.

Four major categories of forested wetlands are described below, although the categories grade into one another, swamp forests often receiving river floodwater for example.

Peat Bog Forests

These are forests growing on peat-rich soils that are permanently waterlogged. They are formed where there are large inputs of fresh water and low levels of organic decomposition. Aquatic habitats in peat bog forests may be sporadic, seasonal, or permanent.

Distribution The vast majority of inundated forests on peat bogs are in boreal areas – extensively in Canada, Alaska, Scandinavia, Russia, and China. The coast of the southeast USA (Florida to North Carolina) also has considerable amounts, whilst in the tropics substantial peat bog forests are found in Borneo, Sumatra, and Papua New Guinea.

Physicochemical characteristics Peat bog forests that receive water input solely from rain (ombrotrophic) have a low pH and are low in inorganic nutrients. Where there are groundwater inputs in addition to rain, pH is near neutral and there are higher levels of nutrients. Water in all peat bog forests is often darkly colored from the presence of dissolved tannins which reduce light penetration. Water depth is shallow to moderate. Water movement is slight, thus turnover and flushing rates are low. Combined with high levels of organic materials, this leads to anoxic conditions particularly near the benthos.

Aquatic biota Few or no macrophytes are present because of low light levels and/or low pH. Similarly, algal production is low. Invertebrates appear to be specialists with adaptations to deal with low oxygen levels. Trophic food webs are based on detritus. In boreal areas fish are absent or restricted to a very few species. In the tropics there may be considerable fish diversity from families specialized to deal with low oxygen levels with adaptations including air-gulping and labyrinthine organs. There may be considerably greater fish diversity than is presently recognized because sampling effort has been low in these habitats. Other vertebrates such as turtles and snakes may spend time in these habitats but there are few or no obligate species.

Swamp Forests

Swamp forests are found on peat-poor soils that are permanently waterlogged. They may be created and maintained by land topography (basin swamps), hydrological barriers, and/or high water tables. Aquatic habitats in swamp forests may be sporadic, seasonal, or permanent. Palms are a prominent group in tropical swamp forests.

Distribution Swamp forests are distributed widely, but are more common in tropical rather than temperate zones. The largest areas of swamp forest are to be found throughout Central America, Brazil, Argentina, tropical Africa, and Southeast Asia (particularly Borneo, the island of New Guinea, Laos, and Cambodia). There are also substantial swamp forests in central Asia and the southern USA.

Physicochemical characteristics As there is a wide variety of mechanisms that create swamp forests physicochemical characteristics also vary widely. There is generally little or no water movement for most of the hydroperiod, particularly in basin swamp forests, and water depth is shallow to moderate. However, flushing may occur during seasonal or episodic flooding from rivers. Oxygen and nutrient concentration of the water varies considerably depending on source of input, soil, and vegetation type.

Aquatic biota Considerable diversity of aquatic biota may be found in swamp forests. Where there is not a closed canopy some development of rooted or floating macrophytes may occur. Invertebrates from a wide range of taxonomic groups (particularly insects, crustaceans, and gastropods) are present and trophic webs may be based on autochthonous production, terrestrial input from trees, or detritus. Vertebrates including fish, amphibians, and reptiles are present. Fish diversity may be moderately high with specialists on detritus and benthic or terrestrial invertebrates. Caimans, crocodiles, or alligators are often the top predators in the system.

Floodplain (Alluvial) Forests

These are forests that are seasonally or irregularly flooded by changes in river level. In temperate areas flooding is often associated with snowmelt in the upper reaches of catchments, whilst in the tropics monsoonal rainfall is the major contributor.

Distribution Floodplain forests are found throughout the world. The most extensive are associated with very large rivers such as the Amazon, Mississippi, Orinoco, Congo, and Mekong, although they are associated with almost all unregulated rivers. Estimates of the extent of floodplain forests have been generated by satellite imagery during periods of maximum inundation and include 300 000 km^2 for the central Amazon and 70 000 km^2 for the Mekong.

Physicochemical characteristics The predictability of flooding and hydroperiod depends on the gradient and water storage capacity of the rivers and streams. Forests associated with smaller, high-gradient streams and rivers have rapid changes in water level and irregular and short hydroperiods, whereas those through which large, lowland rivers flow have more predictable hydrological regimes. Water depth may be considerable (>12 m), although shallow depths are more common. Rising water levels transport sediment which is deposited in the floodplain and levels of inorganic nutrients are high. Waters are usually oxygen-rich during initial phases of inundation, although thermal stratification, anoxic conditions, and pH changes can develop over time. River regulation often changes the areas inundated and the hydroperiod substantially.

Aquatic biota Invertebrates, fish, amphibians, and other mobile riverine animals rapidly move into newly created floodplain habitats. This movement can be to escape high-flow conditions in the main stem of the river but is more often related to exploitation of the floodplain habitat for food, reproduction, or avoidance of predators. Where the hydroperiod is of sufficient duration, algae and aquatic macrophytes will become established and may add additional habitat and trophic complexity. Floating mats of vegetation may develop if the light environment is suitable. Aquatic insects, crustaceans, gastropods, and many other groups may reach high abundance levels and complex food webs based on autochthonous production, terrestrial input, detrital material and fruits and seeds develop. In the tropics, high diversity of fish, amphibians, and reptiles are found. These form the basis for well-known fisheries in the Amazon and Southeast Asia. The Amazon basin is home to more than 3000 species of fish, the majority of which spend at least some period of their life history in floodplain forests. It has been suggested that some of this extraordinary diversity is related to additional habitat and trophic interactions that occur during flooding of the forest. Similarly, there are at least 1200 species in the Mekong basin and 700 in the Congo basin, many of which are dependent on floodplain forests.

Mangrove Forests

Mangrove forests are found on the coastal fringes of land on sheltered shores. They are characterized by regular inundation by salt water during the tidal cycle and are composed of a specialized group of trees with adaptations to cope with this. Aquatic habitats in mangrove forests fluctuate in extent over short time periods.

Distribution Mangrove forests are exclusively coastal and predominantly found in the tropics. They are particularly abundant in Australia and Southeast Asia, the Indian subcontinent, Mexico, Central America and Brazil, and equatorial Africa.

Physicochemical characteristics The dominant abiotic factors in mangrove forests are tidal fluctuations in water level and salinity gradients related to proximity to the coast. Water levels change regularly on short timescales following tidal inundation with saline, marine water. Salinity decreases moving inland from the mangrove margin, dependent on levels of freshwater input. Soils are anoxic with large amounts of organic material present (primarily mangrove-derived).

Aquatic biota Plant and animal life in mangroves has to withstand large daily changes in abiotic conditions. Almost all species are of marine origin rather than freshwater origin and may undergo daily migrations or retreat to refugia in response to these variations. Distinct zonation in communities is seen with boundaries orientated parallel to the coast. There are few aquatic macrophytes although marine algae may be found on submerged parts of mangroves. Invertebrates (mostly gastropods and crustaceans) are abundant, with their production based on detritus. Marine fishes move into inundated mangrove areas on the rising tide to feed on invertebrates or detritus. However, there are few species that are restricted solely to mangrove areas, mudskippers being an exception. Crocodiles are characteristic top-level predators. Mangrove areas are very productive, exporting large amounts of carbon and contributing to substantial coastal fisheries through energy transfer or acting as 'nursery habitats' for exploited fishes.

Water Bodies in Forests

These aquatic habitats are found in virtually all forest ecosystems throughout the world, thus no distributional information is given. For ponds, lakes, rivers, and streams the forest is restricted to a fringe around or along the edges and the influence of the forest (shading, chemical, and biological inputs) is restricted to these areas. Obviously, the relative effect of the forest on the water body is dependent on the latter's size relative to the height and extent of the forest. Thus, smaller water bodies or those surrounded by large areas of forest may be profoundly influenced whereas large lakes and rivers may be similar to those in unforested areas. Three types of water bodies in forest are described on the basis of their origin and water movement.

Container Habitats (Phytotelmata)

Phytotelmata are water-retaining structures formed by hollows in plant materials. These containers may be holes in tree stems or branches, the leaf axils of plants (particularly epiphytic bromeliads), leaves of pitcher plants, or fruit husks. They are generally ephemeral although some 'tank' bromeliads may have water in them for their entire lives (>20 years).

Physicochemical characteristics The volumes of phytotelmata are small (up to $1300\,cm^3$) and the water contained within them shows no movement. Water quality is strongly influenced by the surrounding plant material. Most contain decaying plant material – leaves, wood, or fruit – and drowned animals. Leachates from this material and the forest canopy make the water acid and rich in organic nutrients. Oxygen concentrations are low because of decaying organic material.

Aquatic biota Algae may be found in phytotelmata that are in bromeliads located in the forest canopy. Aquatic insect larvae are often the dominant animal forms in phytotelmata, particularly flies and mosquitoes. Many of these are specific to particular phytotelm habitats and are not found elsewhere. Microcrustaceans (such as ostracods), gastropods, and aquatic mites are also found. In tropical areas, juvenile and/or adult frogs may be present. Food webs can be based on algae, detritus, or drowned animals.

Ponds and Lakes (Lentic Habitats)

Lakes and ponds are habitats that are enclosed by land with outflows small in comparison to their volume. They also have water movement that is not unidirectional. In the smallest ponds there may be little or no water movement, but in larger lakes wind and/or convection currents create water movement. Lentic habitats may be created by depressions in bedrock and sediment or by barriers and they are fed by a combination of one or more of the following water sources: streams and rivers, groundwater, and rain. Water depth in lakes in forested areas can be far greater than the other aquatic habitats considered in this article, reaching over 700 m for Lake Mjösen in Norway. There is a large range in surface area from tens of square meters to hundreds of square kilometers. Lentic habitats, particularly larger ones, share a number of similarities with marine habitats such as thermal stratification. Lakes can be sporadic, seasonal, or permanent.

Physicochemical characteristics The dominant abiotic factor in all but the shallowest lentic water bodies is stratification. Heating of the surface water (epilimnion) makes it less dense and it floats on top of cooler water underneath (hypolimnion). Mixing depth is dependent mainly on wind action. Stratification affects not only temperature but also oxygen and nutrient levels across the thermocline. Deep lakes are often anoxic below the thermocline. Turnover, where all of the water in the lake mixes, is strongly influenced by latitude. Cold temperate lakes may turn over twice a year, warm temperate lakes once, and tropical lakes daily or occasionally. In deeper lakes light may be rapidly absorbed. The influence of surrounding forests on ponds and lakes is greatest on the water quality entering through groundwater or rivers. Nutrient levels, pH, and organic input are dependent on the type of forest and soil. Effects on shading and temperature are minimal in comparison with streams and rivers.

Aquatic biota An important component of the flora of lakes is plankton. Autochthonous production by phytoplankton is the major source of organic material in large and/or deep lakes. Macrophytes may be found in shallow zones around the edge of the lake and occasionally may be an important source of organic material. There is a clear distinction in many lakes between benthic and pelagic animal communities. Benthic invertebrates include aquatic insects, crustaceans, and gastropods. These latter two groups may be of greater abundance, diversity, and importance than in lotic habitats. Where the hypolimnion is anoxic there are few benthic invertebrates. Benthic food webs are dependent on detrital input. Pelagic invertebrates include high abundance of zooplankton, particularly crustaceans (cladocerans and copepods) and rotifers, dependent on autochthonous phytoplankton. Aquatic insects – water beetles and water bugs – are also found in the pelagic zones. Fish are found in both the pelagic and benthic zones where there is sufficient oxygen. They may be specialized planktivores or generalist detritivores or omnivores. Reptiles, particularly turtles, are common in shallow areas. Wading and piscivorous birds are also conspicuous aspects of the fauna. There appear to be few generalizations possible about differences between lotic water bodies in forested and unforested ecosystems. Small ponds and the fringes of larger lakes may have faunal elements specialized to take advantage of terrestrial input (fruit, leaves, flowers, invertebrates), but these influences rapidly decrease in importance moving away from the shoreline.

Figure 1 Stream in primary forest, Sabah, Malaysia. Photograph courtesy of Keith Martin-Smith.

Streams and Rivers (Lotic Habitats)

These aquatic habitats are characterized by an overall unidirectional movement of water. However, there is considerable heterogeneity within most rivers and streams with areas of fast unidirectional flow (such as cascades, riffles, and runs), slow unidirectional flow (glides and reaches), and multidirectional flow or gyres (eddies, slacks, and pools) (**Figure 1**). These latter habitats may behave as lentic environments. Streams may be ephemeral, only flowing at certain times of year or after heavy rains, or permanent. There is a large size range from a few centimeters in width to a few kilometers for the biggest rivers such as the Amazon. Patterns in physicochemical and biotic characteristics are strongly related to position along the river course (river continuum concept) as well as temperate–tropical differences.

Physicochemical characteristics These parameters vary widely between different types of river. Depending on the geology, morphology, and forest cover of the catchment, there can be large differences in levels of suspended sediment, dissolved nutrients, oxygen, and pH. However, when compared to rivers running through nonforested areas, there are a number of generalities that can be made. Forests intercept and store water so that flows are moderated. Light levels are lower and the spectral composition is different because the forest intercepts much of the incident light. This effect is more pronounced in smaller rivers which may have completely closed forest canopies. Water temperatures are lower for the same reason. Inputs of dissolved, particulate, and large organic matter are greater than in nonforested catchments and have a different elemental composition. In deciduous forests there is a pulse of organic input with leaf fall, either seasonally or related to drought conditions. Thick layers of leaf litter can build up in temperate and tropical rivers providing an additional habitat for animals. Large woody debris is a significant structural aspect of forested rivers with important effects on hydrology (debris dams), nutrient retention and cycling, and animal microhabitat. Large woody debris is introduced into rivers by physical disturbance such as storms or floods and activity of animals, particularly the actions of beavers in northern temperate areas. Forestry activities have pronounced effects on water quantity, quality, sediment, and debris input.

Aquatic biota The aquatic biota of forested streams has been well studied around the world, particularly in temperate areas. Algae and aquatic plants may be present where current velocity is sufficiently low and there is adequate light penetration. Autochthonous production may peak in intermediate-size rivers where there is open canopy and shallow water depth while larger rivers often have floating mats of vegetation. Invertebrates from a wide range of taxonomic groups (insects, crustaceans, molluscs, and annelids in particular) are present although diversity tends to increase with decreasing latitude. Mayflies, stoneflies, caddis flies, dragonflies, beetles, and true flies are the dominant invertebrates in terms of numbers and biomass in many systems. Invertebrate production is dependent on leaf litter input in small streams, although grazing on autochthonous production may contribute in larger streams and rivers. The fauna in the streambed (hyporheic zone) is also an important component of the ecosystem, responsible for nutrient processing among other functions.

Fish and amphibians are generally present in all but the smallest and most ephemeral streams, again exhibiting distinct longitudinal zonation. Diversity increases moving from headwaters downstream and taxonomic composition changes through both species additions and replacements. The trophic structure of the fish community also changes with greater dependence on invertebrates and herbivory in upland streams while omnivory and piscivory are more important in lowland rivers. Additional food sources are available to fishes in forested streams, particularly terrestrial insects and fruit and leaves from trees. In north temperate streams migratory salmonid fishes may provide a large additional trophic subsidy, transferring production from the marine to the freshwater environment.

Reptiles, birds, and mammals may also be present either obligately or facultatively. Many snakes and most turtles spend large amounts of time in watercourses while crocodiles, alligators, and caiman are important predators in subtropical and tropical areas. Beavers are a conspicuous feature of north temperature forested streams with a profound influence on the structure of water bodies through their dam-building activities while otters may be found in temperature and tropical areas. River dolphins are a feature of large tropical rivers as are manatees in Central and South America.

Human Interactions with Aquatic Habitats in Forested Ecosystems

In many parts of the world there are intimate connections between human populations and the aquatic habitats described above. A large proportion of the annual protein intake may be derived from aquatic organisms, mainly fish. In the Amazon and Southeast Asia, floodplain forests support very large artisanal fisheries and human activities are synchronized with particular phases of the hydrological cycle. Very sophisticated methods of capture and exploitation exist to ensure maximum use of resources. For example, in the flooded forest system of Danau Sentarum, Kalimantan, only two of more than two hundred recorded species of fish are not used in some way by the several thousand people dependent on the system (**Figure 2**). Dozens of different fishing gears are used from lift and cast nets through gill nets and seines to large, semipermanent fish traps. Fry of certain large species (catfish and snakeheads) are captured and raised in floating cages where they are fed on smaller species. Highest catches are taken during the falling phase of the hydrological cycle and these fishes are preserved for use during the remainder of the year. Similarly, in northern temperate areas, salmonids from streams and rivers in forests are a vital part of the diet of native peoples.

Figure 2 Human use of aquatic resources in flooded forest, Kalimantan, Indonesia. Photograph courtesy of Keith Martin-Smith.

Conversely, many human activities threaten the integrity of aquatic habitats in forested ecosystems and individual species within them. The most prominent of these are resource overexploitation, habitat degradation from land-based activities (primarily logging), and the introduction of exotic species. Overexploitation of fishes has been documented as human populations increase and/or greater access to water bodies is created. The giant Mekong catfish and the Asian bonytongue are both considered threatened from overfishing. Logging, both selective and clear-cut, alters water quantity, timing, physicochemical parameters, and the aquatic biota. Sedimentation increases dramatically following logging and profoundly alters the ecosystem. Exotic species can also cause major, irreversible changes, with infamous examples including the water hyacinth and Nile tilapia.

While these threats are serious and immediate, they can be overcome if appropriate, sustainable solutions are developed. This will require adequate funding, political will and the application of multidisciplinary approaches.

Further Reading

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ENTOMOLOGY

Contents

Population Dynamics of Forest Insects

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Population dynamics is the study of changes in the number of organisms in populations and the factors influencing these changes. It thus, by necessity, includes the study of the rates of loss and replacement of individuals and of those regulatory processes that can prevent excessive changes in those numbers.

A wide variety of factors can affect the population dynamics of a particular species. These can be divided roughly into two categories. First, the extrinsic or environmental influences on populations, such as temperature, weather, food supply, competitors, natural enemies, diseases, and all possible combinations of the preceding; and second, the interactions between members of the same populations, be these direct or indirect, e.g., intraspecific