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## Introduction

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### Abstract

This introduction presents an overview of the key concepts discussed in the subsequent chapters of this book. The book is motivated not just by the Amazon's scientific interest but also by its role in these various ecosystem functions critical to life on Earth. It highlights several of its interactive and higher-order linkages among both abiotic and biotic ecosystem components. The book provides summaries of the author's research in Western Amazonia over the last two decades, in both non-flooded forests and forests flooded with white water and with black water. The Amazonian rainforest is located in the equatorial regions of the South American countries of Brazil, Colombia, Ecuador, Bolivia and Peru. In addition, the Amazonian rainforest influences the entire world's precipitation and weather patterns and, over the longer term, the world's climate. Flooding differs within the Amazon landscape in frequency, timing, duration, water quality, and maximum water depth and height.

**Keywords** *Amazon landscape; Amazon's scientific interest; biotic ecosystem; black-water floodplain forests; equatorial regions; non-flooded forests; South American countries; world's climate*

The Amazon Basin contains the largest and most diverse tropical rainforest in the world. In particular, the Western Amazon basin is the most pristine and, perhaps, the most complex within the Amazon Basin. This book is motivated not just by the Amazon's scientific interest but also by its role in these various ecosystem functions critical to life on Earth. In this introductory chapter, I first describe that complexity and highlight several of its interactive and higher-order linkages among both abiotic and biotic ecosystem components. Then I include summaries of my own research in Western Amazonia over the last two decades, in both non-flooded forests (e.g. *terra firme*, white sand, palm) and forests flooded with white water (generally referred to as *várzea*) and with black water (generally referred to as *igapó*). Finally, I outline the chapters to come.

## 1.1 The Amazon

When the first Europeans visited the middle of South America in the 1500s, they saw women warriors and named the area after those same figures in Greek Mythology, the Amazons. The two Iberian powers, Spain and Portugal, then fought for control of the Amazon. The Spanish were mainly interested in the wealth of the Incas and so approached the Amazon from the west, but because the Amazon is so flat the Portuguese could colonize (from the east) a much larger part of it. All this was finally resolved by the Treaty of Madrid in 1750, establishing the general boundaries we see today between Brazil (colonized by Portugal) and Bolivia, Peru and Ecuador (colonized by Spain: Hecht 2014).

One may speak of the river itself (the Amazon), the large depression/watershed which surrounds the Amazon and the smaller rivers and streams which drain into it (the Amazon Basin) or the forest that grows in that basin (the Amazonian rainforest). The Amazon river has the greatest discharge of fresh water in the world and is also its second longest river (~6,400 km). It originates in the foothills of the Andean Mountains of South America (Figure 1.1) and runs east into the Atlantic Ocean. It is not constant, however, and has changed over time. For example, climate change during the Pleistocene (2,588,000 to 11,700 years ago) led to a drop in sea level which changed its course, and also a rise in sea level that filled its connecting rivers with sediments, creating large floodplains. The Amazon Basin predates the separation of South America from Africa some 110 million years ago (Junk *et al.* 2010) and is generally found below 200 m above sea level (a.s.l.), covering over 8 million km<sup>2</sup> (Hoorn and Wesselingh 2010).

The Amazonian rainforest is located in the equatorial regions of the South American countries of Brazil, Colombia, Ecuador, Bolivia and Peru. Besides the Andes and the Atlantic Ocean, the rainforest is bounded to the north by the Guiana crystalline shield and to the south by the Brazilian crystalline shield



Figure 1.1 Photograph of the Amazon river near where it “officially” begins in Iquitos, Peru.

(Pires and Prance 1985), marked at their edges by cataracts in the rivers and often dominated by grasslands (Myser 2012a). This rainforest is the world's largest tropical rainforest and it is the largest continuous forest of any kind, encompassing over 6 million km<sup>2</sup> (Holdridge 1967; Junk *et al.* 2010; Walter 1973). It produces approximately 20% of the world's oxygen and approximately 10% of the net primary productivity of the entire terrestrial biosphere. Its biodiversity is legendary (present at least since the Pleistocene), having at least 11,200 tree species (Fabaceae the most common family: Daly and Prance 1989; Hoorn and Wesselingh 2010) and more than 10% of all the species on the planet (Pires and Prance 1985).

Perhaps most importantly for the future of humans, the rainforest interacts intimately with the Earth's carbon (C) cycle, acting both as a carbon "sink", by taking in large amounts of CO<sub>2</sub> through photosynthesis (~15% of the world's total), and as a carbon "source" as, for example, when its plants decay or burn (Rice *et al.* 2004). The Amazonian rainforest contains 20–25% of the world's terrestrial C, with one-third below ground in the soil and two-thirds in the above-ground vegetation (McClain *et al.* 2001). The Amazon rainforest will continue to be a major C player in the future by both contributing to, and suffering the effects of, global warming (Shukla *et al.* 1990).

In addition, the Amazonian rainforest influences the entire world's precipitation and weather patterns and, over the longer term, the world's climate (Keller *et al.* 2004). Evaporation and condensation over Amazonia are engines of global atmospheric circulation (Malhi *et al.* 2008) and this rainforest may even control how much rainfall it itself receives (Pires and Prance 1985). Daily fluctuations in temperature are greater than seasonal fluctuations, that is 27.9°C in the dry season and 25.8°C in the rainy season. Humidity also varies little seasonally, 77% in the dry season and 88% in the rainy season (Prance and Lovejoy 1985) and its prevailing winds come from the east. Because the rainforest is located on the Equator, it has a day length which varies little during the year, as does solar energy input of 767–885 calories per cm<sup>2</sup> per day. Up to 6 m of rain falls every year on the Amazon Basin with a pronounced rainy season that begins in the south. One study showed that 25.6% of that precipitation was intercepted by plants and returned to the atmosphere by evaporation, 45.5% was taken up by plants and transpired, and the rest was absorbed into the soil and/or ran off (through the litter and the soil) into rivers and streams (Salati 1985).

White-water runoff from the Andes appears white because of the high concentrations of dissolved solids, mainly alkali-earth metals and carbonates. This white water has the highest concentration of total electrolytes, phosphorus (P), potassium (K) and other trace elements, of all the Amazonian flood waters, with a pH of around 7 (neutral). Conversely, black water is transparent due to its low amount of suspended matter and has the lowest concentrations of these ions, with high amounts of humic acid (resulting in a pH of between 4 and 5) and clear water is between these two in amounts of sediments and pH. Productivity follows these nutrient trends (Junk and Furch 1985). The resulting Amazonian floodplain forests are the most diverse flooded forests in the world with at least 1,000 tree species, existing since the early Cretaceous (145–66 million years ago: Junk *et al.* 2010). In general, forest in black- and clear-water areas are less

diverse, with less litter production, smaller trees and less herbaceous growth than forests in white-water areas (Junk *et al.* 2010). Clear-water rivers come from areas where erosion is less intensive but the more sandy a soil is, the more likely it is to give up its humic substances and create black water. Most leaching occurs during the rainy season and when human activity increases erosion.

The large rainfall results in low fertility soil (and has for millions of years: Jordan 1985), which leads to most of the nutrients being stored in the plant biomass with a fast, efficient closed system of nutrient cycling. P availability mostly limits productivity in *terra firme* forests (McClain *et al.* 2001). The large rainfall also leaches out significant nutrients, such as nitrogen (N), calcium (Ca), P and K out of the leaves and stems of trees and shrubs, adding soluble inorganic and organic substances which allow epiphytic plants to live without a root system. This makes the water cycle a significant interactive link between the soil and the biota. Trees adaptations (e.g. dense root mats at the soil surface) must then be “fine-tuned” (niche-packing) in order to take up and store nutrients efficiently, and this may be one of the reasons for the large biodiversity found in the Amazon. Other reasons may include the relatively constant wet and warm climate (including a predictable flood pulse) and a heterogenous edaphic substrate. Other common adaptations found in Amazon trees include:

- tough, leathery, long-lived leaves;
- supporting colonies of algae and lichens which help recover leached nutrients; and
- sprouting roots from branches and leaves.

Human activities (logging with or without burning and agriculture) can affect many different aspects of the ecosystem – making it another significant interactive linkage – by leading to large losses of biomass (up to 90% C loss compared to the primary forest), with nutrients leaching out of the necromass and into the rivers and streams. Large species diversity may also lead to a large diversity of plant community types, many as yet unknown (Myer 2009, 2012b).

Within the Amazonian rainforest is the dominant, unflooded *terra firme* forest. The *terra firme* has the same physiogomy and many of the same structural characteristics of similar unflooded rainforests throughout the rest of the Neotropics (Everham *et al.* 1996; Kalliola *et al.* 1991; Lopez and Kursar 1999; Whitmore 1989). For example, the Amazonian *terra firme* forest also contains a large amount of above-ground biomass (AGB) and a complex strata of emergent trees, canopy trees, understory trees, palms, understory shrubs, climbing vines, saplings, seedlings, epiphytes, hemi-epiphytic stranglers, lianas, herbs and ferns. Along with this vertical structure, it also has an extensive horizontal structure of various-sized “gaps”, light flecks, micro-topological relief and patchy soil nutrient availability in acid, clayey-loamy shallow soils with extensive organic matter in its upper layers. As is true for trees elsewhere in the Neotropics, many of the *terra firme* trees have large buttresses and shallow roots, complex growth/sprouting architectures, and large epiphyte and liana communities (Janzen 1984). Within the broad classification of *terra firme* forest are different types of forest which differ in soil characteristics, for example *terra firme* proper on clay or loam soils,

white-sand forests on soils with large amounts of quartz, and palm or swamp forests on standing water (Tuomisto *et al.* 2003).

Flooding within the Amazon Basin generates floodplains and flooded forests, which cover approximately 3 million km<sup>2</sup> (Junk 1989; Parolin *et al.* 2004). Most of this water is the nutrient rich “white” water from the Andes, which creates forests generally called *várzea* (Junk 1984) and the rest is “black” and “clear” water, which is nutrient poor forest runoff and creates forests generally called *igapó* (Junk 1989; Prance 1979; Sioli 1984). There are also forests created from a mixing of the water types (Myster 2009). Differences in nutrient availability in the water may thus be as important in determining the structure, function and dynamics of flooded forests in the Amazon as is the nutrient availability in the soil for unflooded *terra firme* forests. The more studied *várzea* has light levels on the forest floor similar to *terra firme* (1–3% of ambient: Wittmann *et al.* 2010a,b), but flooding creates oxygen deficiency, reduced photosynthesis and low water conductance, so that flooding may be a greater source of mortality than desiccation. In addition, high nutrient levels within these *várzea* forests can lead to trees with rapid growth rates and low wood densities (Parolin *et al.* 2010). Importantly trees within these forests must time their reproduction cycles in relation to the flooding, where some species grow mainly during the flooded times of the year and reproduce when the waters subside, while other species merely “endure” flooding and reproduce only during the dry times of the year (Junk *et al.* 2010). White-water areas are used more than black- or clear-water areas for agriculture – because of more nutrients and the predictability of the flood pulse (Junk *et al.* 2010) – but effects of human land use (Myster 2007a) in white-water areas may be reduced due to flooding (Pinedo-Vasquez *et al.* 2011).

Flooding differs within the Amazon landscape in frequency, timing, duration, water quality, and maximum water depth and height (Junk *et al.* 2010; Myster 2009). Such variation within the flooding gradient (Myster 2001) greatly affects the distribution and abundance of plant species (Ferreira and Stohlgren 1999; Junk 1989; Lamotte 1990), leading to inundated vegetative associations created by the rise of the water table on a regular, seasonal basis. In general, flooded forest types, vegetation formations and plant communities lie on a continuum defined by:

- the duration of the aquatic and terrestrial phases of the annual cycles; and
- the physical stability of the habitat influenced by sedimentation and erosion processes (Junk *et al.* 2010).

In general, the soils in the floodplain are less acid than those of the *terra firme*, but may have a greater concentration of exchangeable cations such as Mg<sup>+2</sup> and Na<sup>+2</sup> (reviewed in Honorio 2006).

Because the Amazon and its tributaries are very dynamic – often changing their routes within a time span of a few decades (Junk 1989; Kalliola *et al.* 1991; Pires and Prance 1985) – it may well be that forests that are unflooded today were flooded in the past and *vice versa*. It is not surprising that many *terra firme* species establish ecotypes (Myster and Fetcher 2005) in the flooded forest (Wittmann

*et al.* 2004; 2010a,b). For example:

- the *terra firme* species *Guazuma ulmifolia* and *Spondias lutea* have developed flood-resistant ecotypes now found in *várzea*;
- *várzea* species such as *Ceiba pentandra* and *Pseudobombax munguba* occur in *terra firme*; and
- several species of the genus *Maquira* occur in both unflooded and flooded forests.

This ecotropic dynamic and the high species richness of the surrounding Amazonian *terra firme* rainforest, which disperse seeds into flooded forests – when combined with flooding and its associated environmental heterogeneity – suggests that flooded forests will have a unique biology and ecology (Kalliola *et al.* 1991). Furthermore, it is expected that flooding creates specific tree species zonal distributions (Whitmann *et al.* 2010a), largely determined by the submergence tolerance of their seedlings (Parolin *et al.* 2004). Finally the predictability of the flood “pulse” (Junk *et al.* 2010) – both past and present – facilitates adaptation and thus, along with differences in the surrounding biota and a variety of soil types (Honorio 2006; Junk 1989), may help create complex and diverse forest associations throughout the Amazon Basin (Myster 2009).

## 1.2 The Western Amazon

Studies of tree endemism in the Amazon (ter Steege *et al.* 2006; Whitmann *et al.* 2013) show that there is a natural division between the Western Amazon rainforest (Myster 2009) and the Central Amazon rainforest (Junk *et al.* 2010), where the Japurá river joins the Amazon river (Figure 1.2). In this book, I will accept that evidence and define Western Amazonia as everything in the Amazon Basin west of latitude 65°W, including the Mamirauá Reserve in Tefé, Brazil.

This western part of the Amazon Basin is composed of young and relatively fertile sediment, which makes the flora of more recent origin than that of Eastern Amazonia (reviewed in Dumont *et al.* 1990; Terborgh and Andresen 1998). Furthermore, the higher fertility of these soils may lead to more forest turnover and evolution, resulting in the high biodiversity sampled here compared to Central Amazonia (Bierregaard *et al.* 2001; Gentry 1993). Indeed the Western Amazon rainforest contains some of the most diverse areas or “hotspots” on Earth (Myers *et al.* 2000; Myster 2007b) due, in part, because it is largely intact, pristine and unaffected by human activity (<5% of its total area is in secondary forest: Gorchoff *et al.* 2004; Neff *et al.* 2006; Soares-Filho *et al.* 2006) and so suffers the smallest loss of biodiversity and forest fragmentation (Bierregaard *et al.* 2001) in all of the Amazon. The large biodiversity of the Western Amazon may also be a consequence of the large areas within it, which have been surrounded by only rainforest for millions of years, without border effects or edge effects. Because the Western Amazon rainforest has extensive variation in edaphic, climatic, topographic and geological conditions, a large number of distinct plant communities are expected (Myster 2009, 2012b). Indeed, sampling has shown



**Figure 1.2** Map of the Amazon river and some of the other rivers that drain into it, including the Japurá river, with an outline of the Amazon Basin.

that up to 59% of recorded species are found in only one plot among the many sampled (Duivenvoorden 1995), and shared species between wetland and upland forests is very low (Dumont *et al.* 1990).

All tropical rainforests are hot and humid with large biodiversity. However, in addition to the global and ecosystem issues raised before, the Amazon in general, and the Western Amazon in particular, are also unique because of their high level of complexity – the many ways that different components of the Amazon ecosystem interact – and often at a higher-order than other tropical forests. Some of those interactions are outlined above, and in coming chapters authors will discuss many more Amazonian interactions within their own area of interest. I also point to these recent studies that have highlighted important Amazon ecosystem interactions among:

1. soil type, land use and tree growth (Moran *et al.* 2000);
2. water availability and forest biodiversity (Paine *et al.* 2009);
3. deforestation, fire and drought (Davidson *et al.* 2010);
4. recruitment and scatter-hoarding (Russo *et al.* 2005);
5. recruitment and seed dispersal by fish (Anderson *et al.* 2009);
6. hunting of large primates, richness and density (Nunez-Iturri and Howe 2007);
7. soils, geography distances and floristics (Ruokolainen *et al.* 2007);
8. flooding duration and the availability of phosphorus, iron and aluminum (Chacon *et al.* 2008);
9. soils, herbivory and plant defenses (Fine *et al.* 2004);

10. forest responses, drought and the C cycle (Phillips *et al.* 2009; Saleska *et al.* 2007); and
11. climate change and flooding patterns (Langerwisch *et al.* 2012).

With this ecological background in mind, and as background to the chapters that follow, it may be useful to review the ideas and different approaches used in the past to investigate Neotropical forests. First, it has certainly been a positive development over the last few decades of Neotropical forest research that several permanent forest plots has been set up and sampled on a regular basis for a considerable time. These have included large – usually 25–50 ha – plots in *terra firme* forest (i.e. Barro Colorado Island in Panama, Yasuní National Park (YNP) in Ecuador, La Planada in Colombia, Luquillo Experimental Forest in Puerto Rico: Brokaw *et al.* 2012) and smaller plots/transects in various Neotropical forests (Balslev *et al.* 1987; Myster 2007b, 2010; Parolin *et al.* 2004; Worbes *et al.* 1992; author unpub. data). The data collected has advanced our understanding of the structure of these forests and how that structure changes through time (Brokaw *et al.* 2012; Junk *et al.* 2010; Losos and Leigh 2004). I applaud those efforts and hope they will continue. In addition to plot sampling, approaches have included tabulation of common, or otherwise defined important, species traits (ecophysiological: Parolin *et al.* 2004; Poorter 1999; phenology: Parolin *et al.* 2010; mycorrhizal association: Falster *et al.* 2015; Meyer *et al.* 2010; Myster *et al.* 2013), measurement and estimation of different aspects of the C cycle (Baker *et al.* 2007; Schongart *et al.* 2010; Townsend-Small *et al.* 2005) and other biogeochemical cycles (Calle-Rendon *et al.* 2011; Kern *et al.* 2010), remote sensing used to discover large-scale vegetation patterns and tree associations (Melack and Hess 2010; Peixoto *et al.* 2009) and seed/seedling mechanistic experiments (e.g. Kubitzki and Ziburski 1994; Paine and Beck 2007; Wittmann *et al.* 2010b).

While these plots and other research approaches have had success, field experimentation and modeling approaches tried in Neotropic forests over the last 30–40 years (Carson and Schnitzer 2008) continue to be a challenge, especially for those trying to discover what controls forest dynamics: in particular, those approaches that include hypotheses about static, unchanging patterns of biodiversity (Connell 1971; Janzen 1970), which then need to be “maintained” over time (McDade *et al.* 1994; Zimmerman *et al.* 2008), and co-existence of species (Dalling and John 2008; Maberley 1992). Alternatively, the authors in this book will progress with better methods of investigation into forest structure, function and dynamics, which I will put together into a new and better synthesis of Neotropic rainforest investigation, in the concluding chapter.

### 1.2.1 Case study: Sabalillo Forest Reserve

I now review my own studies in the Western Amazon. My first study site was Sabalillo Forest Reserve (SFR: 3°20'3''S, 72°18'6'' W: Frederickson *et al.* 2005; Moreau 2008) established in 2000 and operated by Project Amazonas. SFR is located on both sides of the upper Rio Apayacu, 172 km east of Iquitos, Peru. The reserve is part of 25,000 acres set aside over the last decade and is comprised of low, seasonally inundated river basins of the upper Amazon. The substrate



of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation has been measured as 3,297 mm per year (Choo *et al.* 2007). Within the SFR are areas of black-water runoff, which create *igapó* forests of differing frequency, duration and maximum water column height, where the rainy season is between November and April. In addition, *terra firme* forest is common as well as white-sand forest and palm forest (which exists on standing water: Holdridge 1967). White-sand forests form on white-sand soils of extreme infertility, made up mainly of quartz podzols. The SFR white-sand forest is called “varillal”, which is defined as a dense forest with straight and thin trees between 10 and 20 m high (Honorio 2006; Myster 2009). White-sand forest has a species diversity between *terra firme* forest (which is higher) and palm forest (which is lower: Duivenvoorden *et al.* 2001), and common families include Leguminosae, Clusiaceae, Malvaceae, Euphorbiaceae and Icacinaceae (Honorio 2006).

#### 1.2.1.1 White-sand forest and palm forest plot studies

In my first investigation at SFR in June 2013, my two student field assistants and I set up a 1-ha plot (200 m × 50 m) in a white-sand forest and in a palm forest at SFR. We tagged and measured the diameter at breast height (dbh) of all trees at least 10 cm dbh in a hundred 10 m × 10 m continuous subplots using the protocol as for the 1-ha plot at Yasuní and subsequent plots. Plots of this size have been used to study forests in the Amazon for decades. The tagged trees were identified to species, or to genus in a few cases, using Romoleroux *et al.* (1997) and Gentry (1993) as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana herbarium and the website of the Missouri Botanical Garden ([www.mobot.org](http://www.mobot.org)).

In the white-sand forest I found:

1. there were a total of 15 families and Clusiaceae was by far the most common family, which also had the most genera and the most species;
2. Malvaceae, Myrtaceae and Rubiaceae were also common, and there were 2 families with only 1 stem;
3. most families had a monotonic decline in stem number as stems became thicker and the species *Pachira brevipes* and *Caraipa tereticaulis* were the most common;
4. stems conformed to a “reverse J” size distribution pattern for all stems, as was true of *terra firme* samplings;
5. the average stem dbh was slightly less than *terra firme* plots, but basal area and AGB was greatly reduced compared to *terra firme* plots; and
6. the forest canopy was 14% closed and the trees were randomly dispersed.

In the palm forest plot I found:

1. there were a total of 6 families and Arecaceae was by far the most common family, which also had the most genera and the most species, but Clusiaceae, Fabaceae and Lecythidaceae were also common;
2. all families had a monotonic decline in stem number as stems became thicker and the species *Socratea exorrhiza* and *Lepidocaryum tenue* (both palms) were most common;

3. total number of stems was a bit more than white-sand forest, but much less than each of the three *terra firme* plots;
4. stem size distribution was comparable to white-sand forest, but average stem size was much reduced when compared to both white-sand and one *terra firme* sampling;
5. whereas species richness was much less for palm as well (compared to the other forests), the reduction in basal area and AGB was smaller; and
6. palm was a dimmer, denser forest than white-sand and showed no clumping.

I conclude that:

1. white-sand forest is less complex in floristics and various aspects of structure compared to *terra firme* forests, which may be due to its soils being of low fertility, but similar in number of families and species to some black-water *igapó* forests that are under water at least five months of the year, and
2. palm forest is less complex in floristics compared to both white-sand and *terra firme* but was mixed for other structure characteristics, which may be due to its soils being water-logged and lacking in oxygen for roots (author, unpublished data).

#### 1.2.1.2 Black-water flooded forest (*igapó*) soil and vegetation studies

I next investigated the floristics, and how soil bulk density affects physical structure, of successional *igapó* forests at SFR. In June 2013, my field assistants and I sampled five successional areas – island, oxbow lake, river margin, sandy beach, side creek – close to a black-water river at SFR. In each area we set up 105 m × 5 m continuous plots for a total sampling area of 250 m<sup>2</sup> per area. We measured the dbh of each tree at least 1 cm dbh within each plot. The dbh measurement was again taken at the nearest lower point where the stem was cylindrical and for buttressed trees it was taken above the buttresses. We identified its species, or to genus in a few cases, using Romoleroux *et al.* (1997) and Gentry (1993) as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana herbarium and the website of the Missouri Botanical Garden ([www.mobot.org](http://www.mobot.org)).

In addition, we collected three soil samples in each area by driving a 3-inch diameter ring into a depth of 10 cm and extracting the soil. Back in Iquitos, each soil sample was dried for three 4-minute cycles in a microwave and then weighed. Soil bulk density was computed as weighed soil sample/volume of container, expressed as g/cm<sup>3</sup>. I found (author, unpublished data):

1. a total of 24 plant families where Urticaceae was the most family present, but Rubiaceae and Euphorbiaceae were also common. Most families had a monotonic decline in stem number as stems became thicker and there were no stems with a dbh greater than 29 cm. The most common species were *Cecropia membranaceae*, *Sapium glandulosum*, *Pourouma guianensis* and *Byrsonima arthropoda*.
2. soil bulk density was highest in the sandy beach and lowest in the forest under water for the longest duration. The greatest number of stems was 47 in the island area and 18 in the forest under water for the longest duration.

Mean stem size, species richness, Fishers  $\alpha$ , basal area and AGB were lowest in the sandy beach and highest in the forest under water for the shortest duration; and

3. linear regression analysis showed that soil bulk density could best predict mean stem size, species richness and Fishers  $\alpha$ . Results showed that as soil became less sandy and with more clay content, all structural parameters except stem number increased, suggesting an increase in forest community complexity as soil increases in water retention capacity and nutrients.

I conclude that the severe and unpredictable flooding seen in these successional areas reduces forest structure more than the predictable and seasonal flooding that black-water floodplain forests receive.

### 1.2.2 Case study: Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo

My second study site in the Western Amazon was the Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: [www.perujungle.com](http://www.perujungle.com), Gottdenker and Bodmer 1998; Myster 2007b, 2009, 2010) located in Loreto Province, 80 miles southeast of Iquitos, Peru ( $\sim 2^{\circ}\text{S}$ ,  $75^{\circ}\text{W}$ ) with an elevation of 106 m. The reserve is part of one of the largest (270,654 ha) protected areas in the Amazon, containing wet lowland tropical rainforest of high diversity (Daly and Prance 1989). It is comprised of the low, seasonally inundated river basins of the upper Amazon and named after two of the major white-water rivers (the Tahuayo and the Tamshiyacu), which form boundaries to the north and west and create large fringing floodplains (Junk 1984). The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation ranges from 2,400–3,000 mm per year, and the average temperature is relatively steady at  $26^{\circ}\text{C}$ .

The rainforest itself is divided into distinct communities defined by their flooding regime where the rainy season is between November and April (Kalliola *et al.* 1991), for example non-flooded *terra firme*, *igapó* forest under water 1–3 months per year and *igapó* forest under water 4–6 months per year. Common tree genera in high restinga are *Chorisia*, *Eschweilera*, *Hura*, *Spondias* and *Virola*. Low restinga and tahuampa contain tree species such as *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata*, *Phytelephas macrocarpa*, with under-story palms such as *Guazuma rosea* and *Piptadenia pteroclada* (Daly and Prance 1989; Myster 2007b; Prance 1979; Puhakka *et al.* 1992).

#### 1.2.2.1 Plots in *terra firme* forest and black-water flooded forest (*igapó*)

Within each of three forest types which differed in flood duration and maximum water depth (unflooded *terra firme*, *igapó* forest under water 1–3 months per year, *igapó* forest under water 4–6 months per year), five areas were selected in June of 1997. These were primary, unlogged forest and had fresh average-sized (100–300 m<sup>2</sup>: Brokaw 1982) gaps within them. I sampled all tree stems at least 10 cm in dbh within each of 100 m<sup>2</sup> (10 m  $\times$  10 m) microsites. This makes a total of 30 microsites, the three forest types with their gaps and five reps (6  $\times$  5). This

data is housed in the archives of the LTER site in Puerto Rico (LTERDBAS #150) and may be accessed through their website ([luq.lternet.edu](http://luq.lternet.edu)).

I found (Myster 2007b):

1. common species existed between the two *igapó* forests and their gaps and between the gaps of the two *igapó* forests;
2. tree richness was maximum in *terra firme* forests, medium in the least flooded *igapo* and their gaps, and smallest in the most flooded *igapo* gaps;
3. there were less stems in gaps compared to forests and less stems in forests as flooding increased, except again in the least flooded *igapo* gaps; and
4. dominance-diversity curves have more dominance by single species in the *terra firme* gap plots compared to other gaps and in *terra firme* forest compared to other forests.

In general, while some aspects of structure such as tree stem density is largely determined by treefall gap dynamics, tree composition is determined by the flooding regime. Finally, a jump in tree richness in wet forests and wet gaps compared to other plots suggests a “mass effects” hypothesis where species from dry and very wet forest and gaps have overlapping ranges in the wet forest and gap. This effect may help explain the high species diversity seen in this part of the Amazon.

Further analysis of this dataset (Myster 2010) showed a significant effect of treefall gap formation (gap, no gap) on canopy average height, canopy maximum height, basal area, density, AGB, turnover and alpha diversity, and a significant effect of forest type on species richness, genera richness, density, turnover and alpha diversity. In general, there were fewer trees, but they were larger, and more productive in the forest plots compared with the gap plots; and the most flooded plots had fewer trees, species and genera compared with both the less flooded forest and non-flooded forest. Also the greatest amount of turnover was found in the most flooded forests, and the intermediately flooded forest had the greatest richness and alpha diversity. Canopy structure was determined by traditional gap dynamics, but much of canopy diversity depended on the type of forest, tree density decreased as flooding increased, especially among the smallest stems, and there was evidence to suggest that the high biodiversity of the Amazon may be maintained in part by the existence of moderately flooded forest and gaps.

In the third in this series of papers from the same sampling (Myster 2015b), I found:

1. trees became less dense as flooding increased, more than due to tree fall;
2. trees were dispersed uniformly in the forest and clumped in the gaps for the least flooded forest, but became random as flooding increased;
3. canopy coverage followed the same trends as stem density;
4. tree stem size distribution showed smaller stems in gaps compared to adjacent forest for all forest types, where gaps were more consistent in maintaining this pattern than forests as flooding increased; and
5. canopy cover was dominated by smaller stems in gaps compared to forests and forests lost some of their smaller stems – with their canopy contribution – as flooding increased.

I conclude that flooding placed a greater stress on these forests than tree fall, where Amazonian forests may be an ecosystem where gradients and disturbances overlap in their traditional roles and present plants with similar cues.

Finally, I set up a 1-ha plot in the most flooded *igapó* forest in 2010 and sampled it in the same way as the previous 1-ha plots (Myster 2013). I found that stems conformed to the reverse J-size pattern, total stems were lower than other *igapó* forest ranges with a slightly larger average dbh, trees were clumped at a higher degree than that found in the 1-ha plot I sampled in *várzea* forest with 12% canopy closure, while the basal area and AGB was less than both other *igapó* samplings and the 1-ha *várzea* study plot, and flooding produced reduced basal area in *igapó*, and smaller stems, stem densities and AGB for both flooded forests. I conclude that in both study plots, there was a reduction of tree stem density and structure (basal area, AGB) with flooding, which reduced even more as months under water increased. More sampling in these forests is needed, however, before a conclusion about which aspect of the flooding regime – for example, water quality, flooding duration or frequency – is most important in determining different aspects of forest structure.

#### 1.2.2.2 Seed predation studies in *terra firme* forest and black-water flooded forest (*igapó*)

I set out seeds on transects for a week in seven different tropical forests. I found:

1. seed predation took more seeds than either seed pathogenic disease or germination for most seed species, but there were a few species that lost more seeds to pathogens than predators. Germination had the lowest percentage (%) for most species, but again there were a few species where germination % was higher than pathogens;
2. within the unflooded forests, there was the most predation in *terra firme* forest, palm forest (at SFR) lost more seeds to pathogens than predators, and white-sand forest (at SFR) predation levels were between the other two forest types;
3. within the flooded forests, predation decreased as water went from white to black (at the same inundation levels) and predation decreased monotonically (and pathogens increased monotonically) as months under water increased in black-water forests; and
4. there was significantly more seed predation in the unflooded forests compared to the flooded forests, but significantly more germination in the flooded forests compared to the unflooded forests.

I conclude that seed predation is the major post-dispersal filter for regeneration in these forests, but pathogenic disease can play a major role, especially in forests that have water in them for long periods each year, so that flooding may change those forests dramatically by altering the actions of seed mechanisms and tolerances (author, unpublished data).

#### 1.2.3 Case study: Centro de Investigacion de Jenaro Herrera

My third study site in the Western Amazon was the biological station Centro de Investigacion de Jenaro Herrera (CIJH) operated by the Instituto de

Investigaciones de la Amazonía Peruana ([www.iiap.org](http://www.iiap.org)) and located 2.5 km from the town of Jenaro Herrera, 200 km south of Iquitos on the east margin of the Ucayali river in the Province of Requena, Department of Loreto, Peru (4°54'S, 73°40'W: Honorio 2006). The mean annual temperature is 26.0°C with a range between 25.1°C and 26.5°C. The mean annual rainfall is 2,724 mm with two dry seasons, the more severe between June and September and the less severe between December and March. Here the non-flooded *terra firme* forests have soils that are highly weathered, acidic, nutrient-poor and clayey-loamy (oxisols: Spichiger *et al.* 1996).

Dominating the non-flooded portions of the study site are low terrace broad leaf forest (*terra firme*-low) and high terrace broad leaf forest (*terra firme*-high) with scattered patches of white-sand-varillal (with dense growth and trees up to 20 m tall), white-sand-chamizal (with shrubs and scattered trees less than 8 m tall), and low terrace palm (dominated by palms such as *Mauritia flexuosa*, *Oenocarpus bataua*, *Euterpe precatoria* and *S. exorrhiza*). Common genera in the high and low terrace broad leaf *terra firme* forests include *Eshweilera*, *Pouteria*, *Oenocarpus*, *Miconia* and *Protium*, in white sand-varillal *Pachira*, *Haploclathra* and *Macrolobium*, and in white-sand-chamizal *Caraipa*, *Pachira*, *Macrolobium*, *Calophyllum*, *Haploclathra* and *Platycarpum* (Honorio 2006). *Terra firme*-high terrace forest is located adjacent to rivers (Pires and Prance 1985), but is rarely flooded. *Terra firme*-low terrace is not located on ridges adjacent to rivers and has clay soils. Palm swamps (Montufar and Pintaud 2006) occur in depressions or low-lying patches with poor drainage. White-sand soils consist mainly of quartz with individual trees having slender boles and roots concentrated at the soil surface (Klinge *et al.* 1990). These forests are divided into varillal (dense with straight and thin trees between 10 m and 20 m high) and chamizal (shrubs 3 m high and scattered trees more than 8 m high: Honorio 2006).

### 1.2.3.1 Soil sampling in various forest types

To better understand Amazon soils and how they differ between non-flooded and flooded forests, I took soil samples (author, unpub. data) in eight different forests at two locations in the Peruvian Amazon. In May 2009, I established transects in each of the eight study forests found at CIJH (*terra firme*-low, *terra firme*-high, white-sand-varillal, white-sand-chamizal, palm) and at ACRCCTT located also in Peru and discussed in Section 1.4 (high restinga, low restinga, tahaumpa). Along each transect at microsites of approximately 10-m intervals, I took five soil samples without litter. Data was used for one-way analysis of variance tests for each soil parameters between the flooded forests (pooled for all three types) and the most common non-flooded forests, *terra firme*-low and *terra firme*-high. I found:

1. soil pH of the non-flooded forests was very similar to flooded forests, but became more basic with increased flooding;
2. soil organic matter was lowest in the two non-flooded *terra firme* forests and also increased with flooding;
3. N was lowest in the palm forest, P was lowest in *terra firme*-low terrace forest and K was lowest in the *terra firme*-high terrace forest;

4. while N decreased sharply with flooding, both P and K increased with length of the flooding period; and
5. for some non-flooded forests there was a correspondence between soil fertility and floristic similarity.

I conclude that flooding has significant effects on nutrient availability of Amazonian forest soils, by increasing the concentration of some nutrients but decreasing it for others.

#### 1.2.3.2 Seed rain sampling in various forest types

Because of the importance of seed processes in determining rainforest regeneration and dynamics, I sampled the seed rain (Myster 2015c) in six different tropical forests across the Amazonian landscape. I set up seed traps and took seed samples in three unflooded forests at CIJH (*terra firme*, white-sand-varillal, palm) and three flooded forests at ACRCTT (high restinga, low restinga, tahaumpa) in Peru over a period of one year. I found:

1. all forests except tahaumpa contained seeds of tree species that have been sampled in other studies within a forest of the same type, but in all forests there were seeds of several tree species that have not yet been sampled within their forest type;
2. total seed load peaked in the early part of the year – near the end of the rainy season – and then decreased monotonically over the remainder of the year for all forests;
3. species richness was greater in unflooded forests compared to flooded forests and the largest number of species were found in *terra firme*;
4. seeds were more evenly distributed among species in the unflooded forests compared to the flooded forests; and
5. alpha diversity was much greater in *terra firme* compared to all other forests.

I conclude for the unflooded forests that seed species number and richness increased with soil fertility, but for the flooded forests seed species number and richness decreased with months under water. When taken together, results suggest that for forests across the Amazonian landscape, differences in flooding regime may have a greater effect on both seed rain load and seed species richness than differences in availability of soil nutrients.

#### 1.2.4 Case study: Yasuni experimental station

My fourth and last study site was the Yasuni Experimental Station (0°41'S, 76°24'W), operated by the Pontificia Universidad Católica of Ecuador and located within the YNP of eastern Ecuador (Duivenvoorder *et al.* 2001; Metz *et al.* 2008; Myster 2012c; Myster and Santacruz 2005; Svenning 1999). Most of the YNP is *terra firme* forest, classified as lowland tropical rainforest (Holdridge, 1967). The mean annual rainfall is 3,081 mm, with the wettest months April to May and October to November. August is the driest month and the mean monthly temperature varies between 22°C and 35°C. Soils in the park have been described as clayey, low in most cations but rich in aluminium and iron, whereas soils at the station in *terra firme* forest are acidic and rich in exchangeable

bases with a texture dominated by silt (Tuomisto *et al.* 2003). The park has low topographic variation with a mean elevation of approximately 200 m a.s.l.

The station is also the site of a long-term 50-ha vegetation plot in *terra firme* forest, maintained by the Smithsonian Tropical Research Institute (Losos and Leigh 2004), parts of which have been sampled with summaries of species found, densities and aspects of forest structure reported (Valencia *et al.* 2004a,b,c, 2009). Also found is floodplain *várzea* forest – located next to the nutrient-rich white-water Tiputini river – which is underwater off and on between the months of October and April for a few weeks to a maximum depth of 3 m.

#### 1.2.4.1 Yasuní *terra firme* forest studies

My research in *terra firme* forest at Yasuní began by investigating how tree seedlings respond along a 100-m transect set up 10 m outside and parallel to the 50-ha plot (Myster 2012c), in order to better understand availability of plant resources on the forest floor in the Amazon, and also to show the effect of their heterogeneity on tree seedlings. I first described the spatial and temporal variation of light and soil water along a 100-m transect, 10 m outside the southern border of the 50-ha plot, in *terra firme* forest for 6 months, and then recorded seedling responses of 3 common tree species planted on that transect after 1 years' growth. I found that:

1. the spatial heterogeneity across the transect was greater than the temporal heterogeneity at any given microsite on the transect for both light and water and there was a positive correlation between them;
2. *Couepia obovata*, the largest seeded and the only subcanopy tree, survived best and showed both the largest relative height growth rate (RHGR: Falster *et al.* 2015) and the largest specific leaf area (SLA), while among the two early successional trees, *Tapirira guianensis* had the largest leaf area ratio (LAR) and the largest leaf mass ratio (LMR) and *Duguethia spixiana* had the largest root/shoot ratio (RTOS);
3. for *T. guianensis*, SLA increased with increasing light and soil water potential predicted both increasing LMR and decreasing RTOS with increasing soil water; and
4. soil water potential could also predict increasing LAR with increasing water for *D. spixiana* and, for *C. obovata*, soil water potential predicted more survivorship, LMR and RHGR but less RTOS, all with increasing soil water.

I conclude that some sub-canopy trees may survive and grow more than open-canopy trees when presented with water stress in the forest understory, and that within the ranges of light and soil water sampled here, plants responded more to spatial variation in water compared to light.

My research continued by investigating regeneration (Grubb 1977) in closed *terra firme* forest and within its gaps by setting out seed traps and collecting soil samples in those microsites (Myster 2014). I also set out seeds and seedlings in the same forest and gaps and later collected them scoring various survivorship and growth parameters. I found that:

1. total number and richness of dispersed seeds was greatest in the *terra firme* gaps compared to *terra firme* forest;



2. *terra firme* forest had less seedlings germinating from soil samples than *terra firme* gaps;
3. on average, 30% of seeds remained after two weeks in the field and species seed losses were significantly different in both forest and gap;
4. more large seeds than small seeds were lost to pathogens and those losses were greater in the *terra firme* forest than *terra firme* gap;
5. as seed mass increased, seedlings survival rates also increased but growth rates declined in both forest and gap; and
6. more seedlings survived in gaps compared to closed forests, but they grew faster in *terra firme* forest with a larger LAR.

My last research project in *terra firme* forest was a sampling of insects (Myster and Santacruz 2005) as possible agents of the seed predation just reported. We sampled in the same closed *terra firme* forest and *terra firme* gaps, where seed dishes were placed. In the closed *terra firme* forest, we found arthropods in the orders Diptera (92 individuals), Hymenoptera (60), Collembola (5), Orthoptera family Grillidea (5), Coleoptera (1), Acaros (1) and Aracnida (1). In the *terra firme* gaps, we found insects in the orders Diptera (80 individuals), Hymenoptera (52), Collembola (21), Coleoptera family Staphilinidae (4), Orthoptera family Grillidea (2) and Hemiptera family Cydhidea (1). Number of individuals and orders was similar between these two areas. The rankings of these orders became different only among those with the smallest abundances.

#### 1.2.4.2 Yasuní white-water flooded forest (*várzea*) studies

My *várzea* research began in May and June of 2010, when I set up a 1-ha plot next to the Tipitini river (a tributary of the Napo river) and also located a few hundred meters from the 50 ha plot. The 1-ha plot was subdivided into 100 continuous 10 m × 10 m subplots. In each subplot I and my field assistants tagged, identified and measured the dbh of all trees at least 10 cm dbh, expanding on past sampling of Amazon flooded forests (Balslev *et al.* 1987; Myster 2007b, 2010; Parolin *et al.* 2004; Worbes *et al.* 1992). The dbh measurement was taken at the nearest lower point where the stem was cylindrical and for buttressed trees it was taken above the buttresses. The data are archived at the Luquillo Experimental Forest, Puerto Rico as LTERDBAS#172, part of the LTER program funded by the US National Science Foundation. One may visit their website (<http://luq.lternet.edu>) for further details.

I found (Myster 2013, 2015a) in the 1-ha plot that:

1. the seven most common families sampled were also among the top ten families sampled in the 50-ha plot, but most of the rare families were not;
2. at the genus and species taxonomic level, similarities with the 50-ha plot disappeared, except for the genera *Cecropia*, *Lachornea*, *Inga*, *Zygia*, *Eschweilera* and *Virola* and the species *Iriartea deltoidea* and *Coccoloba densifrons*;
3. the 1-ha plot lost stems with flooding but that loss was mainly in the smaller size classes, leading to a proportionally greater number of larger trees than the *terra firme* forest and a larger basal area for stems at least 40 cm dbh; and

4. because the flooded forest loses families, genera and species proportionally more than they lose stems, Fisher's  $\alpha$  was lower in the flooded forest compared to *terra firme* forest.

In addition, stems conformed to a reverse J-size pattern for stems less than 40 cm dbh, trees were clumped at a low level with 45% canopy closure, basal area was within other *várzea* forest ranges, and above-ground biomass was lower, and flooding produced smaller stems, stem densities and above-ground biomass compared to the *terra firme* forest sampled as part of the 50-ha plot.

Next I investigated (Myster 2014) on how *várzea* forest regeneration is affected by treefall gap formation, by setting out seed traps and collecting soil samples in the forest and its gaps. I also set out seeds and seedlings in the same forests and gaps and later collected them, scoring various survivorship and growth parameters. I found that:

1. the total number and richness of dispersed seeds was greater in the *várzea* gaps compared to the *várzea* forest;
2. likewise, a greater number of seedlings germinated from *várzea* gap soils compared to the *várzea* forest;
3. on average, 30% of seeds remained after two weeks in the field and species seed losses were significantly different;
4. more large seeds than small seeds were lost to pathogens, and those losses were greater in the *várzea* forest compared to the *várzea* gap microsites;
5. as seed mass increased seedlings survival rates also increased but growth rates declined; and
6. more seedlings survived in *várzea* gaps compared to closed *várzea* forests, where they grew faster with a larger LAR.

When we combine these regeneration results with those in *terra firme* forests (discussed earlier), we see that most regeneration mechanisms had the greatest seed and seedlings losses and the slowest growth rates in intact *terra firme* forest, medium losses and growth rates in *terra firme* gaps and intact *várzea* forest, and the smallest losses and fastest growth in *várzea* gaps. These results are consistent with viewing flooding as a disturbance, like gap formation, both of which structure the Amazon rainforest (Myster 2007, 2010, 2015).

Finally, I compared *igapó* sampling at ACRCTT and *várzea* sampling at YRS (Myster 2016). There was species variation among the plots within both forest types, but little variation in physical structure. The *igapó* plot had 16 families, 29 genera and 31 species, with Fabaceae the most common family which also had the most genera and the most species. The *várzea* plot had 42 families, 91 genera and 159 species with Fabaceae again the most common family, which also had the most genera and the most species. There were only four species in common. In general, the *várzea* plot had more stems, and more large stems (at least 40 cm dbh) than the *igapó* plot, but mean stem size was very similar. Structural comparison to *terra firme* 1-ha plots showed it had more stems, thicker stems and more above-ground biomass compared to either of these pooled 1-ha flooded plots. Finally, all study plots conformed to the reverse J-stem size distribution pattern for all stems.

### 1.3 About this book

Here I take advantage of my many years working in Ecuador and Peru, and my three awards from the Fulbright Foundation, to edit a book based solely on the Western Amazon which has never been done. While all tropical rainforests are hot, humid places with large biodiversity, the Amazonian rainforest in general and the Western Amazonian rainforest in particular are different and important. They are places of more complex linkages and higher-order interactions among components than other, even tropical, ecosystems. I mentioned several of these interactive links in the first section of this chapter, but more will be illuminated in the coming chapters. The Western Amazon is also intimately involved with the basic biogeochemical cycles that make the Earth a place full of life and thus tied to our shared human future.

The book contains both flooded (e.g. *várzea*, *igapó*) and unflooded (e.g. *terra firme*, white-sand, palm) Western Amazonian forests. Authors will prepare chapters that consist of reviews of what is known about their topic, of the research they have done, and of what research needs to be done in the future, often with a new conceptual and/or mathematical model. My organizing theme will be the structure, function and dynamics of the various kinds of forests found in the Western Amazon: how they were in the past, how they are changing today, and how they are likely to change in the future. Authors will ask if the drivers for those changes (e.g. climate change, human disturbances, tree recruitment mechanisms, stress) differ now compared to the past. Conceptual models will make use of tree replacement, or barriers to replacement, by individual trees within these forests (Myster 2012d). My concluding chapter will first summarize the results from each of the preceding chapters, then synthesize those results adding to the general conceptual model, and finally suggest future avenues for research.

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