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The anthropogenic impacts on tropical forest ecology and dynamics

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INTRODUCTION

Africa, topical forests, climate changes and biodiversity

Africa is the second-largest continent on Earth after Asia. With about 30 million square kilometres including adjacent islands and the Sahara, the world's largest desert, Africa covers over 20 per cent of Earth's total land area. Africa is also the second most populous continent after Asia.

With over 965 million people it accounts for about one-seventh of the world's human population. The vast landscape of Africa contains a host of natural wonders and rich resources such as coltan and platinum, which are currently considered the most strategic minerals. Its grasslands, wetlands, mountains, deserts, rainforests and marine areas are home to thousands of species of plants and animals. It is also a land of unparalleled natural beauty and its rainforests are an important storehouse of carbon. Its vast mineral and natural resources provide immense opportunities for economic growth, development and human well-being. The high economic growth of over 4.6 per cent witnessed in the region since 2004 is largely underpinned by the region's environmental resources—oil exploration, improved agricultural performance, and tourism (AMCEN & UNEP, 2008).

Africa is also a land of increasing population and rapidly changing land-use patterns; changes that have deep local, regional and global environmental significance. Sustaining a reasonably high economic growth rate to match the human population growth rate coupled with ensuring the environmental and natural resources integrity is one of the key challenges (UNEP, 2008).

Climate change is likely to intensify some conditions like land degradation and desertification, water stress, declining biodiversity, deforestation, increasing dust storms, rising pollution and rapid urbanisation and alter the environment even further. Although Africa emits only four per cent of total global carbon dioxide emissions, its inhabitants are projected to suffer disproportionately from the consequences of global climate change. Given its economic constraints, Africa's capacity to adapt to climate change is relatively low making the region exceptionally vulnerable to potential impacts. In many areas, even small changes in precipitation and water availability could have a devastating effect on agricultural output and therefore on food security. As climate change intensifies and its impacts deepen, adaptation will become increasingly difficult. Correspondingly, achieving targets set by the United Nations Millennium Development Goals (MDGs) will become more challenging. Africa is particularly vulnerable to climate change. Computer models project major changes in precipitation patterns on the continent, which could lead to food shortages and increased

desertification. Yet on the whole, African nations lack the resources and technology to address such changes (Adger et al., 2007; UNECA 2001).

According to this vulnerability, converting forests to agricultural land is necessary for food production but such deforestation negatively impacts local ecosystems as habitats are lost. Deforestation also impacts the global carbon cycle; carbon released when trees are cut, burned, or as they decompose enters the atmosphere as CO_2 and contributes to global warming (Willcocks 2002).

Moreover, land degradation and desertification processes result from both human activities and climatic variability. For example, people use controlled fire to manage grasslands and savannahs for livestock production and wildlife, control pests, clear dying vegetation, and convert wild lands to cropland (Trollope and Trollope 2004).

Another important environmental aspect, in Africa, is the rise of population. An increasing population and a decreasing water supply leads to water scarcity and stress. Water scarcity is defined as less than 1000 m^3 of potable water available per person per year, while water stress means less than 1700 m^3 of potable water is available per person per year (UNEP 2002). In terms of agriculture, water consumption can be defined as the amount of surface and groundwater absorbed by crops and transpired, or used directly in the building of plant tissue, together with water that evaporates from the area where crops are located. Water consumption also includes all activities where the use of water results in a loss of the original water supplied, such as industrial or community consumption (UNESCO, 2007).

There are few data concerning wetland losses in Africa. A 2005 review of wetland inventories in ten countries in southern Africa found significant losses in two areas in KwaZulu Natal: Tugela Basin, where over 90 per cent of wetland resources have been lost in parts of the basin, and the Mfolozi catchment (10 000 km2), where 58 per cent of the original wetland area (502 km2) had been lost (Taylor and others, 1995). Another study in 1992 reported an overall loss of 15 per cent of wetland area in Tunisia and 84 per cent wetland loss in the region's Medjerdah catchment (Moser and other, 1996). Losses may be due to land conversion, water extraction and climate change.

Furthermore, biological diversity in Africa continues to decline (UNEP, 2002). Over 120 plant species are extinct, with another 1771 threatened (Bird and Medina, 2002). Threats to species are both direct (such as bushmeat hunting) and indirect (such as habitat loss). Some species, such as the Bonobo or pygmy chimpanzee *(Pan paniscus*), exist in very limited areas. Loss of habitat in these relatively small areas can lead to the rapid extinction of species (Brooks and others, 2002).

All this data show that Africa is already a continent under pressure from climate stresses and it is highly vulnerable to the impacts of global change. Many areas in Africa are recognized to have climates that are among the most variable in the world on seasonal and decadal time scales. Floods and droughts can occur in the same area within months of each other. These events can lead to famine and widespread disruption of socio-economic well-being.

Many factors contribute and compound the impacts of current climate variability in Africa and will have negative effects on the continent's ability to cope with climate change. These include poverty, illiteracy and lack of skills, weak institutions, limited infrastructure, lack of technology and information, low levels of primary education and health care, poor access to resources, low management capabilities and armed conflicts. The overexploitation of land resources including forests, increases in population, desertification and land degradation pose additional threats (UNDP 2006). In the Sahara and Sahel, dust and sand storms have negative impacts on agriculture, infrastructure and health.

As a result of global warming, the climate in Africa is predicted to become more variable and extreme weather events are expected to be more frequent and severe, with increasing risk to health and life. This includes increasing risk of drought and flooding in new areas (Few *et al*. 2004, Christensen *et al*. 2007) and inundation due to sea-level rise in the continent's coastal areas (Nicholls 2004; McMichael *et al*. 2006).

Africa will face increasing water scarcity and stress with a subsequent potential increase of water conflicts as almost all of the 50 river basins in Africa are transboundary (Ashton 2002, De Wit and Jacek 2006). Agricultural production relies mainly on rainfall for irrigation and will be severely compromised in many African countries, particularly for subsistence farmers and in sub-Saharan Africa. Under climate change much agricultural land will be lost, with shorter growing seasons and lower yields. National communications report that climate change will cause a general decline in most of the subsistence crops, e.g. sorghum in Sudan, Ethiopia, Eritrea and Zambia; maize in Ghana; millet in Sudan; and groundnuts in Gambia. Of the total additional people at risk of hunger due to climate change, although already a large proportion, Africa may well account for the majority by the 2080s (Fischer *et al*. 2002).

Africa is vulnerable to a number of climate sensitive diseases including malaria, tuberculosis and diarrhoea (Guernier *et al*. 2004). Under climate change, rising temperatures are changing the geographical distribution of disease vectors which are migrating to new areas and higher altitudes, for example, migration of the malaria mosquito to higher altitudes will expose large numbers of previously unexposed people to infection in the densely populated east African highlands (Boko *et al*. 2007).

Future climate variability will also interact with other stresses and vulnerabilities such as HIV/AIDS (which is already reducing life expectancy in many African countries) and conflict and war (Harrus and Baneth 2005), resulting in increased susceptibility and risk to infectious diseases (e.g. cholera and diahrrhoea) and malnutrition for adults and children (WHO 2004).

Climate change is an added stress to already threatened habitats, ecosystems and species in Africa, and is likely to trigger species migration and lead to habitat reduction. Up to 50 per cent of Africa's total biodiversity is at risk due to reduced habitat and other human-induced pressures (Boko *et al*. 2007). The latter include land-use conversion due to agricultural expansion and subsequent destruction of habitat; pollution; poaching; civil war; high rates of land use change; population growth and the introduction of exotic species. For example, the habitat of the great apes, including the western lowland Gorilla – identified as critically endangered on the World Conservation Union's (IUCN) red list of threatened species, is likely to seriously decline in the next four decades.

Future sea level rise has the potential to cause huge impacts on the African coastlines including the already degraded coral reefs on the Eastern coast. National communications indicate that the coastal infrastructure in 30 percent of Africa's coastal countries, including the Gulf of Guinea, Senegal, Gambia, Egypt, and along the East-Southern African coast, is at risk of partial or complete inundation due to accelerated sea level rise.

In Tanzania, a sea level rise of 50 cm would inundate over 2,000 Km^2 of land, costing around USD 51 million (UNEP 2002a). Future sea level rise also threatens lagoons and mangrove forests of both eastern and western Africa, and is likely to impact urban centres and ports, such as Cape Town, Maputo and Dar Es-Salaam.

Predicting the impact of climate change on complex biophysical and socio-economic systems, that constitute agricultural sectors, is difficult. In many parts of Africa it seems that warmer climates and changes in precipitation will destabilise agricultural production. This is expected to undermine the systems that provide food security (Gregory et al., 2005). Whilst farmers in some regions may benefit from longer growing seasons and higher yields, the general consequences for Africa, are expected to be adverse and particularly adverse for the poor and the marginalized who do not have the means to withstand shocks and changes.

Effective adaptation strategies and actions should aim to secure well-being in the face of climate variability, climate change and a wide variety of difficult to predict biophysical and social contingencies. In pursuing this aim, climate adaptation should focus on support for the decision-making and capacity building processes that shape social learning, technology transfer, innovation and development pathways. Adaptation is most relevant when it influences

decisions that exist irrespective of climate change, but which have longer-term consequences (Stainforth et al., 2007).

A key component of climate adaptation involves building resilience, where resilience is the capacity of a system to tolerate disturbance without collapsing into a qualitatively different state that is controlled by a different set of processes: a resilient system can withstand shocks and rebuild itself when necessary.

An important aspect of the capacity to rebuilding itself sets up on energy. Sub-Saharan Africa is home to the world's lowest electricity consumption rates per capita; here poverty and the under-development of modern energy services are clearly linked. Between 1990 and 1999, average per capita consumption fell from 695 kilograms of oil equivalent (kgoe) to 410 kgoe. Although Africa is home to 13% of the world's population and produces 7% of the world's commercial energy, it accounts for only 2% of the world's GDP and 3% of global commercial energy consumption. In 1990 the total primary energy use in sub-Saharan Africa—including South Africa— was: 53% biomass; 26% petroleum; 14% coal; 3% large-scale hydro; 2% natural gas; and, 2% other renewables.

Moreover, according to the latest African Water Development Report, a total of five countries—South Africa, Egypt, Algeria, Nigeria, and Libya—were responsible for 84% of all energy production in Africa and for 78% of total energy consumed. Because of their centralised, non-renewable energy reserves—and high level of government involvement in energy generation—these countries have managed to develop at a faster rate than most other African countries. Conversely, due to the unavailability of comparable, traditional energy reserves, other African countries have had to import energy or rely primarily on renewable energy sources, e.g., hydro-electric generation, solar thermal and wind technologies. This development disparity illustrates a direct relationship between energy security and economic growth in Africa: energy security is a correlation of livelihood security.

As rural and urban low-income households do not have access to alternative energy sources they are the most vulnerable to climate change. This vulnerability is further compounded by national policy development that does not adequately address the needs of the rural population in general or rural energy needs in particular. There is, then, a real need to ensure sustainable energy supplies while also increasing access and affordable energy services for Africa's poor—both rural and urban.

In the face of projected climate impacts, the need is even more pressing. Problems of inefficient energy production and use undermine the income-generating potential of entrepreneurs and small-scale farmers. Studies show that small and medium enterprises (SMEs) in sub-Saharan Africa still depend on biomass for 84% of their energy needs. The

increased threat of climate change on natural fuel resources reinforces the need for urgent action to provide alternative and sustainable energy generation and supply for this economic sector.

In terms of energy generation and supply, the impacts of climate change on the energy sector will be felt primarily through: changes in the growth rates of biomass for fuel use; increased runoff and siltation from land degradation on hydro-generation; and, losses or fluctuations in hydropower production due to increased stresses on water supply systems and changing rainfall patterns.

Hydropower generation is likely to be the most heavily impacted because it is sensitive to the amount, timing and geographical pattern of precipitation as well as temperature—rain or snow, timing and speed of melting, etc. As hydropower is the primary source of electricity in East Africa and Central Africa—and supplying about half of West Africa's needs—the impact on development will be significant. This high dependence on water resources for energy generation further highlights the vulnerability of energy systems across Africa.

Although climate change seems marginal compared to the pressing needs of poverty alleviation, health, hunger and economic development, it is becoming increasingly clear that achieving development goals, such as those related to food, water and energy, can be seriously impeded by climate impacts. As a result, linkages between climate change and development are receiving more attention in political and scientific circles. Development can and should be planned in such a way that development goals are achieved, while simultaneously reducing vulnerability to climate change. It is essential that the potential impacts of climate change be mitigated in Africa where levels of poverty will be worsened by extremes of climate change. Countries with the fewest resources are most likely to bear the largest burden of climate change in terms of morbidity, loss of life, adverse effect on income and growth and damage to general living standards, such as access to safe water, energy and shelter.

Africa must explore mitigation options against greenhouse gases (GHG) emissions by developing solar, wind, hydro- and bio-energy sources; simultaneously the region must also consider the impacts of climate change on these energy sources.

The extent to which a community is able to adapt to climatic changes depends on its relative vulnerability—the degree to which a community is susceptible to the adverse effects of climate change—and adaptive capacity. Adaptive capacity is the ability of a community to adjust to the evolving challenges of climate change. It is also the ability of a community—or system—to adjust to climate change, to take advantage of opportunities, or to cope with the consequences.

To be successful, adaptation responses must be consistent with sustainable development. However, historically, little reference is made to climate impacts in development plans other

than in disaster management plans for droughts and floods. Most of the work done to date looks at the impacts on natural resources that affect the livelihoods of Africans. While energy has received lots of attention, the main focus has been on energy access and ensuring a sustainable energy path for Africa. The linkage between sustainable energy and climate impacts has not been explicitly made. Longer-term impacts due to climate change, such as the gradual change in rainfall patterns, do not fit into most planning horizons which are usually politically and financially constrained. The uncertainty of future projections such as population growth, energy demand and future energy supplies, further complicates adaptation responses.

All levels of government should ensure that policies, programmes, budget frameworks and projects take account of climate change and adaptation strategies. To date, much has been invested in Africa in terms of capacity building; however, more new efforts are needed to enhance the adaptive capacity of institutions, organisations and individuals. Even where climate change is recognised as a crucial concern, it is viewed as a long-term issue and therefore not consistently considered.

Thus, Africa has a huge burden to bear: it has been deemed "the continent most vulnerable to the impacts of climate change" by the UN Intergovernmental Panel on Climate Change (IPCC). Political, social, environmental and economic realities complicate the problem despite, or because of the region's abundant natural resources. One thing is clear however: Africa must not be allowed to slip into climate-induced chaos because of the industrialised world's addiction to fossil fuels. From the country reports, we can see that energy development for Africa in a changing climate will require greater emphasis on small-scale, decentralised and diversified supply and increased distribution to households and enterprises alike. As has been discussed, hydro-dependency will become problematic if rain patterns change. Similarly, renewable technologies such as wind and solar could be affected by changing climate patterns. A diversified and distributed energy mix is the best insurance policy against climate change.

But adaptation of energy policies and systems is only part of the solution; building up the resiliency of local populations and energy systems is equally important.

Despite the obstacles facing Africa, hope is not lost. There are numerous positive characteristics upon which successful programmes can—and should be—built. Culturally, Africa has strong social networks. These networks serve an important function in educating communities, disseminating information and serving as substitutes for collateral in micro-loans. Women—in particular—play an important role in the management of natural resources. As primary collectors and users of biomass and water, women are well-placed to monitor and manage resources, spur innovation on adaptive techniques and experiment with new management approaches. Ironically, it may be Africa's decades-long experience coping with

poverty that may be its strongest resource. By its collective survival the region has shown itself to be adaptive and resilient despite enormous obstacles. It is now our collective responsibility to ensure that this rich, diverse region develops to its fullest potential (Helio International, 2007).

Superimposed on the many other anthropogenic impacts on forest ecosystems is surely human-forced global climate change. Climate has a major influence on rates of photosynthesis and respiration (Law et al. 2007), and on other forest processes, acting through temperature, radiation, and moisture regimes over medium and long time periods. Climate and weather conditions also directly influence shorter-term processes in forests, such as frequency of storms and wildfires, herbivory, and species migration. As the global climate changes, forest ecosystems will change because species' physiological tolerances may be exceeded and the rates of biophysical forest processes will be altered (Olesen et al. 2007, Kellomaki et al. 2008, Malhi et al. 2008).

If climate change results in a significant reduction in water availability, then the forest system will naturally change species composition (or state – see definition below). For example, the vegetation will reach a threshold beyond which the vegetation structure is not sufficiently tall and dense to comprise a forest, along with the concomitant changes in the dominant taxonomic composition of the plant community. Several studies have established that resilience in ecosystems is related to the biological diversity in the system and the capacity that it confers to maintain ecosystem processes (Hooper et al. 2005, Drever et al. 2006, Bodin and Wimen 2007). Most ecosystem processes are controlled by, or are the result of, biodiversity. However, not all species are

necessarily equally important in maintaining these processes (Walker 1992, 1995, Diaz et al. 2003) and there is some redundancy at multiple levels within most ecosystems (Hooper et al. 2005). Loss of functional species in the absence of redundancy has negative consequences for the ecosystem to the point of ecosystem collapse (Chapin et al. 1997). Bazazz et al. (1995) demonstrated the potential for populations to respond to varying levels of CO_2, and the genetic complexity and magnitude of genetic responses to population factors such as density and competitive interactions. The first aim of this Ph.D. thesis is to investigate the impact of selective logging, which alter forest dynamics and cause loss of functional species, and could seriously affect tropical forests under a changing climate. I carried out researches on African tropical forests trying to find a significant answer to this issue.

There is considerable ongoing debate over the role that biodiversity plays in ecosystem function and stability owing to the highly complex nature of the relationships among species and the synergistic roles of extrinsic factors and intrinsic factors, including genetic factors, in

ecosystems (see e.g., Waide et al. 1999, Kinzig et al. 2001, Loreau et al. 2002, for summary discussions). Further, there is evidence that complex forest ecosystems are more productive than less diverse ones (under the same conditions) (e.g., Phillips et al. 1994), and generally that forest systems comprised of few species are highly prone to various catastrophes including disease and invasion (Scherer-Lorenzen et al. 2005).

Much of the work done to understand the relationship between species diversity, ecosystem processes, and production has necessarily been done in highly controlled low-diversity systems at small scales, especially using grasses (e.g., Tilman and Downing 1994, Tilman et al. 1996, Hector et al. 1999, Hector 2002), or in other controlled systems (e.g., Naeem et al. 1995). Few studies have examined more connected systems with multiple trophic levels and complex production webs, such as forests, nor have they considered larger scales.

The second aim of this Ph.D. thesis is to understand the relations between forest structure, productivity and biodiversity.

Up to now, two main competing hypotheses have been identified to predict the relationship between biodiversity and productivity in ecosystems: the niche complementarity hypothesis (Tilman et al. 1996, Tilman and Lehman 2001) and the sampling effect hypothesis (Aarssen 1997, Doak et al. 1998).

Under either hypothesis, a certain level of saturation is expected where no more effective use of resources can be achieved regardless of increased species richness (Hooper et al. 2005).

The niche complementarity (or niche differentiation) hypothesis predicts that as species are added to a system, the productivity in the system will increase until vacant niches are filled because of effective partitioning of resources. The coexistence of species then is assured through interspecific differentiation as a direct response to competition for resources. If species are able to avoid competition by occupying different niches, then production in the system will increase accordingly (e.g., Tilman and Lehman 2001, Tilman et al. 2002). Niche differentiation models also consider the concept of facilitation, where one or more species may enhance the capacity of another species to survive and reproduce (e.g., ectomycorrhizal fungi on tree roots or legumes in grasslands). However, few keystone functional roles among plants are known (e.g., C3 and C4 grasses, nitrogen fixers).

A competing model, the sampling (or selection) effect hypothesis, suggests that dominant competitors (“sampled” from the regional species pool) will play the greatest roles in ecosystem functioning and as diversity increases, functioning in the system will be controlled by these dominant species because of their greater likelihood of being present in a diverse system (e.g., Aarssen 1997, Huston 1997). This result is achieved because the best competitors will always control resources within a system. Niche differentiation models predict coexistence

among species, while sampling effect models predict dominance by one or a few species, especially for systems in equilibrium. Various studies suggest support for one or the other of these models (e.g., Hooper and Vitousek 1997, Tilman at al. 2002, Hooper and Dukes 2004) or suggest that the capacity to conduct the experiments has been limited by almost intractable design problems or analysis constraints (e.g., Huston 1997, Allison 1999, Schmid et al. 2002). By studying tropical forest of Africa and of the Earth I tried to shed light on this two competing hypothesis and to develop a unified theory which could explain the relations between forest structure, niche volume, climate and biodiversity.

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CHAPTER 1

The impact of selective logging on African tropical forests*

Abstract

Tropical deforestation for timber market is well known to have serious negative consequences on local biodiversity, terrestrial carbon sink and the balance of atmospheric greenhouse gases. In contrast, selective logging of tropical forests is often regarded as a management practice that has less dangerous effects on the ecosystem, even though researches are scanty in critically evaluating its impact on forest structure, biodiversity and ecosystem services. We compared field data that we collected in Africa (Cameroon, Gabon, Sierra Leone and Ghana) from 511 plots of tropical forest subject to different forest management practices (old-growth primary forests, selectively logged and secondary forests). Our findings suggest that the vertical structure and plant diversity of the logged forest are not largely different from those of a primary forest, while a remarkable difference in forest density, synthesized in some indicators, together with a concomitant invasion by vines, climbers and other weeds is pointed out. We show that the effects on species richness and biomass are greater than those expected from the simple removal of commercial species, implying that selective logging, unless it is practiced very carefully at very low harvest intensities, may significantly reduce the biomass density of a tropical forest for time scales spanning decades, and possibly longer, seriously diminishing the aboveground carbon storage and richness of the forest.

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Introduction

Tropical forests are key biomes for crucial ecosystem services. Such biomes attain the highest level of biodiversity among terrestrial ecosystems (1), protect hill slopes, strongly influence local climate and represent the most productive ecosystems on Earth, accounting for 59% of the global carbon pool in forests (2, 3). However, tropical forest areas are also characterized by very high rates of deforestation, conversion to agriculture, logging, and degradation by continuous withdrawal of wood by local population for subsistence (4).

In recent decades, many tropical countries have changed forest resource extraction management from clear cutting to selective logging (5, 6, 7), in response to the scientifically recognized role of deforestation activity in the increase of CO2 atmospheric concentration (8, 9) and following the concept that . the close relationship between biodiversity and productivity makes policies which support preservation of forest integrity a win-win approach for both carbon sequestration and biodiversity protection (10, 11, 12).

Selective logging is defined as the harvest of valuable timber trees above a threshold trunk diameter with methods designed to maintain the forest cover, including a significant understock of living biomass. Currently, selective logging is considered to be a "sustainable forest management" (SFM) practice and it is increasingly embraced as an approach to protect forest integrity while allowing an appropriate use of resources. Overall, there appears to be a consensus on viewing selective logging as causing only minor disturbance (13, 14, 15, 16), and thus acceptable within the requirements of certification schemes such as the Forest Stewardship Council (FSC), a highly regarded SFM standard established in 1993 and now included in REDD programs (17).

At the moment, there is not an extensive knowledge on the short and long-term effects of selective logging on carbon sequestration and biodiversity, as well as the trade-off between these two ecosystem variables as functions of the intensity of timber harvesting, despite its increasingly wide adoption.

Generally, available studies focus on specific and confined areas of South or Central America (18, 19, 20), or South-East Asia (21, 22), or Africa (23, 24, 25, 26, 27, 28), where the practice of selective logging is rapidly increasing (29).

In some cases, the intensity of the disturbance caused by selective logging was solely quantified in terms of diversity of the logged forest (30, 31, 32) with results that were encouraging for that practice. However, other studies show significant changes of species composition (33, 34, 35, 36) and genetic diversity (37), variations in forest structure (38, 39, 40) and nutrient cycling (41). Remote sensing techniques have been applied to quantify large-scale physical forest damage, extent of canopy openings (caused by logging operations and the

construction of access trails) and changes in the carbon stock (42) showing that selective logging definitely has non-negligible impacts.

An important aspect in evaluating forest damage is the assessing of the extension of canopy gaps by selective timber harvests. In tropical forests, canopy gaps have immediate impacts on light interception, heat fluxes, water stress and plant productivity (43). In computer simulations the rate of forest regeneration strongly depends on the size, the number and the spatial arrangement of canopy gaps following harvest (44). Recent studies also suggest that canopy openings decrease in size with distance from each felled tree crown, but in recently logged forest the area initially affected by harvesting of each tree is at least 50-100 m in radius (45).

One of the main effects of canopy gaps discontinuities appears to be the creation of spaces readily invaded by weeds, vines and climbers at the expense of the late-successional state cenosis (46). Typically, fragmentation and selective logging opens up gaps of light in which weeds displace or suppress native species. Conversely, natural gaps (e.g. due to big broken branches or naturally died trees) are usually smaller than logging gaps, and tree saplings seems to be prepared to grow fast enough to fill the canopy opening (47, 48, 49, 50, 51). This reduces the likelihood of vines, weeds and climbers invasion (52). Here we argue that changes in native cenosis caused by the selective removal of the tallest trees induce a local variation of forest structure with relative consequences on biodiversity and carbon stocks.

To support our thesis we compare three different types of forest management (old-growth/untouched, clearcut and subject to selective logging) of tropical forests in Western and Central Africa looking for statistically significant differences. For this purpose we collected data of tree heights, diameter at breast height (d.b.h) and species composition from 33 forest plots, each one of 500 m^2 located in Ghana, Gabon and Cameroon (which we call Dataset1), and we processed 478 additional plots with data of d.b.h. located in Sierra Leone (Dataset2). The data allow us to form 12 distinct indices (summarized in Table 2) on forest biomass, diversity, density, etc. that we examine in order to determine which of them show statistically significant differences among the forest types, and which do not.

Study sites

Our data were collected in four tropical forest countries, located in West and Central Africa: Ghana, Cameroon, Gabon and Sierra Leone. In West Africa forest plots were selected along the border between Ghana and Ivory Coast (Bia National Park and surrounding areas), and on the Ghana coast (Ankasa Forest Reserve). We also analysed data collected in the Gola Rainforest National Park (located in Sierra Leone close to the border with Liberia) within Kenema district. In Central Africa forest plots were selected within the Congo river basin, on

the border between Cameroon and Congo (Sangha Tri-National Forest) and in Gabon (Woleu-Ntem and Moyen-Ogooué regions).

The first sampling site in Ghana, Bia National Park, is part of a protected area of 306 km^2, which includes 77.7 km^2 of national park in the north, and 227.9 km^2 of Resource Reserve (where logging is permitted) in the south. The area is located in the transition zone between the southern mixed evergreen forest and northern mixed semi-deciduous forest. The average annual precipitation ranges from 1500 mm to 1800 mm and the average monthly temperatures range between 24° and 28°C, with the rainy season during the months of May, June, September and October. More than 300 plant species per hectare can be observed; species from the *Tieghemella*, *Ceiba*, and *Khaya* genera are widespread.

The second sampling site in Ghana, Ankasa Conservation Area, is twin Wildlife Protected Area comprising Nini-Suhien National Park and the Ankasa Resource Reserve with the Nini-Sushien river forming the boundary between the two. Selective logging and clearcutting occurred in area surrounding the current boundaries of the protected areas. Its extension is about 500 km^2 and it is situated in the Western Region of Ghana. Being the area with the highest rainfall in Ghana (1700-2000 mm per year), Ankasa is the richest forest of the country in terms of botanical diversity. About three hundred plant species have been recorded in a single hectare. Notable among the trees are *Tieghemella heckelii, Ceiba pentandra and Khaya ivorensis.* The vegetation of the two conservation areas is respectively wet evergreen and semi-deciduous evergreen. The southern parts of Ankasa were logged from the early 1960s up to about 1974. Logging intensity was, however, relatively low due to the small amounts of commercially valuable timber. Nini Sushien contains one of the few remaining blocks of relatively untouched forest in the country (53).

The first sampling area in Central Africa is bordered to the east by the Sangha River, an affluent of the Congo River, and it belongs to the surrounding areas of the Lobeké National Park. It is located in the East Region of Cameroon. The forest covers an area of 184,000 hectares with an altitude ranging between 300 m and 750 m above sea level. The area consists of semi-evergreen forests, with over 300 species of trees, the largest ones including *Ceiba pentandra* (L.) Gaertn, *Terminalia superba* Engl. & Diels and members of the family *Sterculiaceae* (*Triplochiton*, *Pterygota*). The average annual precipitation is 1400 mm, with the dry season occurring from December to February (54).

The second study site in Central Africa is located in North and Central Gabon in the Provinces of Woleu-Ntem and Moyen-Ogoouè. These forest areas of about 180,000 hectares have an equatorial climate, with year-round high temperatures and humidity. Rainfall varies from an annual average of 1750 to 3050 mm, with almost all of it falling between October and April. In

the period from May to September there is little, if any, rainfall, but humidity remains high. Temperature shows little seasonal variation, the daily average being about 27° C. The areas in the provinces surveyed for this study are moist and semi-evergreen forests.

In all of these study sites, the commercial tree species most commonly harvested are *Enthandrophragma cylindricum, Terminalia superba*, *Triplochiton scleroxylon* and *Heritiera utilis*. A typical selective logging scheme includes the harvest of trees with diameters bigger than 30–100 cm and logging cycles of 15–30 years. For example, in Central Africa the minimum diameter is 100 cm for *Enthandrophragma cylindricum*, 60 cm for *Terminalia superba* and 80 cm for *Triplochiton scleroxylon* and logging cycle is 15-30 years.

We also expand our study on data sampled from Lindsell and Klop (Lindsell, J. A., & Klop, E. 2013) in the Gola Rainforest National Park, the largest area of lowland evergreen rain forest remaining in Sierra Leone (54). The forest covers 71,000 hectares hilly terrain located at Sierra Leone's eastern border with the Republic of Liberia and it extends for. The forest used to be commercially exploited when was classified as a production forest and more than 20,000 hectares were logged. Logging in Gola started at least by 1961 but possibly earlier. Logging practice in the northern block was good in the 60s and 70s, but it may have been poor in the 80s. Most areas were only logged once and few had two harvests. Offtake was concentrated in accessible areas so impact was patchy. Logging in the western and eastern blocks was much more intensive. It lasted 1963 to 1965, then 1975 to 1989 and in the latter period was patchy, intensive and damaging (55).

Methods

Sampling Methods

In the following we shall distinguish between three kinds of sampling plots: “Primary Forest” (PF) which designates plots sampled in areas of old-growth forest for which we have documented evidence that they were left untouched for at least 300 years; “Secondary Forest” (SF), plots sampled in areas subject to clear cutting in the 1990s and, hence, left to recover for at least 20 years; “Selective Logging” (SL) to label plots sampled in areas, harvested in the 1990s (SL20) or in the 1980 (SL30). Cameroon also include a plot subject to two rounds of logging in the 1960s and 1990s (SLD), while two plots in Ankasa were clearcutted and then selectively logged after about 50 years (SFD). All plots have negligible slope and lie on plains or hilltops, with the exception of two primary forest plots (PFH) lying on hillsides (Table 1).

To collect the data included in the Dataset1, we used a cartographic grid with rectangular cells of 500 m^2 to define field plots (56) for each forest category (primary, secondary and selectively

logged) within each study area above described (57). The grid was overlaid on satellite maps of the study areas of the five countries. Rectangular plots of 500 m2 (20x25 m or 10x50m) were selected by random sampling method (adapted Whittaker sampling method, 58, 59) at a minimum buffer distance of 50 m from access roads and extant logging trails. This sampling design resulted in some plots being placed in forest affected by logging as well as in plots with not direct signs of cutting activities (stumps, roads, skid trails and gaps). Overall, including all three forest management types, we sampled a total of 33 distinct plots (Table 1).

	Dataset 1				**Dataset 2**
Country	**Ghana**		**Cameroon**	**Gabon**	**Sierra Leone**
Location	**Bia National Park**	**Ankasa Forest Reserve**	**South-Est Region**	**North and Central Regions**	**Gola National Park**
N° Plots of primary forest (PF)	**2 (including 1 PFH)**	**4**	**2**	**3 (including 1 PFH)**	**223**
N° Plots in Selective logged forest (SL)	**2**	**4**	**3 (including 1 SLD plot)**	**4**	**119 SL-WM, 136 SL**
N° Plots in secondary forest (SF)	**1**	**4 (including 2 SFD plots)**	**1**	**3**	**--**
Vegetation type	**moist evergreen forest**	**wet evergreen forest**	**moist evergreen forest**	**wet evergreen forest**	**wet evergreen forest**
Meters a.s.l.	**85-104**	**70-130**	**120-400**	**410**	**154-400**
Annual total rainfall (mm)	**1650-2000**	**1850-2000**	**1500-1750**	**2000-2500**	**2000-2500**
Average mean temp (°C)	**23-25°**	**26-28°**	**23-25°**	**24-26°**	**24-28°**
Soil type	**Oxisol-alfisol**	**Oxisol**	**Oxisol-alfisol**	**Oxisol**	**Oxisol**

Table 1. List of site characteristic with regard to location, vegetation type, climate and soil classification of the sampled tropical forest. All the study sites incorporates primary forests (PF, -H: hills) surrounded by managed forest: SL20, area subjected to selective logging 20 years ago; SL30 area subjected to selective logging 30 years ago; SL-WM area subjected to a *well-managed* practice of selective logging; SLD area subjected to a double turn of selective logging (1960s and 1990s); SF area subjected to clearcutting 20 years ago; SFD area clearcutted and then selectively logged after about 50 years.

Within these plots, corner coordinates were collected with a GPS/compass and positions of all trees having diameter not less than 5 cm were mapped. The diameter of each tree was measured at breast height, i.e. 1.37 m above ground (or 50 cm above buttresses if present). D.b.h. and height were measured using a laser hypsometer-dendrometer. The genus and species name was identified directly in field or using specimens in laboratory. Tree positions into the plot were recorded in gridded and geo-referenced worksheets, as well as weed/vines cover.

We collected the available documentation reporting the number of felled tree in the areas of selectively logged forest, which range from 4 trees/ha to 38 trees/ha. Scaling these numbers down to the area of the plots, we estimate the number of felled trees per plot, on average, to be 1±0.6.

The plots from the Gola National Park (Dataset2) that we use in our analysis are a subset of 609 circular plots of 0.125 ha, sampled at 200 m intervals and arranged in 43 transects, surveyed by Lindsell and Klop (27) between October 2005 and May 2007. In each plot the diameter of all trees larger than 30 cm d.b.h. was measured, together with ancillary data such as the slope of the terrain, the distance from the nearest road or trail, etc (see ref. 27 for a full data description). We excluded the plots disturbed by rivers, swamps, trails, farming activities, and those where the slope was not measured. Based on field evidence and on the available records of logging offtake, we classified the remaining plots as "*unlogged*" (223 plots, assumed to be PF), *"well-managed"* (119 plots, SL-WM) and *"logged"* (136 plots, SL). This classification is based on historical records (60) and field observations. "*Unlogged*" areas were untouched by commercial operations and showed no indication of recent illegal activity. "*Well-managed*" and "*logged*" areas were distinguished according to the recorded performance of the relevant concessionaires (60) with "*well*-managed" areas having a largely intact canopy and "over-logged" areas having extensive canopy openings. Because of the different sampling methodologies, we analyse the data from Sierra Leone (Dataset2) separately from the others (Dataset1).

Data analysis

The biometric data (height and d.b.h.) were used for the calculation of aboveground biomass using the allometric equations of Chave et al., 2005 (61) and the Global Wood Density Database (62). The amount of carbon stored in the aboveground biomass was then estimated as the kilograms of biomass multiplied for a conversion factor of 0.47 (63).

We formed 12 indices for each plot, defined in Table 2. The first group of four indices contains the average tree height, diameter and biomass, and the height of the 80th percentile in each

plot. The second group of four indices contains measures of density, that is the sum of height, diameter, biomass and number of individuals normalized by the area of the plot. The third group contains three indices of biodiversity (richness, entropy and evenness, 64) and a measure of the abundance of vines in each plot.

Mean Height	$\frac{1}{N_l}\sum_{i=1}^{N_l} h_{l,i}$	Normalized Biomass	$\frac{1}{A_l}\sum_{i=1}^{N_l} b_{l,i}$
Height of the 80th percentile	$\mathcal{H}_l$ such that $P\{h_{l,i} \leq \mathcal{H}_l\} = 0.8$	Normalized Diameter	$\frac{1}{A_l}\sum_{i=1}^{N_l} d_{l,i}$
Mean Biomass	$\frac{1}{N_l}\sum_{i=1}^{N_l} b_{l,i}$	Richness	R_l
Mean Diameter	$\frac{1}{N_l}\sum_{i=1}^{N_l} d_{l,i}$	Shannon Entropy	$-\sum_{j=1}^{R_l} \frac{n_{l,j}}{N_l} log\left(\frac{n_{l,j}}{N_l}\right)$
Normalized Height	$\frac{1}{A_l}\sum_{i=1}^{N_l} h_{l,i}$	Evenness	$\frac{-1}{\log(R_l)}\sum_{j=1}^{R_l} \frac{n_{l,j}}{N_l} log\left(\frac{n_{l,j}}{N_l}\right)$
Tree Density	$\frac{N_l}{A_l}$	Vines Cover Factor	$\frac{a_l}{A_l}$

N_l: number of tree in the l-th plot;

$h_{l,i}$: height of the i-th tree in the l-th plot;

$b_{l,i}$: above-fground biomass of the i-th tree in the l-th plot;

$d_{l,i}$: diameter of the i-th tree in the l-th plot;

R_l: number of species present in the l-th plot;

$n_{l,j}$: number of individuals of the j-th species present in the l-th plot;

a_l: area covered by vines in the l-th plot

A_l: area of the l-th plot;

Table 2. Definition of the 12 indices used to compare primary vs secondary and primary vs selectively logged forest plots.

For each index, we compare the values scored by primary forest plots with those scored by secondary forest plots, and, separately, by selectively logged forest plots of the Dataset1. The null hypothesis, namely that the index shows no difference between PF and either SF or SL, is tested with a Mann-Whitney *U* test, which is appropriate because it works also if the distribution of data is non-normal or unknown and it is applicable to samples of small size.

From the value of the statistics *U* we compute, using Harding's algorithm (65), the probability *P* of the null hypothesis, namely that the two samples are drawn from the same distribution. We report the value of P any time that it is lower than 0.05.

We complete the analysis of Dataset 1 by computing the Sørensen index to estimate the beta-diversity among primary forest plots and between primary and selective/secondary forests plots (65).

For the Sierra Leone plots (Dataset2) the tree height was derived from the diameter data by allometry. Therefore, height and biomass data are merely a function of diameter data, and we do not include them in our analysis. On the other hand, the abundance of plots, all from the same location, allows us to study the entire distribution of tree diameters (for trees larger than 30 cm dbh), rather than just plot-by-plot averages (or percentiles). For this purpose we form three large samples of diameter data by grouping together the diameter measurements from all the unlogged, all the well-managed and all the logged forest plots. We then perform two pairwise comparisons between the 'unlogged' and 'well-managed' samples, and between the 'unlogged' and 'logged' samples by means of a two-sides, two-sample Kolmogorov-Smirnov test. In addition we use a kernel density estimation (based on the Epanechnikov kernel, using Silverman's rule for bandwidth selection) [66] in order to plot a reliable estimate of the diameter data probability density function (pdf).

Then we use two indices of the second group (measures of density), namely the tree density and the normalized diameter. In this case we have to revert to a plot-by-plot analysis, because we need the plot's area to compute the densities. Following ref. 27, in order to properly weight the contribution of plots on sloping grounds, we use the vertical projection of the surface area, namely

$$A_l = A_0 \cos(\varphi)$$

where A_0 = 0.125 ha is the (constant) surface area of the plot, and φ is the slope of the ground as measured in-situ with a clinometer. We then compare the three groups pairwise, as for the 33 plots discussed above, using the Mann-Whitney *U* test. Note that the actual values of these two indices are not directly comparable with those of the same indices of the 33 plots from the Dataset1, because in the former case the samples include all trees above 5 cm dbh, while in Sierra Leone only the trees above 30 cm dbh were measured and, overall, the sampling protocols are quite different (see section "Sampling Methods").

Results

Figure 1 shows the first group of indices, namely the average values of tree height, diameter, biomass and the 80th percentile of height, for each plot. It is quite evident that these indices do not show striking differences between plots of primary forest and plots of either secondary or selectively cut forest. Although visually the values of selectively logged forest (red symbols) appear to be generally lower than those of primary forests (blue symbols), the probability of the null hypothesis is not as low as to allow for its outright dismissal, except possibly in the case of the mean biomass. In addition, we must observe that one selectively logged plot in

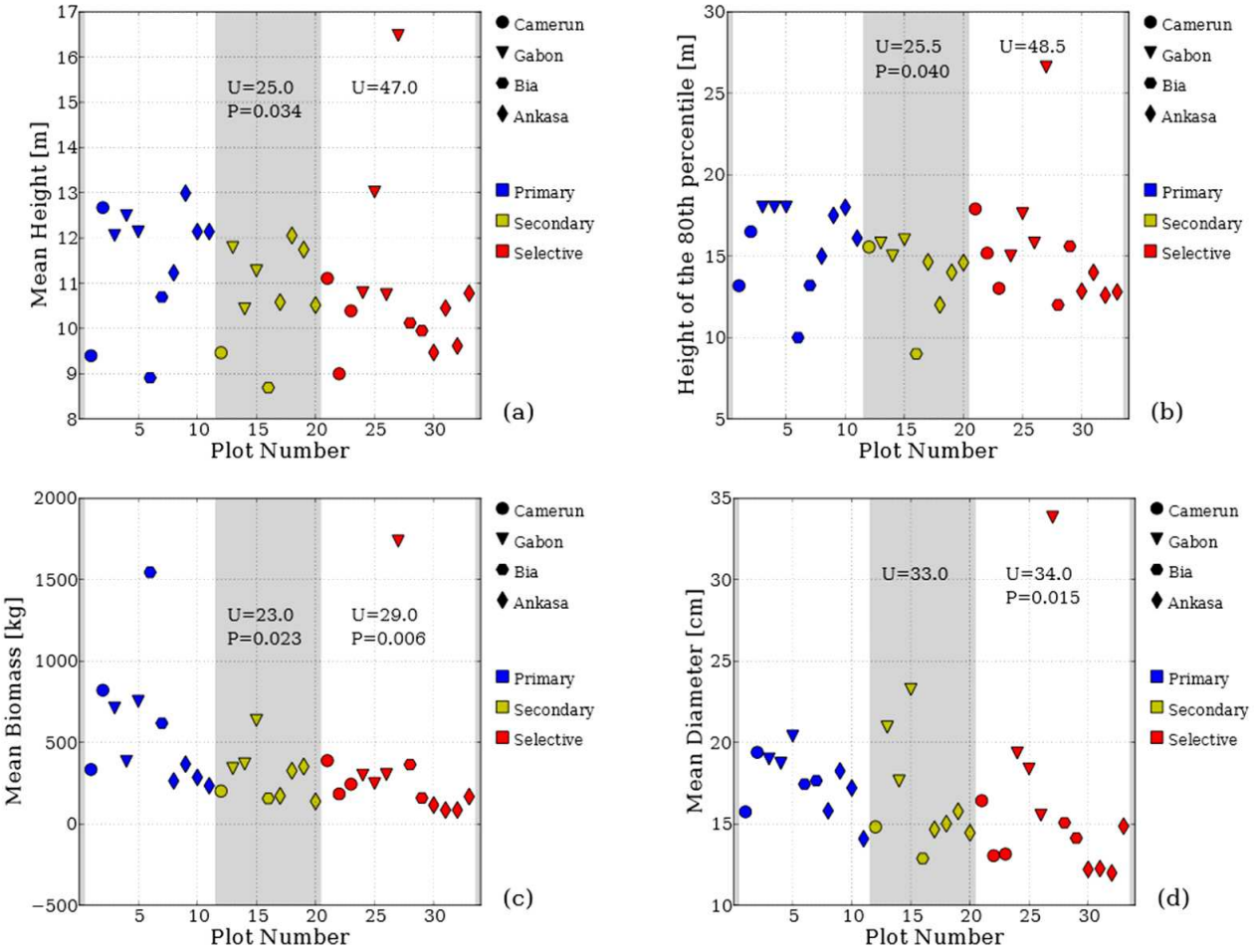

Figure 1. Indices characterizing the distribution of tree height, biomass and diameter in each plot. A) Mean tree height, B) Height of the 80th percentile, C) Mean biomass D) Mean diameter. The abscissa shows a serial number attributed to each plot (which is held the same in all the figures). The marker shape identifies the geographical location of the plot (circles: Cameroon; triangles: Gabon; hexagons: Ghana – Bia; diamonds: Ghana – Ankasa). Plots from Cameroon and Gabon are clumped together in Table 3 as "Central Africa", Bia and Ankasa as "West Africa". The marker color identifies the type of forest management (blue: primary, yellow: secondary, red: selectively cut). We show the values of the Mann-Whitney U statistics, above the yellow symbols when comparing primary vs selectively cut forest plots. If the probability P of the null hypothesis is lower than 0.05 we report it under the value of U.

Gabon scores the highest value in all these four indices, reflecting the fact that selective logging does not always remove all the big trees in a given area.

Figure 2 shows the four density indices, namely the sum of the height, biomass, diameter of each tree, and the number of trees in each plot, divided by the area of the plot. The Mann-Whitney U tests let us conclude, with a very high confidence, that all four densities are systematically higher in primary forests. Therefore, these indices are sensitive to differences between primary forests and the other two types of forest.

The difference in response between the first and the second group of indices may be further illustrated by looking at Figures 3 and 4, which show a representative examples of the vertical profiles and the canopy covers of the trees in two plots of lowland primary forest and two plots of selectively logged forest of Cameroon and Ghana. Even when one compares a primary forest plot containing a few big, tall trees with a selectively logged forest deprived of tall trees, the averages are in both cases dominated by medium and low height trees, that by far

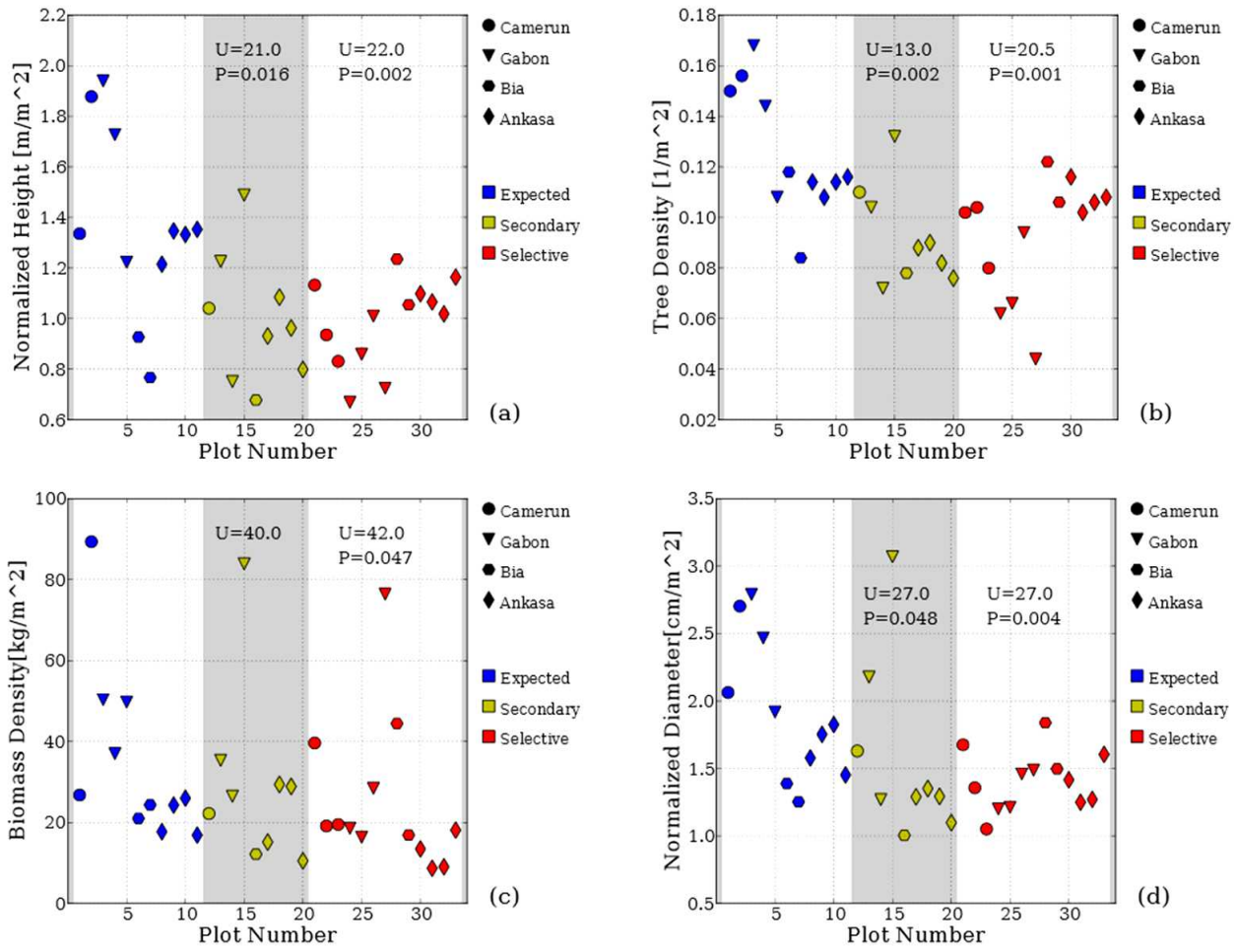

Figure 2. Indices of forest density in each plot. A) Normalized height, B) Tree density, C) Normalized biomass, D) normalized diameter. Symbols, colours and legends as in Figure 1.

outnumber tall trees even in primary forest plots. On the other hand, the visually evident difference between the two types of forest management is the sparseness and lower number of the trees in selectively logged plots compared with the denser, thicker and more uniform spatial tree distribution in primary forest plots.

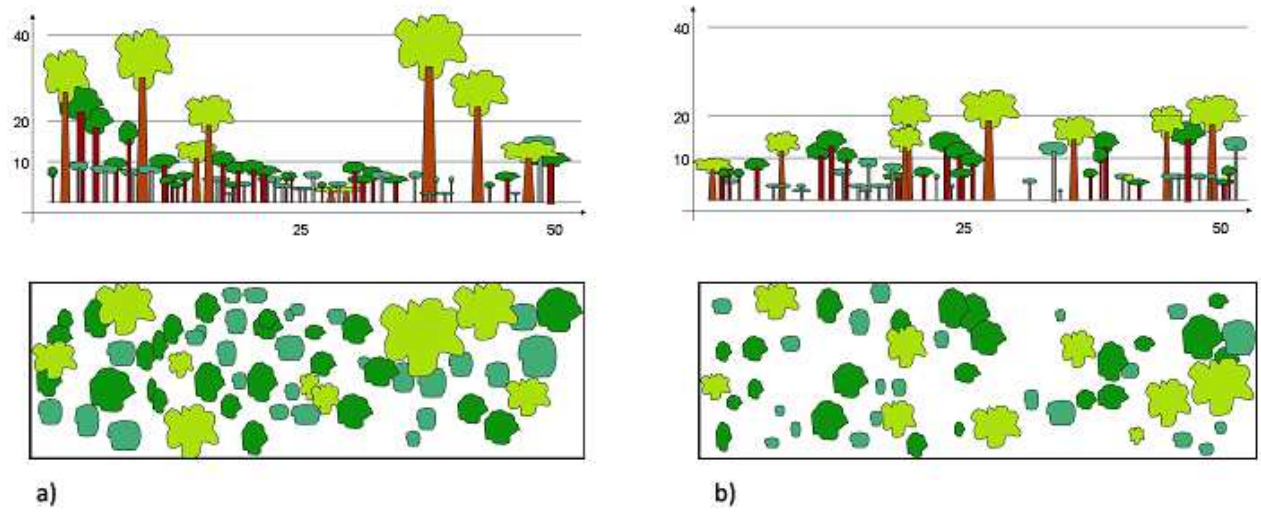

Figure 3. A comparison between vertical profiles (upper) and canopy view (bottom) of two plots of 50 m x 10 m achieved in Cameroon. *a)* primary forest (PFP); *b)* Forest subject to selective logging 30 years ago (SL30).

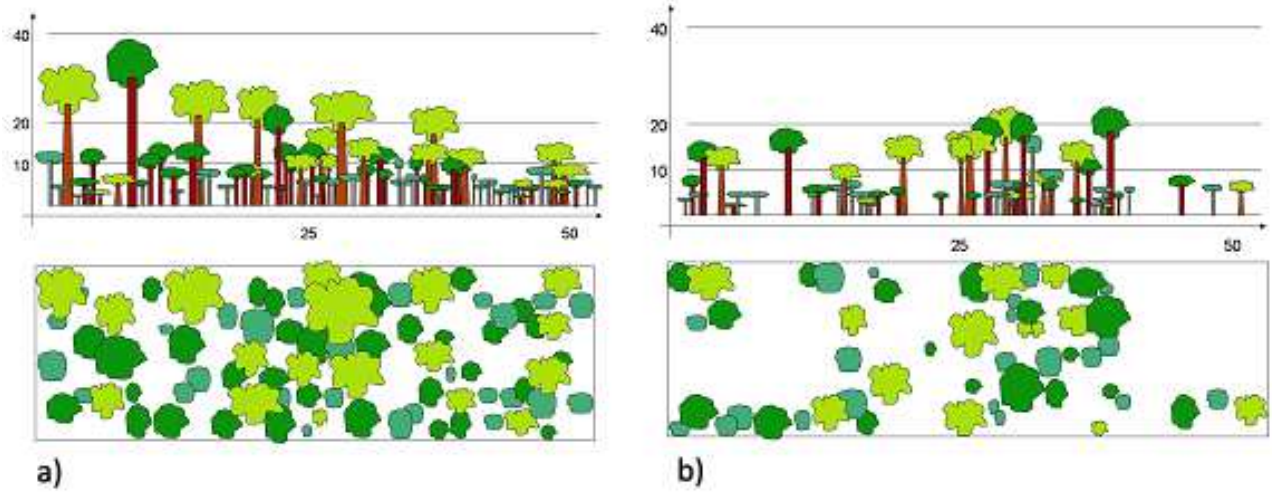

Figure 4. A comparison between vertical profiles (upper) and canopy view (bottom) of two plots of 50 m x 10 m achieved in Ghana. *a)* primary forest (PFP); *b)* Forest subject to selective logging 30 years ago (SL30).

Figure 5 shows the diversity and vines coverage indices. In all cases, with the sole exception of a plot of secondary forest in Cameroon, entropy and evenness of the plots have very high values, signalling that most of the species appear only once in each plot, regardless of the forest management type. Evenness is unable to distinguish between primary and the other two forest types, and entropy does so with a relatively low statistical confidence. This result is consistent with previous studies that did not record large losses of diversity in selectively logged forests (32). Not surprisingly, the species richness is instead significantly lower in plots

of secondary and selectively logged forest than in plots of primary forest: this is the expected consequence of the fact that the number of individuals per plot is less in selectively logged than in primary forests (Figure 4b), and that most species are represented by just one individual. Finally, the fraction of plot surface covered by vines is the index that most reliably singles out the primary forest plots from the other two types: in each primary forest plot the vine coverage is less (usually by a factor larger than ten) than in all non-primary forest plots.

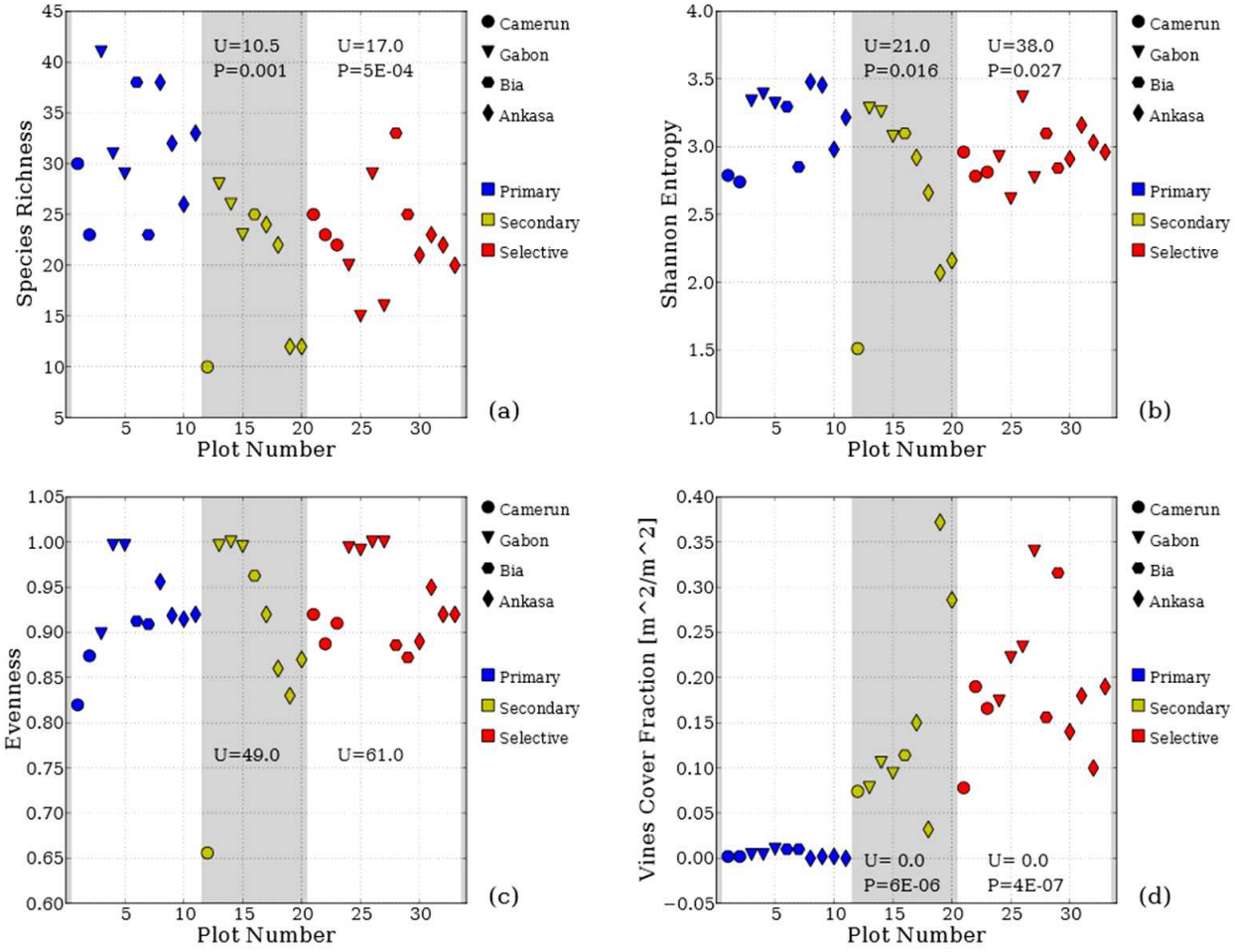

Figure 5. Indices of diversity and vine coverage. A) Species richness, B) Shannon's entropy, C) evenness, D) Vines cover fraction. Symbols, colors and legend as in Figure 3.

In order to exclude that the test results are affected by geographic inhomogeneities, we have applied the Mann-Whitney test grouping together only the plots from West Africa and, separately, only the plots from Central Africa. The results are reported in Table 3. The reduced size of samples raises the *P*-values associated to the computed *U*-values, and makes it difficult to reject the null hypothesis with very high confidence even when the value of *U* is near zero. However, the general pattern appears to be unaffected by the geographic location, namely that the first four indices, together with entropy and evenness are not particularly skilled in distinguishing plots of primary forest from the other two forest types, and that the density

indices, together with species richness and vines cover fraction are generally able to perform the distinction. A notable exception are normalized height and tree density for West Africa plots of primary vs selectively logged forest. In these two cases, however, the value of the *U* statistics is almost completely determined by the low values recorded at a single plot of primary forest in Bia (plot number 7 in the figures), characterized by having relatively few, unusually low trees, probably because it lies on the side of a steep hill.

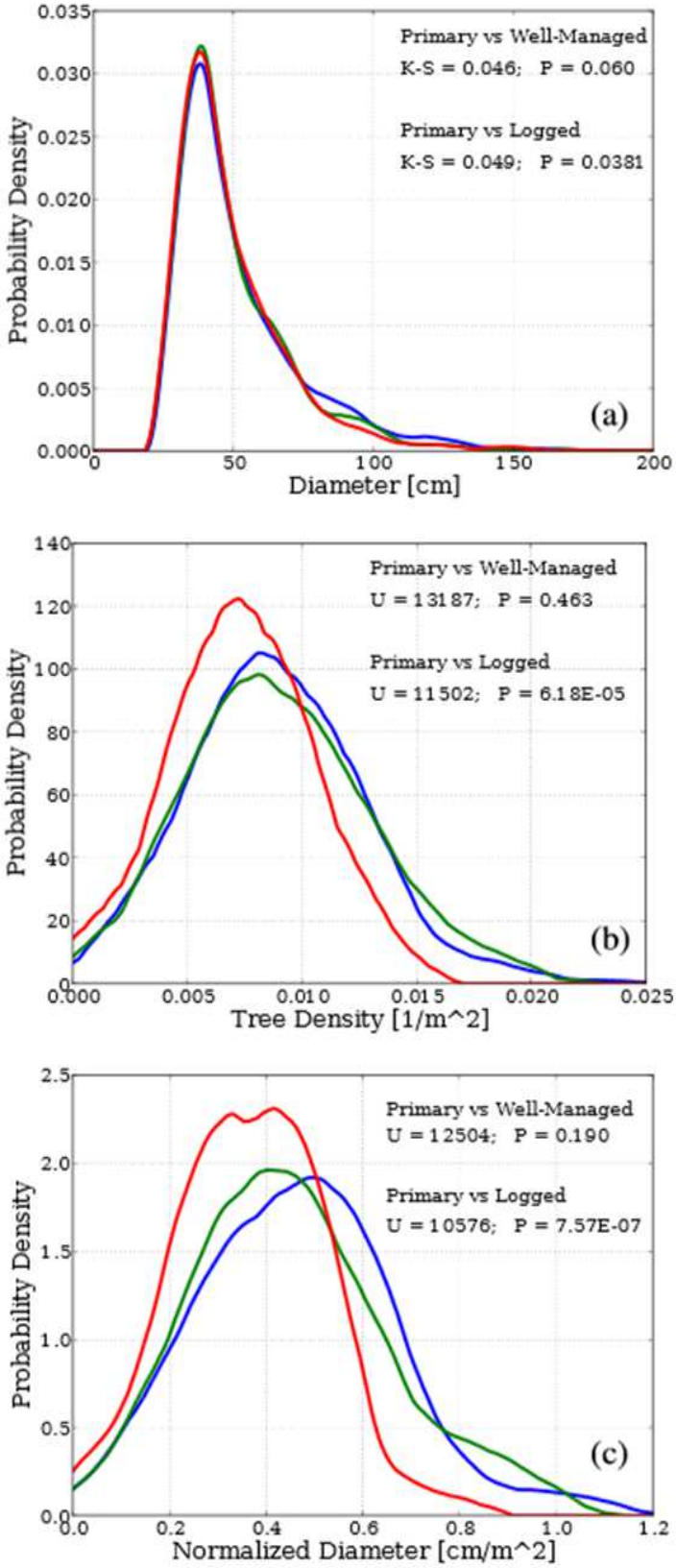

Figure 6. Probability density function (pdf) of data collected in Sierra Leone. a) pdf of trees diameter; b) pdf of tree density; c) pdf of normalized diameter. Blue line: unlogged plots; green line: well-managed plots; red line: logged plots.

Figure 6 shows the results of the statistical analysis of the diameter data of the plots sampled in Sierra Leone. Panel (a) shows the probability density function of the diameter of the trees for the 'Unlogged' (considered as primary forest), 'Well-Managed' and 'Logged' plot types, obtained with a kernel density estimation (the very steep decline to zero on the left side of the curves is due to having sampled only trees larger than 30 cm dbh). The three curves appear very similar to each other, and the *P*-values of the Kolmogorov-Smirnov test confirm that any difference is just marginally significant. The curves, however, do show slight differences for trees above 75 cm dbh, that is in the range of the commercially interesting sizes.

This result is coherent with those of the indices of Figure 1, that also showed just marginally significant differences between primary and the other two forest types.

		Primary vs Secondary			Primary vs Selective		
Indices		*West*	*Central*	*All*	*West*	*Central*	*All*
Mean Height	U	8.0	4.0	25.0	70.	14.0	47.0
	P	-	-	0.034	0.047	-	-
Height 80th Percentile	U	7.0	4.0	23	3.0	7.0	29.0
	P	-	-	0.023	0.008	-	0.006
Mean Biomass	U	6.0	4.0	23.0	3.0	7.0	29.0
	P	-	-	0.023	0.008	-	0.006
Mean Diameter	U	4.0	9.0	33.0	3.0	10.0	34.0
	P	0.026	-	-	0.008	-	0.015
Normalized Height	U	2.0	2.0	13.0	9.0	0.0	12.0
	P	0.09	0.032	0.002	-	0.001	1E-04
Tree Density	U	1.5	1.0	10.5	11.5	0.0	16.5
	P	0.004	0.016	8E-04	-	0.001	4E-04
Normalized Biomass	U	2.0	2.0	12.0	4.0	2.0	15.0
	P	0.009	0.032	0.002	0.013	0.005	3E-04
Normalized Diameter	U	0.0	3.0	16.0	3.0	0.0	4.0
	P	0.002	-	0.005	0.008	0.001	5E-06
Richness	U	2.0	2.5	10.5	5.0	3.0	17.0
	P	0.009	0.032	8E-04	0.021	0.009	5E-04
Shannon Entropy	U	3.0	6.0	21.0	8.0	12.0	38.0
	P	0.015	-	0.016	-	-	0.027
Evenness	U	11.0	9.0	49.0	15.0	11.0	61.0
	P	-	-	-	-	-	-
Vines Cover Fraction	U	0.0	0.0	0.0	0.0	0.0	0.0
	P	0.002	0.008	6E-06	0.001	0.001	4E-07

Table 3. Results of the Mann–Whitney U test comparing plots of primary vs secondary forest (3rd to 5th column) and primary vs selectively cut forest (6th to 8th column) for the indices of Table 2. We apply the test only to the plots from West Africa (3rd and 6th column), or only to the plots from Central Africa (4th and 7th column), or to all plots (5th and 8th column). For each index, the first row reports the values of the U statistics. The second row shows, when it is less than 0.05, the probability that the corresponding U value may occur in two independent samples drawn from the same distribution (null hypothesis).

Panels (b) and (c) show the tree density and the normalized diameter indices. Because of the large number of plots, showing the values scored by each plot with individual markers, as in

Figure 2, would be rather confusing and not very informative. We then opt for showing a kernel density estimate of the probability density function of each index as a function of the index value. It is then visually obvious that the 'Logged' plots score systematically lower values than the 'Unlogged' and the 'Well-managed' plots. This is confirmed by the Mann-Whitney *U* test, which gives vanishingly low values to the null-hypothesis for the pair 'Unlogged' vs 'Logged'. However, it does not show significant differences for the pair 'Unlogged' vs 'Well-managed'.

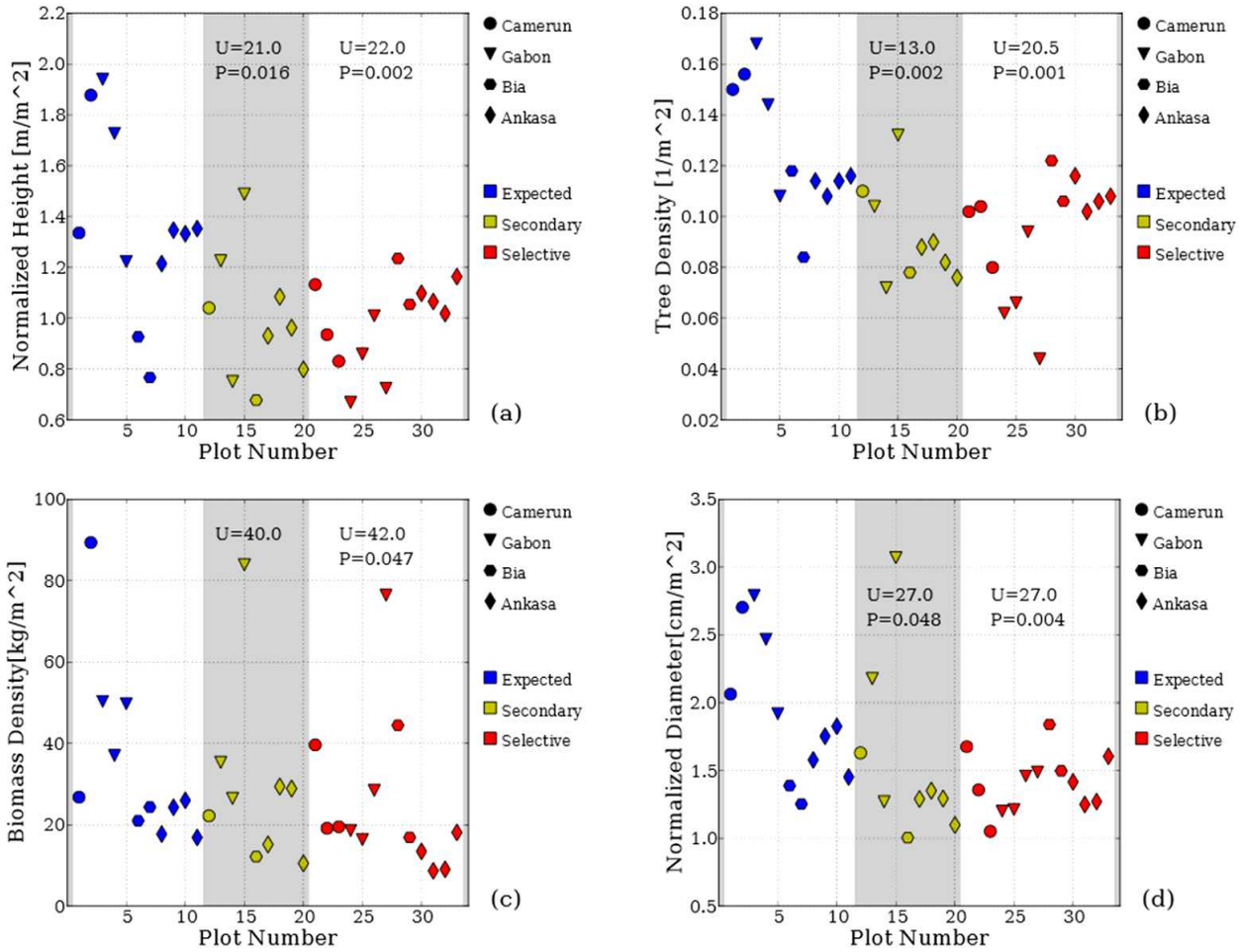

Figure 7. Expected density indices of primary forest *vs* density indices of selective logged and secondary plots. The expected indices are obtaining omitting the two tallest trees of each plot for the normalized height, the two heaviest trees for the biomass density, the two trees with the largest diameter for the normalized diameter, and any two trees for the tree density. Symbols, colors and legends as in Figure 1.

We wonder if the simple removal of tallest trees may have an imp act over time. For this reason we compute, for all the primary forest plots of Dataset 1, the value of the four density indices, but omitting the two tallest trees of each plot for the normalized height, the two heaviest trees for the biomass density, the two trees with the largest diameter for the normalized diameter, and any two trees for the tree density. The reason for this choice lies in the fact that the estimated number of felled trees per plot in the selectively logged plots of

Dataset 1 is 1±0.6. In this way we have a rather pessimistic estimate of what those indices would be *expected* to score, if those plots were subject to a selective logging whose only effect was the disappearance of the two most valuable trees of each plot. We then compare the scores of the *expected* indices of primary forest plots with those of the other two types of forest in Figure 7. In spite of the simulated logging, they remain significantly above the scores of selectively logged plots, except for biomass density, where the difference, albeit existing, is only marginally significant.

A genus similarity index (β-biodiversity) for species recorded in different management types of forests in each study area was calculated using the Incidence-based Sorensen's index. The results of pairwise comparisons are summarized in Table 5. These results cannot be considered as representative of the whole forest ecosystems because they are referring to small sampling plots (500 mq) which do not reach the Species-Areas Curve saturation (67). Anyway, from the calculated indexes we can argue that selective logging forests genus are more similar to those of primary forest than secondary one. However, primary forests plots have more common genus among themselves than if compared to selectively logged areas.

Cameroon (Forest Plot)	**Sorensen Index**	**Gabon (Forest Plot)**	**Sorensen Index**
PF vs SF	0.086	PF vs SF	0.14
PF vs SL	0.348	PF vs SL	0.571
SF vs SL	0.233	SF vs SL	0.116
PF 51 vs PF 52	0.363	SL 63,64 vs SL 65,66	0.415
SL 53 vs SL 54	0.093	PF 57 vs PF 58	0.558
SL 53 vs SL 56	0.325	PF 57 vs PF 59	0.5
SL 54 vs SL 56	0.272	PF 59 vs PF 58	0.592
		SF 60 vs SF 61	0.571
		SF 60 vs SF 62	0.347
		SF 61 vs SF 62	0.465
Ghana - Bia (Forest Plot)	**Sorensen Index**	**Ghana - Ankasa (Forest Plot)**	**Sorensen Index**
PF vs SF	0.363	PF vs SF	0.415
PF vs SL	0.534	PF vs SL	0.552
SF vs SL	0.441	SF vs SL	0.505
PF 71 vs PF 72	0.472	PF 1,2 vs PF 3,4	0.622
SL 73 vs SL 74	0.339	SL 5,6 vs SL 7,8	0.735
		SF 9,10 vs SF 11,12	0.307

Table 5. Sorensen index (SI) for genus similarity (β-biodiversity) of each study areas of the Dataset 1

Discussion and Conclusion

In recent decades, many tropical countries have changed forest resource extraction management from clear cutting to selective logging ([68], [69], [70]), the latter regarded as a management practice that has less dangerous effects on the ecosystem, even though researches are scanty in critically evaluating its impact on forest structure, biodiversity and ecosystem services. To better understand the effect of selective logging on tropical forests, we compare three different types of forest management: primary forest, namely mold-growth/untouched forest; secondary forest, namely forest subjected to clearcutting management; selectively logged forests. The data allow us to form 12 distinct indices (summarized in Table 2) on forest biomass, tree diversity, tree density, etc. that we examine in order to determine which of them show statistically significant differences among the forest types, and which do not.

Our results indicate that the distribution of heights, diameters and biomasses, and the diversity of trees in a logged forest are not largely different from those of a primary forest, while all indices of density show a marked decrease of the logged forest together with the concomitant invasion by vines, climbers and other weeds. In other words, the forest subjected to selective logging does not seem to suffer any effect on its vertical structure but rather shows a well-markable arboreal rarefaction.

The single exception to these findings are the "*well-managed*" plots of the Gola National Park in Sierra Leone (Dataset 2), where the density indices appear to have roughly the same values than in the "*unlogged"* plots. On the other hand, the "*logged*" plots of Gola show a drop in the density indices even though they were logged in the seventies and eighties. This result suggests the key that allows for an understanding of the observed data. In the "w*ell-managed*" plots of Gola the harvesters took care to minimize as much as possible the amount of canopy damage exerted by the logging activities. No such care was taken in the "*logged*" plots. This, in turn, implies that the amount of extra light filtering to the lower forest layers, and to the ground, was limited for "w*ell-managed*" plots, and more abundant and spread out for "*logged*" plots.

It is reasonable to assume that the extra light caused by canopy openings larger than some threshold, triggers a complex chain of effects on the plant community, of which we may guess a few links: (i) young trees of dominant species (such as *Celtis mildbraedii*) taking advantage of the free space and reduced shade due to the removal of parent plants or other logged, tall commercial species, replace some species of the secondary or tertiary layer (e.g. *Baphia nitida*); (ii) many of the shade-intolerant trees, being suddenly exposed to direct sunlight, experience much increased mortality rates, and leave space for vines and weeds such as *Aframomum alboviolaceus, Halopegia azurea, Manniophyton fulvum* and *Haumania*

danckelmania; (iii) vines, climbers and shrubs, in the occasional spots where they manage to become dense enough, suppress the growth of seedlings of typical primary forest species (71). We further investigate this issue by evaluating the *expected* normalized indices, for all the primary forest plots of Dataset 1, namely how would those indices be if plots were subject to a selective logging whose the only effect was the disappearance of the two most valuable trees of each plot.

We notice that, in spite of the simulated logging, they remain significantly above the scores of selectively logged plots, except for biomass density, where the difference, albeit existing, is only marginally significant. This result suggests a scenario where the logging damage, unless the harvesting is extremely careful, non only persists for decades after the logging, but in some respects (e.g. tree density, normalized diameter, normalized height) becomes worse with time.

If, as a consequence of logging activities, a portion of forest remains locked for decades in a low-density, vines-rich state, undoubtedly there will be effects on its biodiversity. However, those effects may be such to escape easy quantification. At the scale of the plots most species appear only once or twice, regardless of the forest type. Therefore entropy and evenness give very high scores. Richness of the plots appears to drop for logged forests, and this may easily be explained by the reduced density of the forest: a lower number of trees per plot inevitably leads to a reduced number of species, if each species is represented only once or twice (singletons or doubletons).

Among the possible causes of reduction of plant species at the forest-wide scale, there may be changes in the density of suitable animal dispersers, directly or indirectly linked to forest alterations induced by logging activities (Brodie et al 2009; Brodie & Gibbs 2009). In Central Africa, this phenomenon can be due to the reduction of herbivorous populations which are important for seed dispersal. Because many pioneer species are wind dispersed, clear-cutting encourages the establishment of plants which are wind dispersed. These include *Funtumia elastica* and *Terminalia superba*, which were responsible for 65% of the total abundance of the SF in one study performed in Cameroon ([72]). Furthermore, the elimination of species such as those belonging to the genera *Entandrophragma*, *Ceiba*, *Triplochiton* and *Erythrophleum*, removes the main feeding sites of arboreal monkeys and nesting sites of hornbills, which are both important seed dispersers.

Finally, let us say a few words about the plots in secondary forests. In this paper, we present a pairwise comparison between primary forest vs. forest subjected to selective logging and between primary forest and logged ones. Apparently, looking the figures on normalized biometrics (dbh and heigh) and biomass (Figure 1, 2 and 5) this two types of forest management are very similar between them. Anyway the loss of species and the resetting of

the long-term ecological successions of a tropical forest make clearcutting obviously to be the worst in terms of conservation. This is clear analysing the Sorensen values (Tab. 5) which show genus similarity higher (sometimes close to 1) among secondary forest plots themselves than if compared to primary ones.

We can no longer assume that, following selective logging, the forest ecosystem recovers on a trajectory towards its primary (pre-disturbance) state. This research suggests instead that, although in most of the plots analysed only a few commercial trees per hectare are removed, a large structural alteration of the entire ecosystem causes the decline of biodiversity and ecosystem services. Moreover, we wonder if the selective logging cycle of 30 years (the years since logging of most of our plots), commonly used in tropical timber harvesting, is sufficient for a complete recovery of the forest structure and it seems to alter the ecosystem hugely.

It is very likely that changes of the dynamics of niches consolidated over hundreds or thousands of years ([73]) in tropical forests due to the removal of certain key tree species lead to the development of dynamics that decrease the integrity of the system (density-dependent effects). Further investigations on later effects (>50 years after logging) could shed light on these dynamics. Moreover, we showed that the structural changes, vines/weed/climbers growth and alteration of the dynamics among species belonging to different layers are the main consequences of the logging and a clear explanation of the observed effects on biodiversity (74) and carbon stocks. At the same time, the reduction of populations of large herbivorous mammals, the prevalence of wind-dispersed seeds and the increased competition between shade-tolerant species when exposed to sunlight in the forest that have been logged selectively, could be contributory factors that are collectively significant in explaining the effects documented.

Summarizing, this paper suggests that selective logging has several important negative effects on forest structure, dynamics, biodiversity and ecosystem services and that these effects can be truly evaluated only in the long term by analysing the evolving dynamics of repeated logging and not the mean structural values but the normalized indices

The attention should be paid not just to totally destructive practices such as deforestation (clearcutting) for alternative land uses (crops or grazing, commonly in the Amazon, or the palm oil plantations that are typical of South-east Asia), but also to the selective logging of the last virgin forests of Africa, which may be a more serious cause of forest degradation than what has been thought to date. These first results suggest that it will be crucial to increase research about the key question for forest management and conservation: is selective logging really sustainable for primary tropical forests?

Acknowledgments

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Cameroon	PFP	PFH	SL20	SL30	SF20	SLD
Richness (s/500mq)	30	23	25	23	10	22
Richness expected	28,4					
Shannon diversity index	2,788563	2,740624	2,961067	2,78235	1,51032	2,813273
Abundance (n/500mq)	77	80	51	52	55	40
Evenness	0,819877	0,874064	0,919907	0,887372	0,655924	0,910137
Biomass (kg)	25742,91	65711,19	19821,34	9571,725	11106,68	9763,318
Carbon (kg)	12099,17	30884,26	9316,031	4498,711	5220,138	4588,76
Biomass expected (kg)	16045,21					
Biomass variation %	100%	/	76,99729	37,18198	43,1446	37,92624

Gabon	FP	SF40	SL5	SL15
Mean Richness (s/500mq)	33,66667	25,66667	17,5	22,5
SD richness	6,429101	2,516611	3,535534	9,192388
Richness expected	32,06667			
Mean Shannon	3,348375	3,205337	2,771024	3,069942
SD Shannon	0,036405	0,113353	0,21976	0,420521
Mean Abundance (n/500mq)	72	57,2	32	34,5
SD Abundance	15,09967	13,31165	1,095445	13,69306
Mean Evenness	0,963701	0,996965	0,992501	1
SD evenness	0,056531	0,002689	0,001949	0
Mean Biomass (kg)	43890,38	24287,34	8728,983	26215
SD biomass	16473,65	15459,31	781,2501	16961,58
Mean Carbon (kg)	20628,48	11415,05	4102,622	12321,05
SD Carbon	7742,616	7265,874	367,1876	7971,943
Biomass expected (kg)	28011,83			
Biomass variation %	100%	55,33636	19,88815	59,72836

Supplementary Table 1. Data on biomass, biodiversity and carbon stocks (Mg/ha) of trees in Database 1. Expected biomass is calculated as primary forest biomass minus the mean of the highest biomass value for trees in primary forest plots. Expected biodiversity is evaluated as mean richness of the primary forest plots minus 1,6 species (assuming that the logging at the highest estimated rate involve singletons). Carbon stocks and percentage variation are derived from observed biomass (biomass*0.47).

Ghana (Bia)	PFP	PFH	SL20	SL30	SF20
Richness (s/500mq)	38	23	33	25	25
Richness expected	36,4				
Shannon diversity index	3,295296	2,850265	3,097363	2,841976	3,098835
Abundance (n/500mq)	61	44	61	53	39
Evenness	0,912592	0.9090321	0.88584465	0.8722812	0.96270704
Biomass (kg)	94250,41	27230,26	22228,49	8451,275	6085,839
Carbon (kg)	44297,7	12798,22	10447,39	3972,099	2860,344
Biomass expected (kg)	68208,33				
Biomass variation %	100%	/	23,5845	8,966831	6,457095

Ghana (Ankasa)	FP	SL	SF
Mean Richness (s/500mq)	32,25	21,5	17,5
SD richness	4,924429	1,290994	6,403124
Richness expected	30,65		
Mean Shannon	3,317179	3,015	2,4525
SD Shannon	0,216518	0,108474	0,405576
Mean Abundance (n/500mq)	58,5	54	42
SD Abundance	1,566699	2,662876	2,860388
Mean Evenness	0,935474	0,92	0,87
SD evenness	0,457389	0,024495	0,037417
Mean Biomass (kg)	16747,45	2467,052	3868,12
SD biomass	7985,001	2966,263	5505,769
Mean Carbon (kg)	2889,054	1159,515	1818,016
SD Carbon	3752,95	1394,144	2587,711
Biomass expected (kg)	12615,37		
Biomass variation %	100%	14,73091	23,09677

Supplementary Table 1. Data on biomass, biodiversity and carbon stocks (Mg/ha) of trees in Database 1. Expected biomass is calculated as primary forest biomass minus the mean of the highest biomass value for trees in primary forest plots. Expected biodiversity is evaluated as mean richness of the primary forest plots minus 1,6 species (assuming that the logging at the highest estimated rate involve singletons). Carbon stocks and percentage variation are derived from observed biomass (biomass*0.47).

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CHAPTER 2

A model for localized disturbances in tropical forests*

Abstract: Tropical rainforests are among the most threatened ecosystems by large-scale fragmentation due to human activity such as heavy logging and agricultural clearance. Although, they provide crucial ecosystem goods and services, such as sequestering carbon from the atmosphere, protecting watersheds and conserving biodiversity. In several countries forest resource extraction has experienced a shift from clearcutting to selective logging to maintain a significant forest cover and understock of living biomass. However the knowledge on the short and long-term effects of removing selected species in tropical rainforest are scarce and need to be further investigated.

One of the main effects of selective logging on forest dynamics seems to be the local disturbance which involve the invasion of open space by weed, vines and climbers at the expense of the late-successional state cenosis. We present a simple deterministic model that describes the dynamics of tropical rainforest subject to selective logging to understand how and why weeds displace native species. We argue that the selective removal of tallest tropical trees carries out gaps of light that allow weeds, vines and climbers to prevail on native species, inhibiting the possibility of recovery of the original vegetation. Our results show that different regime shifts may occur depending on the type of forest management adopted. This hypothesis is supported by a dataset of trees height and weed/vines cover that we collected from 9 plots located in Central and West Africa both in untouched and managed areas.

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Introduction

Tropical forests provide crucial ecosystem goods and services, such as sequestering carbon from the atmosphere, protecting watersheds and conserving biodiversity. Around 40% to 75% of all biotic species are indigenous to rainforests, half of all the living animal and plant species on the planet live there and about two-thirds of all flowering plants can be found in rainforests.
Tropical forests are among the most threatened ecosystems by large-scale fragmentation due to human activity such as heavy logging and agricultural clearance. Actually the area covered by rainforests around the world is rapidly shrinking. Up to date most studies into the impacts of land use in tropical ecosystems on the global carbon cycle and conservation of biological diversity have focused on deforestation (1).
In several countries forest resource extraction has experienced a shift from clearcutting to selective logging (2; 3; 4). In some regions of the World such as Africa, "selective logging" is of great importance because allows to maintain a significant forest cover and understock of living biomass. Selective logging (i.e. the practice of cutting down one or two largest trees while leaving the rest intact) is increasingly embraced as an approach which protects the integrity of forest ecosystems while allowing an appropriate use of resources. This is a concept specifically designed to reconcile the different interests in forests, including the maintenance of biodiversity (5, 6). However, several studies in tropical forests subject to selective logging have shown changes in species composition (7, 8, 9, 10), genetic diversity (11), forest structure (12, 13) and nutrient cycling (14).
However the knowledge on the short and long-term effects of removing selected species are scarce and need to be further investigated.
One of the main effects of selective logging on forest dynamics seems to be the local disturbance which involve the invasion of open space by weed, vines and climbers at the expense of the late-successional state cenosis (15). In secondary forests (regrowth of clearcutted areas), instead, the development of light-demanding species does not involve vines and weeds, being the secondary succession restarted directly from the pioneer tree stage towards climax. There are some evidence that tropical forests subject to selective logging have suffered a decline of biodiversity, both of animals and plants species (16, 17, 18, 19).
Weeds, vines and climbers forest species exhibit a well-known range of ecological roles (20) and are fundamental components in forest dynamics with respect to natural disturbance regimes, from pioneer phase to mature phase, and they regenerate from a range of sources, including dormant seeds, seed rain, pre-established juveniles, and resprouts from damaged adults (21). Most of weeds, vines and climbers are uncommon in old-grown forest ecosystems.

Disturbance plays a critical role in weed invasions in rainforests because it creates opportunities for weeds to claim previously utilised space and resources. Rainforest weeds rarely tolerate shade, so some kind of minor disturbance resulting in an opening of the canopy is usually necessary for weed establishment. Typically, fragmentation and selective logging open up gaps of light in which weeds displace or suppress native species. Otherwise, in natural gaps (e.g. due to big broken branch or naturally died trees) the light space created is usually smaller than in logging gaps and tree saplings seems to be prepared to grow fast to fill the canopy opening (22, 23, 24, 25, 26). This reduce the likelihood of vines, weeds and climbers invasion (27, 28).

In this work we will derive a simple model to describe the dynamics of tropical rainforest subject to selective logging. For this purpose we developed a quantitative, deterministic model that describe the dynamic of tropical trees coexisting with weeds, vines and climbers. We argue that the selective removal of tallest tropical trees carries out gaps of light in which weeds, vines and climbers can grow suppressing the sprouting tress. This hypothesis is supported by a dataset of trees height and weed/vines cover that we collected from 21 plots located in Central and West Africa both in untouched and managed areas. To our knowledge, this is the first mathematical model that builds on those experimental findings to quantitatively explain the presence of weed on forest subject to selective logging. The model is embodied with two simple ordinary differential equations and does not explicitly describe the spatial structure of the forest. Our results show that different regime shifts may occur depending on the type of forest management adopted.

Materials and methods

This work is based on the concept of the vertical structure of the forest. We mean to “structure” as the vertical composition and stratification of vegetational layers, from the understory to the highest trees. In this sense the vertical structure of a forest may be described by some statistical parameters of height distribution of the tress, like the mean, the standard deviation or a specific percentile. We consider that a forest is well structured when the distribution of trees heights is wide and heterogeneous. Vice versa we consider forest as unstructured when the distribution of the trees heights is concentrated into a small range and the variability is quite low. For the purpose of our work we introduce a vertical vegetational structure index (h) ranging from 1, the maximum value corresponding to a proxy of a well conserved old-growth tropical forest, to 0, the minimum value corresponding to a proxy of a highly damaged forest (e.g. clearcutted). Intermediate values of h should indicate that the forest has decreased its height of some

amount, but the largest contribution to the index must be given by the tall trees. Therefore, a herd of elephants cutting a path below the (untouched) high canopy, should decrease by little or no amount the value of h, while the selective logging of commercially-valuable trees, which are the tallest in the forest, should decrease h by a sizable amount. Such Index may represent a single statistical parameter (e.g. mean canopy height or the standard deviation) as well as a indicator of the combination of more parameters. In this case study, because we are interested to the effects on long term of the selective removal of higher tress, we assign to the vertical structure index (h) the mean of trees height over the 80° percentile. Nevertheless other statistical parameters will be compared and some discussion will be carried out.

The Model

The model includes two state variables: the forest vertical index (h), based on the height distribution of the trees over the 80° percentile, and the weeds, vines and climbers cover (q). In the absence of any other disturbance, when empty space becomes colonized by a forest, we shall assume that the index h is subject to the following simple dynamics:

$$\frac{dh}{dt} = r(h)h$$

where the growth rate r is a decreasing, continuous function of h, it reaches a positive maximum for h = 0, and becomes zero at h = hmax. It is convenient to rescale all the quantities by using $[r(0)]^{-1}$ as the unit of time and hmax as the unit of h. Therefore, the above assumptions on r can be summarized as: $r(0) = 1$; $r(1) = 0$; $r'(h) < 0$.

Because of the vines growth only in gaps of light into structured forest, we take into account three basic assumption: i) the carrying capacity of the vines in a untouched forest (values of h lose to hmax) is quite zero; ii) weeds, vines and climbers cannot growth after a clearcutting , indeed there are evidences that the forest returns to its natural composition after such managing. So we assume a low (or even zero) carrying capacity of weed vines and climbers at h=0; iii) if the upper canopy of the forest is removed without damaging the lowest trees, one or more spots with enough light will appear at the lower levels of the forest, without undo (or shatter ?) the vertical structure. Therefore, we are lead to conclude that the carrying capacity of the vines has a maximum at intermediate values of h.

The above discussion leads to the following conceptual model for the coexistence of forest and vines:

$$\begin{cases} \frac{dh}{dt} &= (r(h) - \alpha q)\ h \\ \frac{dq}{dt} &= \epsilon \left(1 - \frac{q}{K(h)}\right) q \end{cases}$$

where q is the biomass of vines per unit area, ε is their maximum growth rate, and the function K is the h−dependent carrying capacity of the vines, which shall be a positive function for h >0 but may be zero if h = 0. The constant α determines the damping strength of the vines on the (re)growth of the forest.

Study sites

We collected data on vines, weed and climbers densities and tree heights in tropical forests of West and Central Africa. In West Africa forest plots were selected along the border between Ghana and Ivory Coast (Bia National Park and surrounding areas). In Central Africa forest plots were selected within the Congo river basin, on the border between Cameroon and Central African Republic (Sangha Tri-National Forest).

The first study area, Bia National Park, is part of a protected area of 306 km^2, which comprise 77.7 km^2 of national park in the north, and 227.9 km^2 of Resource Reserve (where logging is permitted) in the south. The area is located in the transition zone between the southern mixed evergreen forest and northern mixed semi-deciduous forest. The average annual precipitation ranges from 1500 mm to 1800 mm and the average monthly temperatures range between 24° and 28°C, with the rainy season during the months of May, June, September and October. More than 300 plant species per hectare can be observed; species from the *Makore*, *Dahoma*, *Khaya* and *Marantis* genera are widespread. The second study area in Central Africa is bordered to the east by the Sangha River, an affluent of the Congo River, and it belongs to the Sangha Tri-National Protected Area (STN). The park covers an area of 1,838 km^2 with an altitude ranging between 300 m and 750 m above sea level. The area consists of semi-evergreen forests, with over 300 species of trees, the largest ones including *Ceiba pentandra* (L.) Gaertn, *Terminalia superba* Engl. & Diels and members of the family *Sterculiaceae* (*Triplochiton*, *Pterygota*). The average annual precipitation is 1400 mm, with the dry season occurring from December to February.

In all the study sites, the commercial tree species most commonly harvested are *Enthandrophragma cylindricum* K. Schum, *Terminalia superba* Engl. & Diels *Triplochiton scleroxylon* Sprague and *Heritiera utilis* (Sprague) Sprague. A typical selective logging scheme includes the harvest of trees with diameters bigger than 30–100 cm and logging cycles of 15–30 years. For example, in Central Africa the minimum diameter is 100 cm for *Enthandrophragma cylindricum*, 60 cm for *Terminalia superba* and 80 cm for *Triplochiton scleroxylon* and logging cycle is 15-30 years .

Plots Selection and Data recordering

To identify and outline the sample plots we performed the following protocol: i) the study areas were surveyed to detect each forest category (primary, secondary and selectively logged); ii) 9 plots of 500 m^2 were selected at a minimum buffer distance of 50 m from access roads and logging trails. The selected plots included 2 primary old-growth forests (PF), 5 areas subject to selective logging (SL) and 2 areas subject to clear-cutting in the 1990s and then left to recover (SF); iii) in each plot corners coordinates were collected with a GPS.
For each plots we recorded genus/species name, tree position into the plot and trees height by a laser hypsometer-dendrometer.

Results

Data Analysis

The evidences of the leading role of taller trees on forest structure are shown in Figure 3. The standard deviation of the mean canopy height of the untouched forests (green markers) is higher than those subject to selective logging (red markers), that is, the inviolate forests show greater variability in the distribution of heights.
With regard to the basic assumption of the model listed abov, the data collected give rise to our hypothesis: the correlation between the average of trees height over the 80° percentile and weeds/vines/climbers is quite strong in plots subject to selective logging but not for those subject to clear cutting. In forests subject to clear cutting the weeds/vines/climbers are almost absent, indicating that they do not have important ecological roles in deforested site.
Also the correlation between the mean canopy height and weeds/vines/climbers, although less strong, is not deniable in the pltos subject to selective logging. This result is reasonable since the arithmetic mean takes into account all trees present into the plot and in tropical forests the tallest tree are also the rarest one.

Equilibria

The system of equations 2 has the trivial fixed point $h_o=q_o=0$, corresponding to the absence of both forest and vines. Other fixed points satisfy the following algebraic equation:

$$q_o = K(h_o) = \frac{r(h_o)}{\alpha}$$

In other words, an equilibrium occurs when the growth rate of the forest, rescaled with the damping term α equals the carrying capacity of the vines.

On the other hand, if the upper canopy of the forest is removed without damaging the lowest trees, many more gaps with enough light will appear at the lower levels of the forest, without damaging too much the quality of the soil. Therefore, we are lead to conclude that the carrying capacity of the vines has a maximum at intermediate values of *h*.

In other words, an equilibrium occurs when the growth rate of the forest, rescaled with the damping term α equals the carrying capacity of the vines.

Depending on the shape of the functions K and *r*, the condition 3 may be satisfied never, once, or more than once. Figure 1 shows a case with one non-trivial equilibrium (dashed magenta line), and a case with three non-trivial equilibria (solid magenta line). For simplicity, we have used $r(h)=(1-h)$ and $K(h)=\beta h^2 e^{-\gamma h2}$, with suitable values of the constants β, γ. If our assumptions on the general shape *r* and *K* are correct, three intersections should be not uncommon. This is the interesting case for our discussion. When there are three non-trivial equilibria, linear stability analysis shows that the equilibrium having intermediate values of h_o and q_o is unstable, and, in particular, it is a saddle. The equilibria having low ho and high *qo* (unhealthy forest with dominance of the vines), and high h_o and high q_o (healthy forest with few vines), are stable. The phase state of the system is partitioned into two basins of attractions by the stable manifold of the saddle equilibrium (the U-shaped blue line in Figure (2)). All the orbits starting from the states into the “U” region of the phase space converge to the unhealthy forest equilibrium, and the orbits from the states outside that region converge to the healthy forest state. The particular choice of *r* and *K* does not affect much this partitioning, as long as there are three non-trivial equilibria (two stable ones, and a saddle in between them), and that *K(0)* is sufficiently small. If *K(0)* has a sufficiently high value, I have numerical evidence that a global bifurcation occurs, in which the left-side branch of the stable manifold of the saddle point originates from the trivial fixed point rather than from infinity. In this case, the states

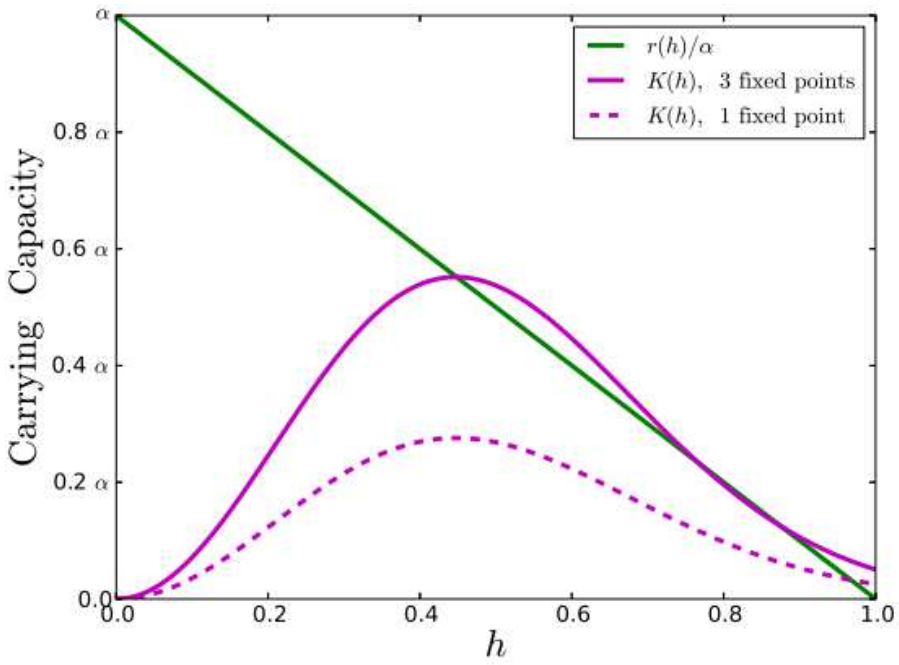

Figure 1: Non-trivial equilibria of model (2) are determined by the intersections between the rescaled forest growth rate $r(h)/\alpha$ (solid green line) with the carrying capacity $K(h)$ of the vines (solid and dashed magenta lines). Two examples are shown: the solid magenta line is a case where the vines carrying capacity is high enough at intermediate values of h as to have three non-trivial equilibria; the dashed line is a case where there is only one non-trivial equilibrium, attained at almost full forest height, and very low vines concentration.

with low values of *h*, but sufficiently high value of *q* will originate orbits converging to the unhealthy forest fixed point.

Discussion and Conclusion

The action of cutting the highest trees leaves the forest with a much lowered value of *h*, but changes little the density of the few vines present in the healthy forest. In other words the cut moves the system along the horizontal dashed line in Figure (2). If the drop in *h* is large enough, the new state (represented by the star at the left end of the dashed line), may belong to the basin of attraction of the unhealthy forest state. Therefore, as time passes, the forest does not recover to a healthy state, but falls into the unhealthy, vine-infested one. It is possible that even the removal of a single big tree is enough to locally move the system to the unhealthy forest basin of attraction (by locally, I mean on a surface of a few thousand square meters). The possibility of recovery, then, depends on the ability of the surrounding healthy forest to invade the unhealthy spot. This calls for an explicit spatial modelling. On the other hand, the action of a fire, or other catastrophic events that destroy most of the biomass in the forest, including the vines, moves the system lose to the origin (the star in the lower left corner of Figure (2)).

Because of the basin of attraction of the unhealthy forest fixed point does not extend up to the axis *h=0* (it is U-shaped) all states having sufficiently small h belong to the basin of attraction of the healthy forest fixed point. From the data collected on canopy height and plant diversity, we have the evidences of a decreasing of plants diversity in tropical forest subject to selective logging respect to the same but untouched forest. Although up to now there is not a well defined correlation between canopy height and biodiversity (which is discussed in Chapter 3) it is clear that the highest levels of biodiversity reside in the untouched forests.

This finding calls for an urgent adaptation and mitigation response aimed at protecting and enhancing the forest conservation through specific interventions, both in terms of policy and management and regulatory mechanisms, to prevent human pressure on tropical areas. Our work confirms the importance of using dynamic, deterministic models for identifying vulnerabilities and thresholds while assessing the impacts of anthropogenic activities. We believe that in the future approaches like this model will have a wider use because they provide simple and clear instruments to policy makers and planning institutions for decision making.

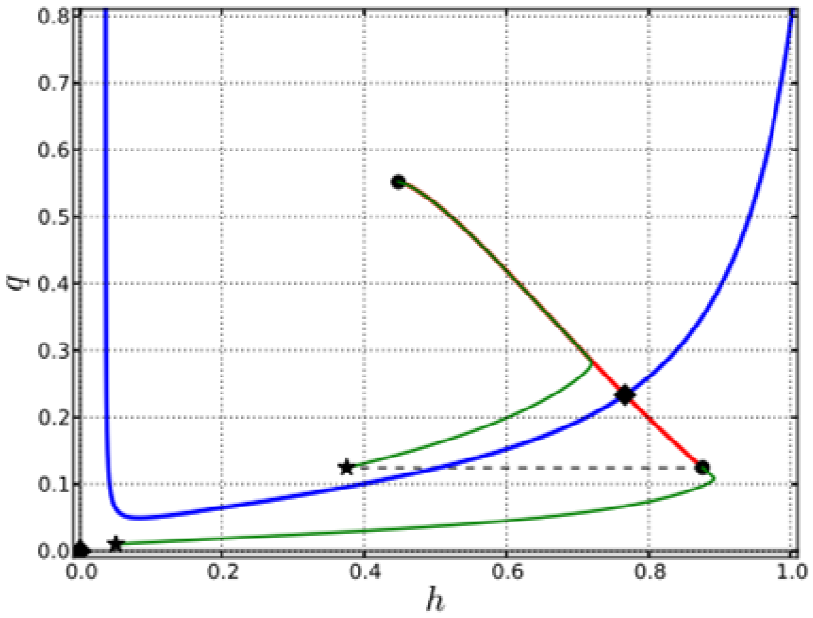

Figure 2: Phase space of model (2) for the case of the solid magenta line in Figure (1). Unstable equilibria are marked by black squares, stable equilibria by black dots. The equilibrium corresponding to intermediate forest height and intermediate vines density is a saddle. Its two unstable manifolds (solid red lines) connect with the two stable equilibria. Its two stable manifolds (solid blue lines) come from infinity. One of them goes close to the trivial equilibrium, without reaching it. Two initial conditions (black stars) belonging to separate basins of attractions are shown, together with the orbits originating from them (thin solid green lines). The thin dashed black line represents the process of removing the tall, commercially-valuable trees, bringing the system from the healthy forest state (lower right black dot) to a state (the star furthest from the origin) which has essentially the same vine density, but a much lower value of h, and that belongs to the attraction basin of the unhealthy forest (upper left black dot). A forest fire would destroy both forest and vines, moving the system to a state (the star closer to the origin) which still is in the basin of attraction of the healthy forest fixed point.

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CHAPTER 3

The global correlation between canopy height and biodiversity*

Abstract: Stratification has important implications in sun detection and microclimate formation within forests. Many observations suggest that there might be an optimum height for the emergent and mid-story trees, reached by responding to signals in the environment. Therefore, it is not surprising that diversity is higher in a forest where different species can spread their crowns over a single point on the ground. We combined data derived from the new global canopy map developed by NASA through the LiDAR survey of Earth and the global map of vascular plant produced by the Nees-Institut für Biodiversität der Pflanzen. Here we show that there is a global positive correlation between forest canopy height and biodiversity and that it follows a latitudinal gradient.

*in preparation as "Gatti Cazzolla R., Paparella F., Valentini R., Di Paola A., *The global correlation between canopy height and biodiversity*"

Introduction

Forest are well known to be organized in a vertical dimension (1). Temperate forests are often poor stratified where tropical rainforests consist of emergent trees, a dense foliage below them and several other layers (treelets, shrubs, lianas) until the herbaceous plants on the ground level (2, 3). The vertical order of forests is a consequence of a predictable allometric rule (4), a design constraint and the tendency of plants to allocate their resources efficiently (5). In fact, most trees will not bloom and bear fruits until they reach a certain height avoiding to be suppressed by neighbours during their growth (6). Stratification has important implications in sun detection and microclimate formation within forests (7). Many observations suggest that there might be an optimum height for the emergent and mid-story trees, reached by responding to signals in the environment (8). Therefore, it is not surprising that diversity is higher in a forest where different species can spread their crowns over a single point on the ground (9). The superimposition of many crowns is one of the mechanism that contributes to the high diversity of plant species in forests (10). However, the vertical dimension can allow high diversity only where the climate and soil conditions permit trees to attain large stature (11). Up to now difficulties to detect tree's height by ground, lack of global canopy data and incomplete flora census has impeded to define general patterns of forest structure and biodiversity. The recent developments of powerful technologies, such as Light Detection and Ranging (LiDAR), and the enrichment of databases of vascular flora allows to develop analyses on global scale on these relations in forest ecosystems. Here we show that there is a global positive correlation between forest canopy height and biodiversity and that it follows a latitudinal gradient.

Materials and Methods

We combined data derived from the new global canopy map developed by NASA through the LiDAR survey of Earth (12; 13; 14, Figure 1) and the global map of vascular plant produced by the Nees-Institut für Biodiversität der Pflanzen (15, Figure 2). The global map of canopy height is has a 1 km spatial resolution, using 2005 data from the Geoscience Laser Altimeter System (GLAS) aboard ICESat (Ice, Cloud, and land Elevation Satellite). The map models the forest vertical structure and reveals a global latitudinal gradient in canopy height, increasing towards the equator, as well as coarse forest disturbance patterns.

The biodiversity map gives an overview on continental to global patterns of land plant diversity. It focus on vascular plants, comparing diversity patterns of large sub-groups like ferns, gymnosperms, or angiosperms. The datasets classify vascular diversity as Diversity

Zones (DZ) expressed as number of species per 10000 km^2 and divide them in 10 diversity classes. Datasets properties are summarize in Table 1.

We converted the biodiversity map (shape file) in a raster data with a resolution of 0.9x0.9 degrees, which is 100x100 km at the Equator. This resolution is an integer multiple of that of Canopy Height map (0.0083x0.0083 degrees, 1x1 km ca. at the Equator). We resampled the high-resolution spatial grid of the Canopy Height on the coarser grid of biodiversity. This allows us to compare the two datasets and carried out some analyses. We selected the maximum geographical common area covered by the data within the maps: 55° S – 83° N.

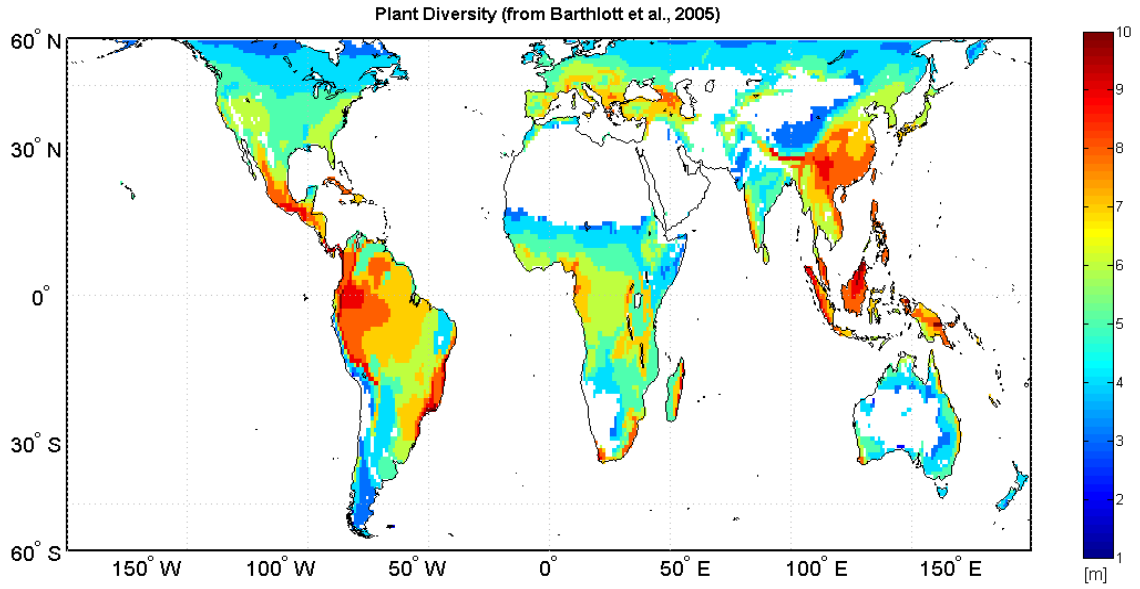

Figure 1 Global map of vascular plant diversity (o to 10 biodiversity classes, incremental)

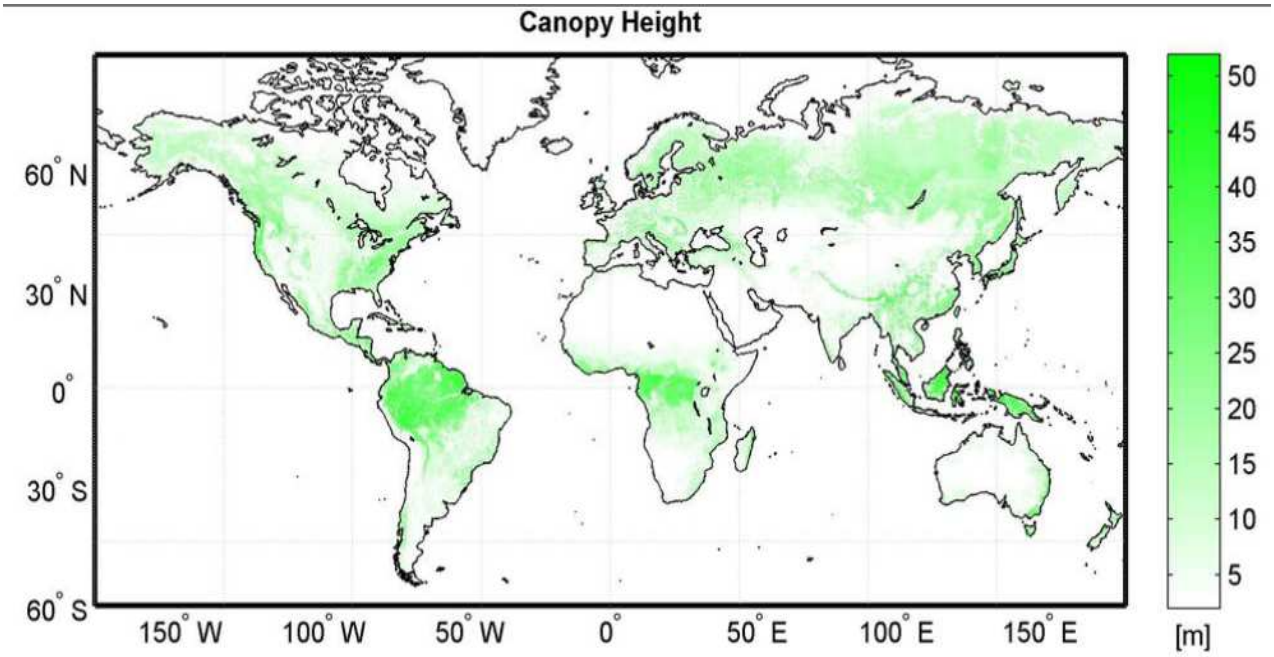

Figura 2 Global map of canopy height derived from LiDAR survey (NASA)

Title	Canopy Height Map (Ch)
Institution	Nasa
Data-type	Grid
Dimention	21600*43200 pixel
Geographic Coordinate System:	GCS_WGS_1984
Geospatial lat_min, lat_max, lon_min, lon_max	 +90.00138889, -89.99853911, -180.00138889, +179.99846711
Geospatial resolution	0.0083°* 0.0083°
Fillvalue	-9999; type: integer (2 bytes)
Main Attribute	Canopy Height
Units	Meters [m]
Format	Tiff (.tif)

Title	Plant Diversity Map (B)
Institution	Nees-Institut für Biodiversität der Pflanzen
Data type	Shapefile Feature Class
Geometry type	Poligon (curve di Livello che individuano 10 classi di Biodiversità)
Geographic Coordinate System:	GCS_WGS_1984
Geospatial lat_min, lat_max, lon_min, lon_max	 -55.07 +83.60 -180.00 +180.00
Unit	Class (from 1 (min Biodiversity) to 10 (Max Biodiversity)
Format	ArcGis® Shape (.shp)

Table 1 Datasets properties of the canopy height map and biodiversity map

Results

We show four different results derived from data analyses and correlations.

The first result is the observation of the correlation and data along the latitudinal gradient, which is one of the most investigated rule of biodiversity in relation to climate, biomass, productivity, number of niches, etc.

We projected the mean biodiversity value (hereto, species richness; red line in Figure 3) with the mean value (green line in Fig. 3), standard deviation from mean (clear green area) and

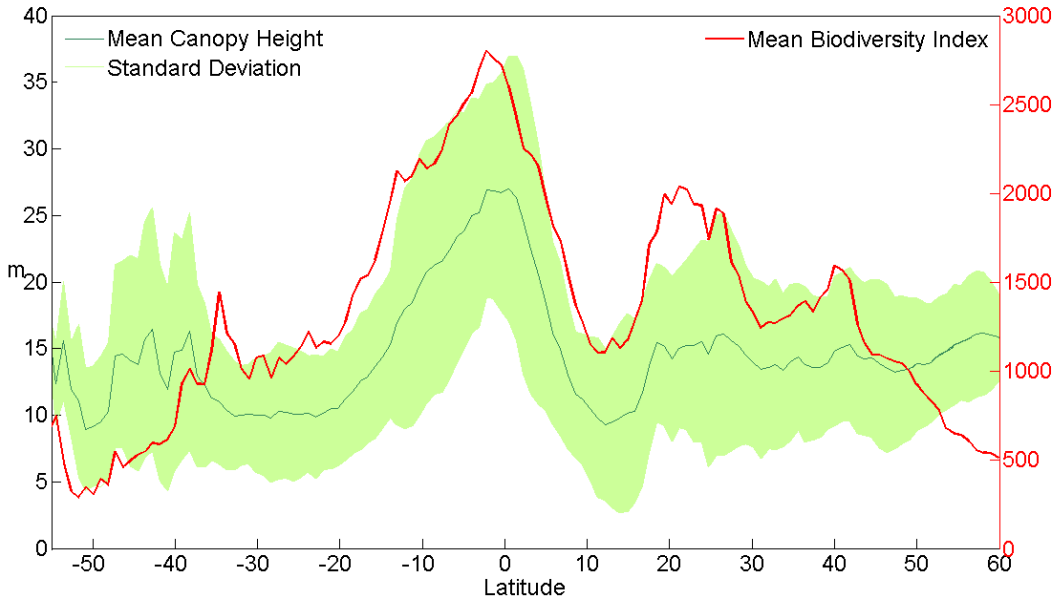

Figure 3 The mean biodiversity value is projected with the mean value (green line), standard deviation from mean (clear green area) and maximum (dotted black line) of the canopy height.

maximum (dotted black line) of the canopy height.

Secondly, we derived the same indices of canopy height from the previous analysis (mean, standard deviation, height max) and we correlate them with biodiversity values. In order to obtain an index able to represent the hypervolume of an ecosystem niche we computed the mean height to the 3rd power (to the cubic power). Correlation results are summarized in Figure 4.

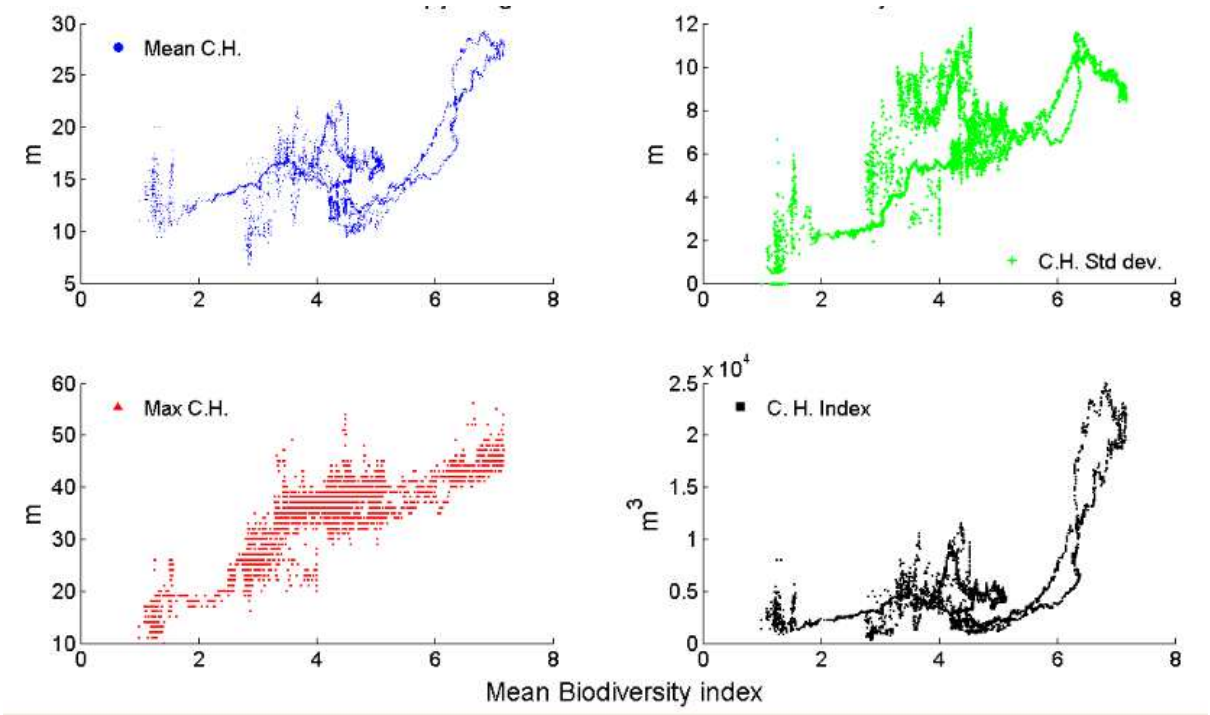

Figura 4 Correlations between mean biodiversity index and canopy height (C. H.) indices

The third result we obtained derives from the relation between canopy height and biodiversity within each class of diversity (instead to use the mean value of it). We selected some sample areas from each continent of Earth and we observed the height data distribution for each diversity class. In Figure 5 we show a clear correlation ($0.76<R^2<0.97$) between mean height and biodiversity in each study areas. The regression is not always linear because residuals are not randomly dispersed.

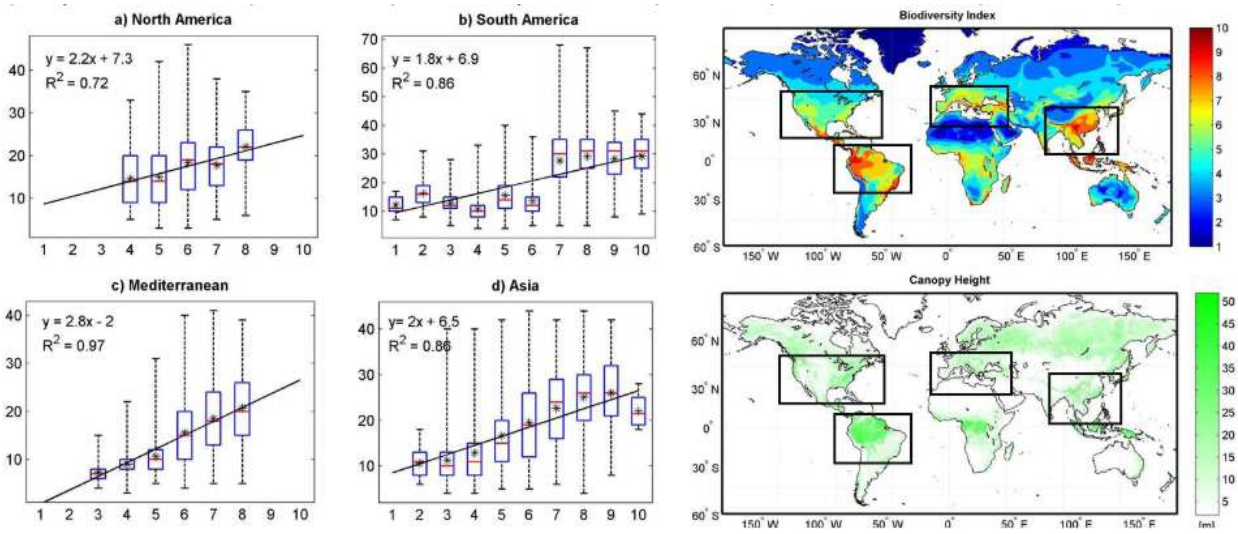

Figure 5 Sampling areas canopy height values plotted against biodiversity classes (red line, median; blue box, 25%-75% percentile; bar errors, maximum and minimum value)

Then, we plotted the mean canopy height values against biodiversity classes of latitudinal gradient transects of 15°. Again, we in Figure 6 show a clear correlation between the two parameters.

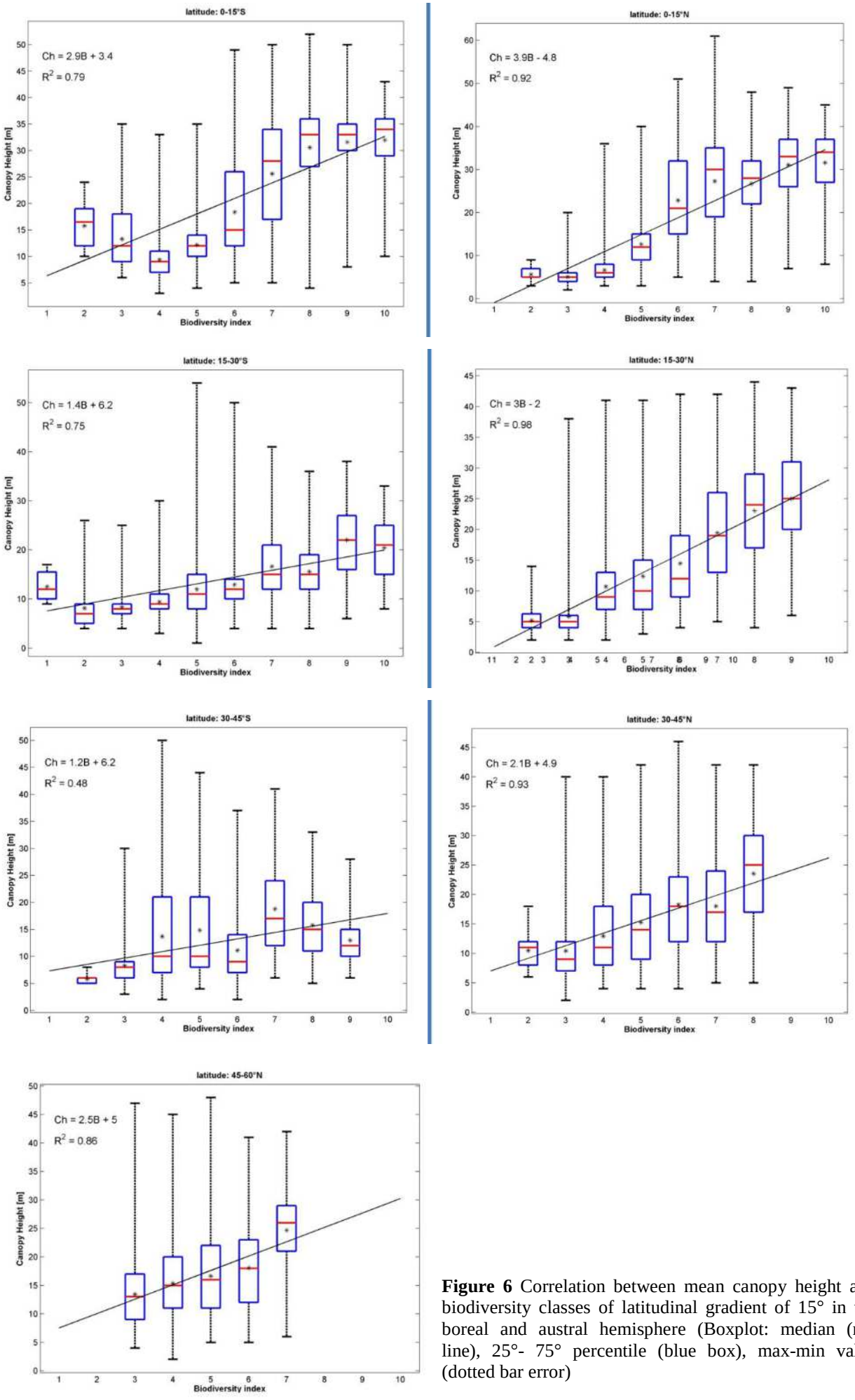

Figure 6 Correlation between mean canopy height and biodiversity classes of latitudinal gradient of 15° in the boreal and austral hemisphere (Boxplot: median (red line), 25°- 75° percentile (blue box), max-min value (dotted bar error)

The abovementioned relations can be evaluated at a global scale. Figure 7 shows the relation between mean canopy height and biodiversity with a sigmoid trend. The relative abundance of data of such groups allow us to perform a kernel density estimation of the probability density function for both datasets, based on the Gaussian kernel and using Silverman's rule for bandwidth selection. Probability density functions are shown in Figure 8.

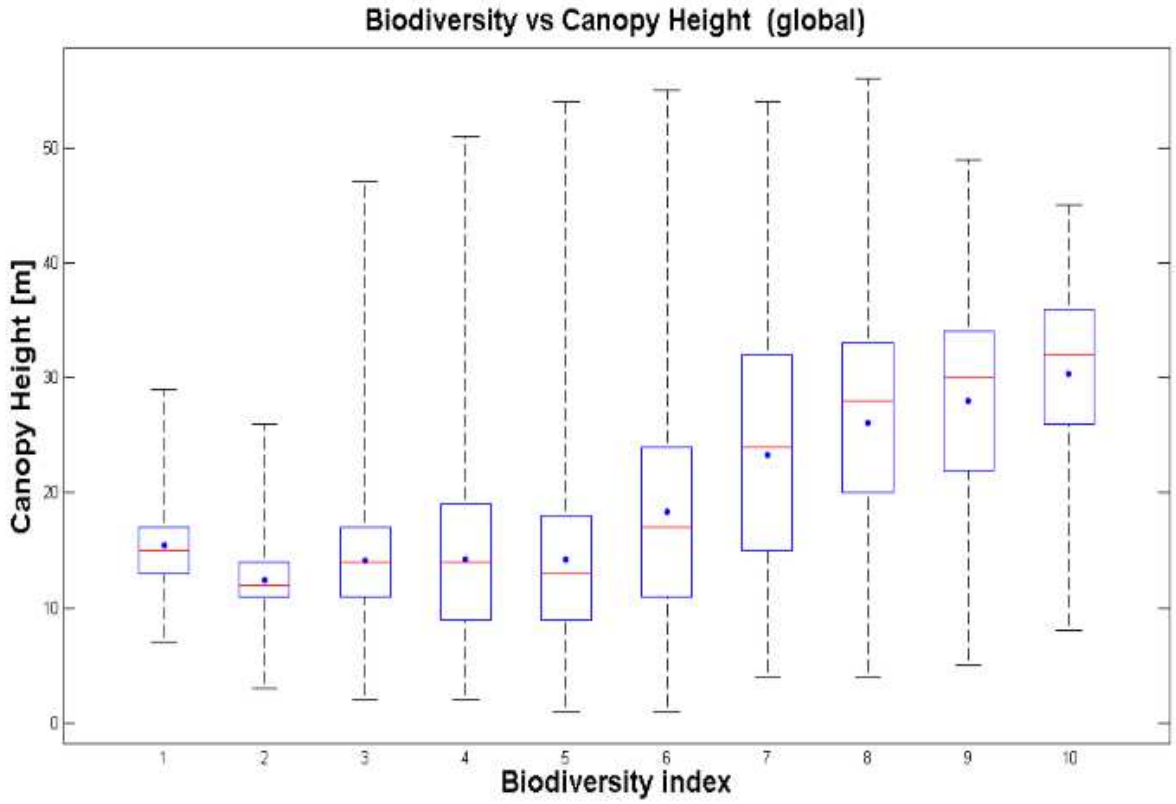

Figure 8 Global correlation between biodiversity and mean canopy height (blue point, mean; red line, median; blue box, 25%-75% percentile; dotted error bars, max-min values)

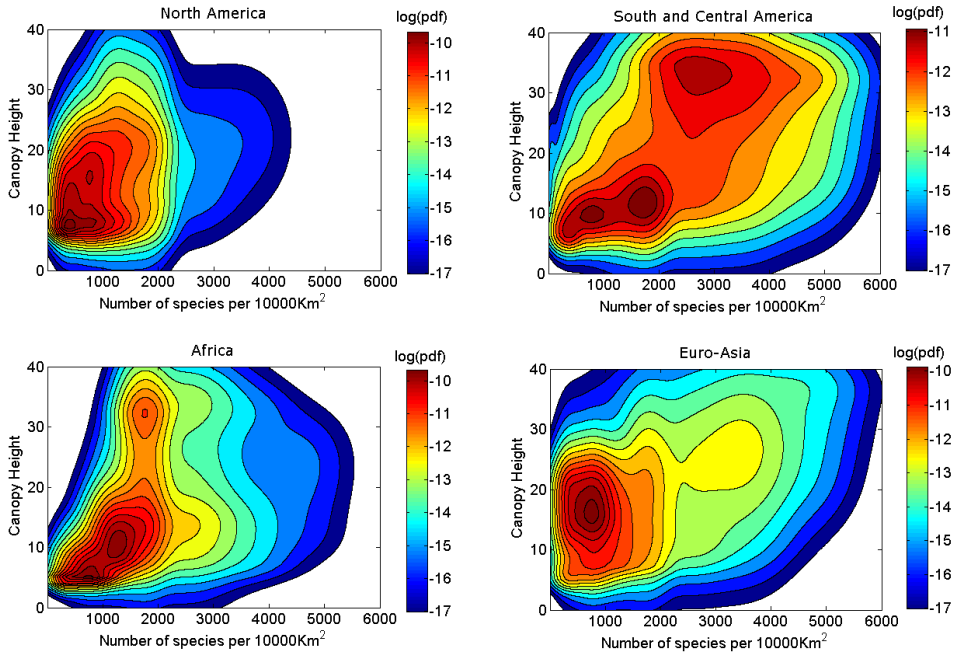

Figure 7 Probability density functions (pdf) of canopy height distribution and number of species per 10000 km^2 at continental scale.

Discussion and Conclusion

From the maps and the correlations presented in this study it seems evident that plant diversity is distributed in different fashions in temperate and tropical forests. In the mid-high latitude this diversity is concentrated in the upper and lower strata but very few species occurred in the middle. In low latitude the herbaceous layer is poor of species whereas the canopy is plenty. It is in the middle strata that tropical forests differ dramatically from temperate ones. This is clear analysing the standard deviation from the mean of the trees canopy height.

We demonstrate that the positive correlation between biodiversity and canopy height is particularly due to the increased vertical partitioning of the light field. Tropical rainforests are taller than temperate forests and therefore offer more space for internal strata. The uniform light field found under the canopy of temperate forests differs from the light that passes through the emergent stratum of a tropical forest, which is spatially heterogeneous. This feature allows species with distinct light-capturing adaptation to coexist at each level and contributes to the high diversity of the middle strata. In tropics the middle-strata "niche", or hypervolume, is consequently larger than that of a temperate forest. The probability distribution curves show a multivariate (multimodal) distribution with positive skew (correlation coefficient R^2>0.7) consistent with the fact that, generally, tree species diversity always increase with canopy height. In some cases, such as Africa, the bimodal probability distribution tell us that multiple causes can contribute to this rule. African forests, for instance, seem have been modified by human beings since 2000 years ago (16) and this can explain the almost exponential relation (instead of linear/sigmoid one as in the other continents) between diversity and canopy height. Thus, the combination of stratification (height/biodiversity relation), climatic factors (humidity and temperature) and productivity and evolutionary history allows species to fill the ecosystem niche in a fractal way and could be the key to understand why tropics are so diverse as discussed in Chapter 4.

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CHAPTER 4

A theory to explain why tropical forests are so diverse*

Abstract: For a long time ecologists have questioned on the variations of biodiversity across the latitudinal gradient. Recently it has emerged that the changes in β-diversity are caused simply by changes in the sizes of species pools. I combined the species pool size and the fractal nature of ecosystems to clarify some general patterns of this gradient. Considering temperature, humidity and NPP as the main variables of an ecosystem niche and as the axis of the polygon in the Cartesian plane, it is possible to build fractal hypervolume, whose the fractal dimension rises up to three moving towards the equator. It follows that the best figure that graphically synthesizes the evolutionary forces that fit this ecosystem hypervolume is the fractal cauliflower.

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One of the most interesting question in ecology is why tropics are so diverse or, in other words, why there are variations of biodiversity across the latitudinal gradient. Since the extent of tropical diversity compared to temperate areas became evident during the XIX century, a large number of different factors have been suggested as possible explanations (for a summary see ref. 1). Recently it has been evidenced that the changes in β-diversity is caused simply by changes in the sizes of species pools. In fact, after correcting for variation in pooled species richness (γ-diversity) the differences in β-diversity disappear. Thus, differences in local assembly processes are not the causes of latitudinal and altitudinal patterns of biodiversity, where the variation in biogeographic processes that set the size of the species pool is a more plausible explanation (2). One of the most corroborate ecological and evolutionary hypotheses is that climate (C) influences Net Primary Production (NPP) in such a way that, by rising/lowering available biomass (B) and so increasing/decreasing the number of individuals (I), it "controls" the number of species (S). So far the Climate→NPP→I→S correlation has not been clearly demonstrated, because it seems to be not mediated directly by biomass. I will show that it is not I or B that influence S, but rather the extent of climatic and NPP on niche variables .

It is possible to extend the ecological niche concept to an ecosystem dimension to better define the size of species pool invoked by (2) . This "ecosystem niche", therefore, can be imagined as the sum of the niches of each species included in the pool. In an Hutchinsonian view an ecosystem niche is an n-dimensional hypervolume, where the dimensions are environmental conditions (C) and the resources (NPP) that define the requirements of all the species in an ecosystem to reproduce themselves.

Furthermore, examples of the fractal nature of nature have been argued continuatively during the last years (3). Different elements of the natural world have been associated to or defined as fractals but only considering them separately and not in an holistic perspective. That ecosystems are structured in a fractal way (made by relationships that are self-similar over a wide range of spatial or temporal scales as well as the single elements whose they are composed), is becoming an intriguing idea in ecology. I combined this two apparently distinct concepts, the ecosystem niche and the fractal nature of them, in an attempt to clarify some general patterns of biological diversity.

Here I show that latitudinal gradient of biodiversity can be explained as differences in fractal dimension of ecosystem niches (Fig. 1A). Let's reduce the variables can shape the ecological niche to the fundamental ones. Temperature (T) is surely one of these (4). Different authors suggested that the richness of species which cannot regulate their internal temperature

(ectothermic) can be predicted from environmental temperature (5,6). The second fundamental variable of an ecosystem hypervolume is humidity (H), which shows different values in terrestrial regions but it is constant in marine environment, where temperature and photic zone depth are the main factors. The latitudinal variation of both these variables is shown in Fig. 1B.

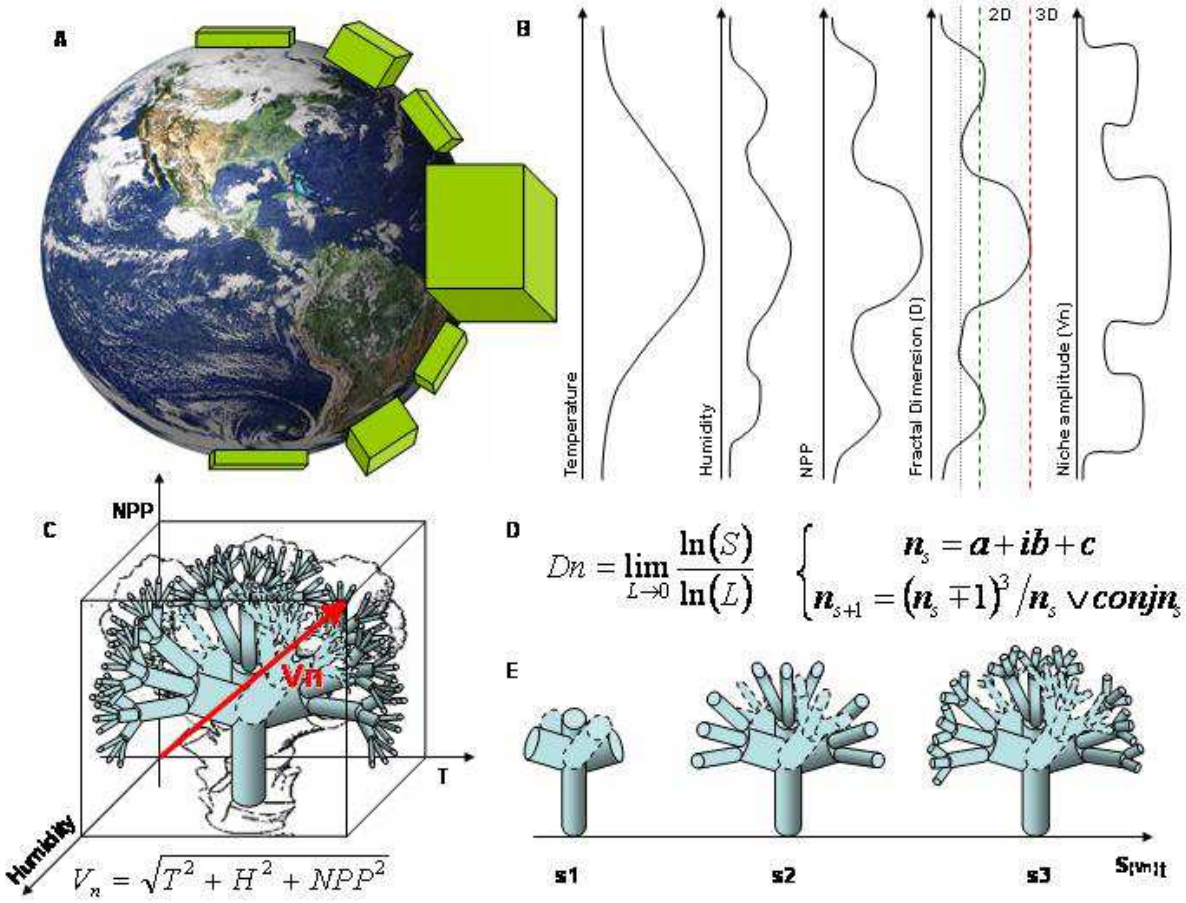

Figure 1. The latitudinal gradient of biodiversity can be explained as differences in ecosystem niche amplitude (*a*) and fractal dimension derived by the combination of T, H and PPN (*b*). These three variables are the axes of the fractal hypervolume (*c* and green polygons in *a*). The fractal 3-D cauliflower (*d*) is the best fitting mathematical object (*e*) that takes into account the addiction of new species within the fractal ecosystem niche (*c*). The number of species in each region are thus dependent on the number of possible iterations of the fractal function (*e*) which is constrained by the ecosystem niche amplitude (Vn).

By merging temperature and humidity from pole to pole it is possible to estimate the curve of Net Primary Production (NPP). This latter shows a triple-humped-shape, with one big hump within about 20°N and S from the Equator and two moderate over the temperate areas. The lowest values of NPP are in polar and tropical (deserts) latitudes where T and/or H are low. Simple models of spatial dynamics (7) accurately predicts the increase in species richness with increasing environmental productivity (i.e. “energy richness hypothesis”). It seems reasonable that autotrophic organisms diversity may be principally driven by humidity (or light in marine

environment), that of ectotherms by temperature, whereas resource availability (NPP) is the fundamental variable that allows differentiation of endothermic species. Thus, both T and H are constituent and co-variables of NPP in the ecosystem niches. Therefore, considering this niche as a polygon in the Cartesian plane where the x, y and z axis are T, H and NPP (Fig. 1C) I demonstrate that where these values, and in particular the NPP are close to zero like in polar or deserts areas, the fractal dimension (D, Fig. 1D where L is the linear scaling and S is the result of size increasing) of this polygon is lower than two (~1.5). This means that there is rather a hypersurface available for species than a hypervolume. Moving along latitude and following the NPP curve, the fractal dimension pass through the value 2.5 reaching the value three (a 3-D shape) at the equator (Fig. 1A and B). Explicitly, here I consider the D value of the ecosystem hypervolume as a proxy of the available space for species pool. Evidently, the greater are T and H, and so the NPP, the higher is D and the bigger is the ecosystem niche amplitude (Vn, Fig. 1B and C). This seems to solve "niche conservatism" (8) and "energy richness" hypothesis problems (such as the misunderstanding influence of B or the weaker correlation between NPP and I than between NPP and S). Defined the ecological causes of "biodiversity dimension", it is then fundamental to focus on evolutionary processes that can fill the niche space available. The best figure that graphically synthesizes the evolutionary forces that fit the ecosystem hypervolume is the fractal cauliflower. In fact, for each iteration, that can be assumed as the addiction/speciation of a new species (s), the niche volume can be filled up to reaching a value close to 3 D (such as 2.7-2.9 of the equations in Fig. 1D). The simple system in Fig. 1D accomplishes in the most efficient way the filling of an available functional space, where ns is the ecosystem niche occupied by species ecological niches and a, b and c the portion of the three fundamental variables (T, H and NPP) used by each species. The branches of the fractal cauliflower are created step by step (Fig. 1E) by the addition/speciation of new species towards the maximum amplitude (Vn) allowed by NPP and consequently by D. Each segment constitutes a new available ecological niche within the ecosystem hypervolume which other species can occupy, as suggested by the hypothesis of the diversity that begets diversity (9, 10).

The patterns described above, can be synthesized as the "cauliflower hypothesis of biological diversity", although they could appear oversimplified, can be also extended to altitudinal gradients and shed more light on ecological and evolutionary processes which shape biodiversity on Earth.

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CHAPTER 5

Growth trends of tropical trees from Pre- to Post-Industrial Age under a changing climate*

Abstract: Knowledge of age and growth rates of tropical trees is necessary for an understanding of forest dynamics and for sustainable management of forest resources. In order to study the impact of climate change due to new practices and industrial emissions (GHG, fires, logging impacts, etc.) on African forests and their role in the forestry-based carbon sequestration processes, it is necessary to track forest -stand changes on the long term trends.

In this respect dendrochronology of tropical trees represent an interesting tool to gather information of trees growth along time series. However, due to the difficulties of sampling and counting rings of tropical species, there is still a lack of dendrochronological complete series in tropical areas.

In this work we analysed samples collected in tropical forests of Africa (Cameroon, Sierra Leone, Ghana and Gabon) to estimate the tree-growth trends of the last century. We measured with the optical dendrochronological methods samples of *Entandrophragma cylindricum* (Sapele, common name) and *Triplochiton scleroxylon* (Ayous, common name) collected respectively in primary and secondary/degraded tropical forests. The oldest samples we had available were a Sapele of 350 ca. years and an Ayous 200 ca. years old. We compared growth trends of old trees born in the pre-industrial age (17th century) with those of younger trees born in the modern age (20th century) to evaluate the changing forests behavior under a modified atmospheric chemistry. We show, as preliminary results, that the Sapele and Ayous species increased their growth trends during the last century (from 1900). Further analyses will clarify this preliminary conclusion and move deeper inside in physiological explication.

* presented as poster at the International Simposium in Wood structure in Plant Biology and Ecology, WSE 2013, 17-20 April 2013 as “Gatti Cazzolla R., Battipaglia G., Castaldi S., Laserre B., Cardellini G., Valentini R., Growth trends of African tropical trees under a changing climate”

Introduction

The role of the African continent in the global carbon cycle, and therefore in climate change, is increasingly recognised (Houghton and Hackler, 2006; Williams et al., 2007). Even if Africa contributes only less than 4% to the global anthropogenic fossil fuel emissions (Canadell et al., 2008), 20% of both global net primary production (NPP) and global land use emissions (mainly from forest degradation and deforestation), and around 40% of fire emissions have been attributed to the African continent, significantly affecting the atmospheric chemistry (Kituyi et al., 2005; van der Werf et al., 2006). Moreover, about 50% of inter-annual variability of global atmospheric CO_2 is attributed to the variability of the African carbon balance (Rödenbeck et al., 2003; Baker et al., 2006; Williams et al., 2007). Despite the increasingly acknowledged importance of Africa in the global carbon cycle and its high vulnerability to climate change due to both ecological and socio-economic factors, there is still a lack of studies on the carbon cycle in representative African ecosystems (in particular tropical forests), and on the effects of climate on ecosystem-atmosphere exchange (Scanlon and Albertson, 2004). Up to now it is not clear whether Africa is a net carbon absorber or emitter, however Williams et al. (2007), in the probably most complete and recent review on African carbon cycle, showed that Africa's decadal scale mean carbon balance appears to be neutral, whereas latest results by Ciais et al. (2008) showed that in the last decade Africa has probably been acting as a net carbon sink. Lewis et al. (2009) have provided evidence that increasing carbon storage in old-growth forests is a pan-tropical phenomenon. The only way to extend time series more rapidly is to look backwards. Tree ring analysis allows this approach by reconstructing annual growth rates over the full lifetime of trees, easily spanning more than a century. Tree ring research in the tropics is not new, but its wide application has been hampered by the common belief that several tropical forest trees do not produce annual rings. Fortunately, tropical dendrochronology has developed rapidly over the last decade and has revealed that many tree species do form such rings (Rozendaal & Zuidema, 2011).

Such climate–growth analyses can be used to project potential tree responses under climate change scenarios. Long-term growth increases have been observed for several species and are consistent with an expected positive response to increased atmospheric CO_2-pressure or nutrient supply (Zuidema et al., 2012)

We used a combination of tree ring analysis, 14C dating and potential biogeochemical signals from plant biomass to reconstruct the growth patterns of trees in the last few centuries and to provide a mean carbon flux to the atmosphere. In particular, for this study we used some selected African tree species for the comparison of the pre-industrial age growth analysis with

the current time growth to prove a likely role of carbon dioxide fertilization on the increased sink of carbon in tropical rainforests.

Study sites

The study was carried out in four tropical forest areas, located in West and Central Africa. In West Africa wood samples were collected along the border between Ghana and Ivory Coast (Ankasa and Bia National Parks and surrounding areas) and the border between Sierra Leone and Liberia (Gola National Park).

In Central Africa forest plots have been selected within the Congo river basin, on the border between Cameroon and Central African Republic (Sangha Tri-National Forest) and in North and West Gabon (Figure 1).

Figure 1 Study sites in West and Central Africa

Species selection and matherials

The growth dynamics of tropical forests and tree species is one of the least studied aspects of ecological science in the tropics. In trees of the temperate zone, age and growth rates are usually determined by counting and measuring the tree rings from increment cores or in trunk cross-sections (Ogden 1981). In these environments, the cambium exhibits an annual cycle of activity and dormancy as the consequence of temperature variation, which causes the formation of growth rings (Philipson et al. 1971; Creber 1977). It is widely portrayed in textbooks that in tropical forests the cambium remains more or less active throughout the year, and therefore visible growth rings are not related to annual events (Fahn et al. 1981). Some studies reported

that in tropical regions with distinct annual variation in precipitation and dry seasons of 2–3 months, tree species may exhibit annual growth rings (Coster (1927, 1928); Alvim 1964; Amobi 1973; Worbes (1990, 1999). Alternatively a triggering factor for tree ring formation is the seasonal flooding of extensive areas of tropical forest by the lateral overflow of large rivers like the Amazon and its tributaries (Worbes (1986, 1989, 1992, 1995).

We collected wood samples with electric drill and 60-80 cm Pressler augers of *Entandrophragma cylindricum* (Sapele, common name) and *Triplochiton scleroxylon* (Ayous, common name) in primary and secondary/degraded tropical forests (Figure 2).

Figure 2 Distribution, main features and whole tree of *Troplochiton scleroxylon (left)* and *Entandrophragma cylindricum (right)*

Sampling methods

The wood carrots were collected, preserved and analysed following this protocol:

1. Selects tree species with the aid of a local botanist
2. Measure height and diameter at the breast height (d.b.h.) with a laser dendrometer/hypsometer
3. Collect 5 cm of soil on the ground below the selected tree
4. Collect 2 wood cores with augers at d.b.h. (1,30 cm) at an angle of 120° each
5. Remove the wood sample from the auger and preserve it in a newspaper sheet
6. Note height, d.b.h., species, location and serial number on labels and fieldsheet
7. Protect the samples in rigid plastic or paper tube

Then we analysed samples collected with a stereoscope to date annual growth. The oldest samples we had available were a Sapele of 350 ca. years and an Ayous 200 ca. years old.
We compared growth trends of old trees (born in pre-industrial age, 17th century) with those of young trees (born in modern age, 20th century).

Analytical Methods and Results

All the sampled cores were air dried, glued onto wood supports, and sanded to enhance ring boundaries. Ring-width measurements were made with a resolution of 0.01 mm on each of the cores, using LINTAB measurement equipment (Frank Rinn, Heidelberg, Germany) and analysed with TSAP software package. After visually cross-dated to identify missing rings, common marker years and ring width patterns samples from each site were correlated according to the Gleichläufigkeit, a statistical measure of the year-to-year agreement between the interval trends of the chronologies based upon the sign of agreement (Schweingruber 1988) and a Student t-test which determines the degree of correlation between curves. Crossdating of all the tree-ring series was verified using the Program COFECHA, which assesses the quality of cross dating and measurement accuracy of tree-ring series using the segmented time-series correlation technique (Holmes 1993). To remove the biological age-trend and facilitate examination of climatic extremes in the context of adjacent years and decades, the TRW data were de-trended using a negative exponential or linear function first and 30-year cubic smoothing splines as second option by means of ARSTAN. Afterwards, an autoregressive model was applied to remove the autocorrelation with the previous year's ring width.

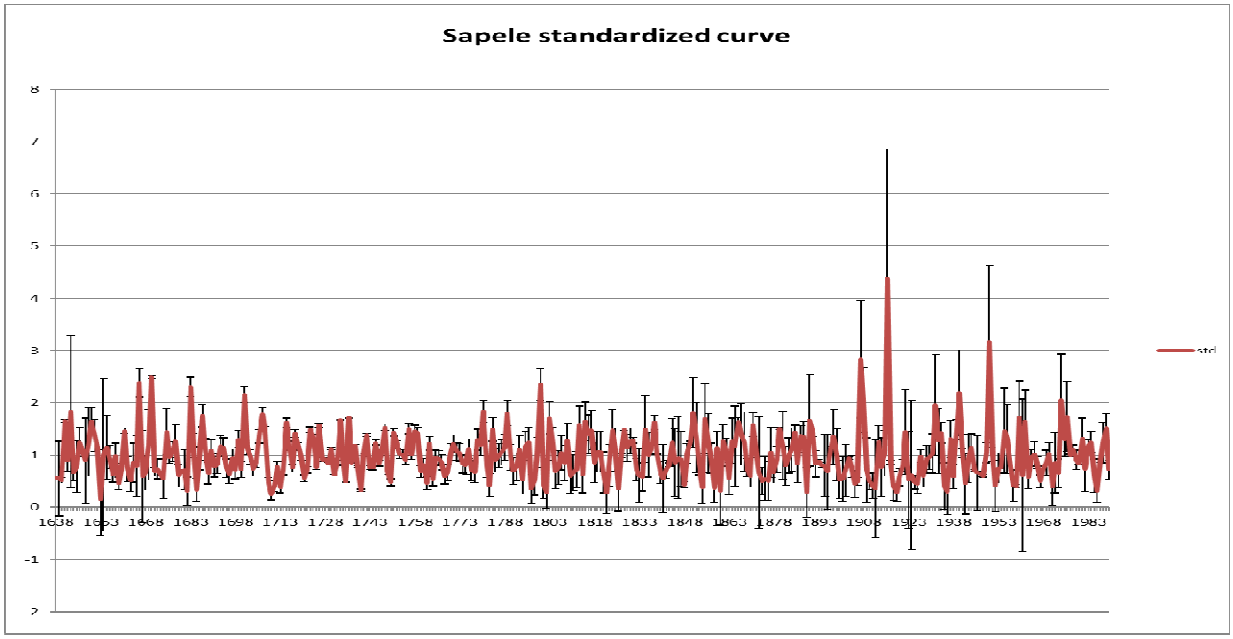

Figure 3 Standardized curve of *Entandrophragma cylindricum*

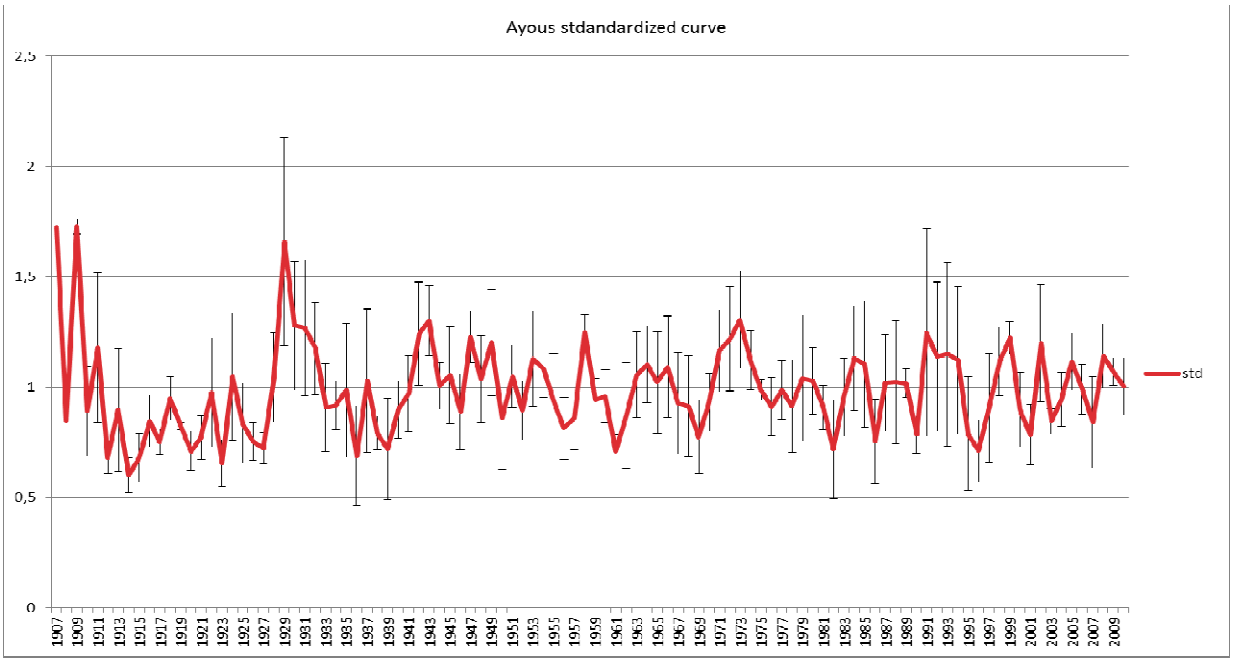

Figure 4 Standardized curve of *Triplochiton scleroxylon*

Individual series within each plant community were averaged with a robust (bi-weight) estimation of the mean. Two standardized curves were derived for both species (Fig. 3 and 4). Annual measurements of raw, standard (STNDRD), residual (RESID) and arstan (ARSTAN) chronology are reported in Table 1 and Table 2. In fact program ARSTAN produces chronologies from tree-ring measurement series by detrending and indexing (standardizing) the series, then applying a robust estimation of the mean value function to remove effects of

endogenous stand disturbances. Autoregressive modelling of index series often enhances the common signal. Extensive statistical analysis of a common time interval provides characterization of the data set. Three versions of the chronology are produced, intended to contain a maximum common signal and a minimum amount of noise.

The 'STNDRD' version of the chronology is computed. Detrended (standardized) tree-ring index series are combined into a mean value function of all series or of those selected in the chronology mask.

The 'RESID' (residual) version of the chronology is computed in the same manner as the STNDRD version, this time using the residual series resulting from step above. Using the autoregressive coefficients selected in the first multivariate autoregressive modelling, the pooled auto-regression (persistence) model is reincorporated into the residual chronology to produce the 'ARSTAN' chronology

The following parameters were calculated within each plant community (Table 3 EPS (Expressed Population Signal; indicates the level of coherence of the constructed chronology and how it portrays the hypothetical perfect population chronology), R-bar (mean correlation among all possible pairings of individual series within a chronology) and MS (mean sensitivity, indicates the degree to which TRW changes from year to year and how it is influenced by high-frequency climatic variations).

year	num	seg	age	raw	std	res	ars	SE
1907	1	104	1	17,06	1,722	1,724	1,775	
1908	1	104	2	7,59	0,846	0,787	0,993	
1909	2	103	2	15,04	1,727	1,728	1,726	0,03404719
1910	3	102,333	2,333	8,537	0,892	0,834	1,026	0,20301962
1911	3	102,333	3,333	10,157	1,178	1,191	1,198	0,33825156
1912	3	102,333	4,333	5,083	0,68	0,639	0,692	0,07139172
1913	3	102,333	5,333	6,317	0,897	0,95	0,869	0,2786599
1914	3	102,333	6,333	3,263	0,599	0,621	0,587	0,07872548
1915	3	102,333	7,333	3,153	0,68	0,754	0,645	0,11109292
1916	3	102,333	8,333	3,487	0,846	0,905	0,812	0,11640942
1917	3	102,333	9,333	2,77	0,752	0,791	0,741	0,05805261
1918	3	102,333	10,333	3,01	0,948	0,993	0,925	0,09760309
1919	3	102,333	11,333	2,397	0,823	0,844	0,825	0,01530607
1920	3	102,333	12,333	1,94	0,71	0,746	0,7	0,0887559
1921	3	102,333	13,333	1,777	0,772	0,82	0,741	0,09953956
1922	4	99	11	5,155	0,976	1,013	0,945	0,24732835
1923	4	99	12	2,84	0,656	0,677	0,663	0,10694427
1924	4	99	13	4,38	1,047	1,104	1,016	0,28820259

1925	4	99	14	2,372	0,837	0,862	0,867	0,17968232
1926	4	99	15	2,092	0,754	0,787	0,753	0,08423648
1927	4	99	16	2,138	0,723	0,76	0,695	0,07071604
1928	4	99	17	2,88	1,045	1,086	1,006	0,2024044
1929	5	95,6	14,6	5,582	1,657	1,649	1,651	0,46984568
1930	6	93,167	13,167	4,95	1,277	1,188	1,361	0,28970787
1931	6	93,167	14,167	4,635	1,268	1,227	1,323	0,30687017
1932	6	93,167	15,167	5,823	1,175	1,136	1,222	0,20888782
1933	6	93,167	16,167	4,672	0,907	0,889	0,948	0,20093238
1934	6	93,167	17,167	4,288	0,918	0,963	0,949	0,11037286
1935	6	93,167	18,167	5,785	0,986	1,011	0,998	0,30512827
1936	6	93,167	19,167	3,66	0,688	0,719	0,718	0,22879903
1937	6	93,167	20,167	4,702	1,029	1,052	0,978	0,32632314
1938	6	93,167	21,167	4,042	0,793	0,797	0,792	0,07474719
1939	6	93,167	22,167	3,255	0,719	0,763	0,709	0,23028555
1940	6	93,167	23,167	4,713	0,898	0,959	0,883	0,12957045
1941	6	93,167	24,167	5,463	0,97	0,985	0,955	0,1720792
1942	6	93,167	25,167	6,833	1,243	1,239	1,228	0,23352206
1943	6	93,167	26,167	7,692	1,301	1,243	1,303	0,15920684
1944	6	93,167	27,167	5,9	1,005	0,943	1,024	0,10422982
1945	6	93,167	28,167	6,8	1,055	1,075	1,081	0,22009682
1946	6	93,167	29,167	5,053	0,887	0,906	0,928	0,17153518
1947	6	93,167	30,167	7,602	1,228	1,247	1,228	0,11636502
1948	6	93,167	31,167	6,673	1,035	0,997	1,058	0,19626108
1949	6	93,167	32,167	7,747	1,201	1,222	1,238	0,24204573
1950	6	93,167	33,167	5,138	0,859	0,861	0,924	0,23197771
1951	6	93,167	34,167	6,478	1,049	1,077	1,058	0,14077532
1952	6	93,167	35,167	5,373	0,895	0,904	0,92	0,13216295
1953	6	93,167	36,167	7,157	1,127	1,144	1,123	0,21626891
1954	6	93,167	37,167	6,542	1,083	1,082	1,115	0,12985822
1955	6	93,167	38,167	5,452	0,933	0,934	0,965	0,21914024
1956	6	93,167	39,167	4,737	0,813	0,825	0,816	0,14047645
1957	6	93,167	40,167	5,068	0,86	0,898	0,85	0,14430309
1958	6	93,167	41,167	7,307	1,25	1,27	1,231	0,078698
1959	6	93,167	42,167	5,365	0,941	0,91	0,971	0,09909352
1960	6	93,167	43,167	5,45	0,96	0,985	0,978	0,12008676
1961	6	93,167	44,167	3,97	0,709	0,71	0,704	0,07548401
1962	6	93,167	45,167	5,303	0,87	0,911	0,833	0,23922673
1963	6	93,167	46,167	5,9	1,056	1,1	1,056	0,19653746
1964	6	93,167	47,167	6,3	1,103	1,091	1,106	0,17465317
1965	6	93,167	48,167	5,615	1,022	0,994	1,023	0,23005458
1966	6	93,167	49,167	6,225	1,09	1,104	1,11	0,23031293
1967	6	93,167	50,167	5,692	0,926	0,942	0,972	0,22943921
1968	6	93,167	51,167	5,243	0,915	0,924	0,917	0,22864985

1969	6	93,167	52,167	4,248	0,774	0,795	0,773	0,16561564
1970	6	93,167	53,167	5,175	0,931	0,987	0,927	0,13137041
1971	6	93,167	54,167	6,758	1,165	1,182	1,164	0,18637108
1972	6	93,167	55,167	7,013	1,219	1,18	1,224	0,23582481
1973	6	93,167	56,167	7,567	1,305	1,246	1,306	0,22029006
1974	6	93,167	57,167	6,41	1,123	1,097	1,178	0,13497506
1975	6	93,167	58,167	5,398	0,988	0,959	1,006	0,04587426
1976	6	93,167	59,167	4,845	0,912	0,919	0,921	0,12976294
1977	6	93,167	60,167	5,165	0,988	1,016	0,996	0,132534
1978	6	93,167	61,167	4,895	0,915	0,932	0,931	0,20986977
1979	6	93,167	62,167	5,615	1,039	1,091	1,073	0,28516638
1980	6	93,167	63,167	5,235	1,028	1,056	1,076	0,15122059
1981	6	93,167	64,167	4,652	0,907	0,919	0,939	0,09993811
1982	6	93,167	65,167	3,723	0,717	0,73	0,714	0,22454806
1983	6	93,167	66,167	4,86	0,953	1,006	0,931	0,17684413
1984	6	93,167	67,167	5,657	1,13	1,139	1,121	0,2369079
1985	6	93,167	68,167	5,512	1,102	1,095	1,128	0,28579619
1986	6	93,167	69,167	3,817	0,753	0,717	0,751	0,19030655
1987	6	93,167	70,167	5,29	1,018	1,041	0,976	0,21921285
1988	6	93,167	71,167	5,553	1,021	1	0,995	0,27950432
1989	6	93,167	72,167	5,358	1,017	1,045	1,044	0,06375442
1990	6	93,167	73,167	4,155	0,785	0,798	0,81	0,08292744
1991	6	93,167	74,167	6,86	1,248	1,288	1,238	0,46954731
1992	6	93,167	75,167	6,303	1,138	1,094	1,157	0,33837136
1993	6	93,167	76,167	6,382	1,15	1,15	1,192	0,41564803
1994	6	93,167	77,167	6,548	1,123	1,129	1,18	0,33457387
1995	6	93,167	78,167	4,743	0,788	0,769	0,817	0,25821317
1996	6	93,167	79,167	4,19	0,711	0,757	0,709	0,13994912
1997	6	93,167	80,167	5,287	0,907	0,952	0,876	0,24627391
1998	6	93,167	81,167	6,887	1,114	1,106	1,074	0,15539324
1999	6	93,167	82,167	7,9	1,223	1,218	1,237	0,07256398
2000	6	93,167	83,167	6,245	0,899	0,871	0,935	0,16799277
2001	6	93,167	84,167	5,307	0,783	0,816	0,799	0,13724898
2002	6	93,167	85,167	8,762	1,199	1,237	1,184	0,26569033
2003	6	93,167	86,167	6,317	0,845	0,843	0,892	0,056841
2004	6	93,167	87,167	7,363	0,944	0,978	0,949	0,12161838
2005	6	93,167	88,167	8,987	1,116	1,129	1,116	0,12924858
2006	6	93,167	89,167	8,212	0,99	0,996	1,027	0,11324838
2007	6	93,167	90,167	6,63	0,84	0,839	0,847	0,20691914
2008	6	93,167	91,167	9,682	1,141	1,15	1,11	0,14473415
2009	6	93,167	92,167	9,453	1,071	1,067	1,097	0,06300701
2010	6	93,167	93,167	9,658	1,004	1	1,026	0,12914665

Table 1 Parameters calculated for the standardized dendrochronology of Ayous

year	num	seg	age	raw	std	res	ars	SE
1638	1	353	1	0,37	0,583	0,638	0,597	0,0198697
1639	1	353	2	0,38	0,554	0,62	0,559	0,71721841
1640	1	353	3	0,38	0,516	0,468	0,514	0,05041671
1641	1	353	4	1,3	1,653	1,526	1,643	0,02588011
1642	1	353	5	0,74	0,889	0,672	0,875	0,19565645
1643	1	353	6	1,6	1,83	1,829	1,818	1,4521852
1644	1	353	7	0,6	0,659	0,615	0,661	0,13823938
1645	1	353	8	0,74	0,785	1,003	0,806	0,49419693
1646	1	353	9	1,21	1,247	1,347	1,281	0,28248916
1647	1	353	10	1,05	1,059	1,057	1,076	0,02998133
1648	1	353	11	0,9	0,893	0,984	0,914	0,8125364
1649	1	353	12	1,28	1,257	1,261	1,255	0,66227621
1650	1	353	13	1,68	1,642	1,65	1,652	0,25936677
1651	1	353	14	1,4	1,369	1,457	1,392	0,30426805
1652	1	353	15	1,16	1,139	1,331	1,164	0,03408255
1653	1	353	16	0,15	0,148	0,362	0,18	0,6873785
1654	1	353	17	1,01	1,003	1,222	1,04	1,45720565
1655	1	353	18	1,15	1,146	1,099	1,172	0,61023315
1656	1	353	19	0,96	0,958	0,917	0,963	0,22273864
1657	1	353	20	0,64	0,636	0,604	0,628	0,1509673
1658	1	353	21	1	0,986	0,929	0,972	0,24084057
1659	1	353	22	0,47	0,458	0,397	0,464	0,11709688
1660	1	353	23	0,75	0,717	0,685	0,718	0,12204663
1661	1	353	24	1,57	1,467	1,297	1,454	0,05437651
1662	1	353	25	0,81	0,737	0,555	0,723	0,23900209
1663	1	353	26	0,58	0,513	0,524	0,507	0,21312198
1664	1	353	27	1	0,859	0,779	0,848	0,37059466
1665	1	353	28	0,95	0,792	0,673	0,792	0,57975685
1666	1	353	29	2,94	2,386	2,306	2,387	0,2721654
1667	1	353	30	0,75	0,594	0,426	0,585	0,87957013
1668	1	353	31	0,85	0,66	0,902	0,666	0,33516861
1669	1	353	32	1,57	1,199	1,268	1,218	0,6688523
1670	1	353	33	3,3	2,489	2,507	2,516	0,02305168
1671	1	353	34	0,91	0,681	0,773	0,722	0,08414571
1672	1	353	35	0,99	0,736	1,051	0,748	0,18455487
1673	1	353	36	0,85	0,629	0,778	0,656	0,00417193
1674	1	353	37	0,74	0,544	0,667	0,585	0,38346401
1675	1	353	38	1,98	1,447	1,468	1,474	0,43529493
1676	1	353	39	1,32	0,958	0,749	0,938	0,11511698
1677	1	353	40	1,48	1,065	1,056	1,054	0,19530289
1678	1	353	41	1,78	1,269	1,24	1,265	0,31777379
1679	1	353	42	0,86	0,607	0,63	0,616	0,21778889

1680	1	353	43	0,98	0,682	0,809	0,705	0,03181981
1681	1	353	44	1,05	0,719	0,678	0,726	0,38417111
1682	1	353	45	0,45	0,303	0,228	0,306	0,27202398
1683	1	353	46	3,49	2,306	2,195	2,297	0,18285781
1684	1	353	47	1,83	1,188	0,899	1,169	0,23082384
1685	1	353	48	0,52	0,332	0,482	0,331	0,22627858
1686	1	353	49	1,49	0,936	1,06	0,943	0,22173333
1687	1	353	50	2,84	1,756	1,718	1,773	0,21718807
1688	1	353	51	1,81	1,104	1,156	1,143	0,21264282
1689	1	353	52	1,08	0,65	0,767	0,656	0,20809756
1690	1	353	53	1,83	1,087	1,163	1,089	0,20355231
1691	1	353	54	1,33	0,779	0,814	0,803	0,19900705
1692	1	353	55	1,44	0,832	0,914	0,857	0,1944618
1693	1	353	56	2,07	1,179	1,126	1,179	0,18991654
1694	1	353	57	2,04	1,146	1,063	1,141	0,18537128
1695	1	353	58	1,35	0,747	0,76	0,753	0,18082603
1696	1	353	59	1,15	0,627	0,657	0,63	0,17628077
1697	1	353	60	1,75	0,941	0,921	0,947	0,17173552
1698	1	353	61	1,35	0,716	0,639	0,723	0,16719026
1699	1	353	62	2,48	1,301	1,231	1,297	0,16264501
1700	1	353	63	1,39	0,723	0,582	0,711	0,15809975
1701	1	353	64	4,16	2,157	2,153	2,151	0,1535545
1702	1	353	65	2,23	1,158	1,087	1,167	0,14900924
1703	1	353	66	1,84	0,962	1,209	0,984	0,14446399
1704	1	353	67	1,39	0,735	0,943	0,77	0,13991873
1705	1	353	68	1,69	0,907	1,05	0,939	0,13537348
1706	1	353	69	2,49	1,361	1,455	1,4	0,13082822
1707	1	353	70	3,2	1,785	1,755	1,792	0,12628297
1708	1	353	71	2,51	1,432	1,485	1,44	0,12173771
1709	1	353	72	0,77	0,449	0,662	0,469	0,11719245
1710	1	353	73	0,43	0,255	0,528	0,29	0,1126472
1711	1	353	74	0,68	0,409	0,501	0,444	0,10810194
1712	1	353	75	1,29	0,778	0,687	0,794	0,10355669
1713	1	353	76	0,63	0,379	0,135	0,359	0,09901143
1714	1	353	77	1,21	0,719	0,459	0,674	0,09446618
1715	1	353	78	2,77	1,619	1,304	1,577	0,08992092
1716	1	353	79	2,06	1,181	0,93	1,155	0,08537567
1717	1	353	80	1,34	0,752	0,75	0,743	0,08083041
1718	1	353	81	2,58	1,416	1,44	1,414	0,07628516
1719	1	353	82	2,17	1,164	1,169	1,184	0,0717399
1720	1	353	83	1,85	0,971	1,122	1,003	0,06719465
1721	1	353	84	1,09	0,56	0,655	0,577	0,06264939
1722	1	353	85	1,42	0,714	0,777	0,726	0,05810414
1723	1	353	86	3,02	1,488	1,465	1,503	0,05355888

1724	1	353	87	2,79	1,35	1,246	1,352	0,04901362
1725	1	353	88	1,61	0,768	0,799	0,767	0,04446837
1726	1	353	89	3,33	1,567	1,653	1,57	0,03992311
1727	1	353	90	1,94	0,904	0,933	0,924	0,03537786
1728	1	353	91	1,99	0,919	1,128	0,953	0,0308326
1729	1	353	92	1,82	0,834	0,913	0,855	0,02628735
1730	1	353	93	2,47	1,123	1,156	1,135	0,02174209
1731	1	353	94	1,37	0,618	0,634	0,636	0,01719684
1732	1	353	95	1,8	0,806	0,814	0,806	0,01265158
1733	1	353	96	3,78	1,679	1,598	1,677	0,00810633
1734	1	353	97	2,03	0,895	0,799	0,896	0,00356107
1735	1	353	98	1,1	0,481	0,593	0,489	-0,0009842
1736	1	353	99	3,95	1,716	1,737	1,717	-0,0055294
1737	1	353	100	1,97	0,849	0,777	0,864	-0,0100747
1738	1	353	101	2,78	1,188	1,355	1,212	-0,01462
1739	1	353	102	1,83	0,774	0,774	0,779	-0,0191652
1740	1	353	103	0,77	0,322	0,397	0,333	-0,0237105
1741	1	353	104	2,43	1,002	1,054	1,023	-0,0282557
1742	1	353	105	3,4	1,38	1,209	1,375	-0,032801
1743	1	353	106	1,9	0,759	0,668	0,756	-0,0373462
1744	1	353	107	1,93	0,759	0,755	0,747	-0,0418915
1745	1	353	108	3,21	1,241	1,179	1,234	-0,0464367
1746	1	353	109	2,21	0,842	0,802	0,854	-0,050982
1747	1	353	110	2,76	1,038	1,078	1,048	-0,0555272
1748	1	353	111	4,11	1,528	1,477	1,526	-0,0600725
1749	1	353	112	1,88	0,694	0,689	0,702	-0,0646178
1750	1	353	113	1,3	0,477	0,627	0,495	-0,069163
1751	1	353	114	3,93	1,439	1,447	1,447	-0,0737083
1752	1	353	115	3,27	1,201	1,112	1,213	-0,0782535
1753	1	353	116	2,75	1,017	1,076	1,029	-0,0827988
1754	1	353	117	2,72	1,018	1,044	1,016	-0,087344
1755	1	353	118	2,38	0,907	0,952	0,917	-0,0918893
1756	1	353	119	3,86	1,505	1,596	1,531	-0,0964345
1757	1	353	120	2,52	1,012	1,022	1,028	-0,1009798
1758	1	353	121	3,53	1,468	1,595	1,483	-0,1055251
1759	1	353	122	3,28	1,422	1,497	1,441	-0,1100703
1760	1	353	123	1,51	0,685	0,863	0,714	-0,1146156
1761	1	353	124	1,71	0,814	1,057	0,85	-0,1191608
1762	1	353	125	0,93	0,464	0,53	0,488	-0,1237061
1763	1	353	126	2,34	1,224	1,267	1,244	-0,1282513
1764	1	353	127	0,99	0,541	0,413	0,542	-0,1327966
1765	1	353	128	1,68	0,953	0,9	0,938	-0,1373418
1766	1	353	129	1,6	0,937	0,79	0,923	-0,1418871
1767	1	353	130	1,43	0,857	0,761	0,846	-0,1464324

1768	1	353	131	0,97	0,59	0,542	0,59	-0,1509776
1769	1	353	132	1,08	0,66	0,57	0,649	-0,1555229
1770	1	353	133	1,73	1,053	0,931	1,048	-0,1600681
1771	1	353	134	2,03	1,221	1,061	1,211	-0,1646134
1772	1	353	135	1,81	1,07	0,971	1,059	-0,1691586
1773	1	353	136	1,8	1,04	1,018	1,033	-0,1737039
1774	1	353	137	1,47	0,827	0,848	0,833	-0,1782491
1775	1	353	138	1,49	0,813	0,872	0,83	-0,1827944
1776	1	353	139	2,13	1,125	1,13	1,138	-0,1873397
1777	1	353	140	1,37	0,699	0,653	0,705	-0,1918849
1778	1	353	141	1,36	0,671	0,674	0,673	-0,1964302
1779	1	353	142	2,71	1,296	1,217	1,291	-0,2009754
1780	1	353	143	2,56	1,189	1,073	1,187	-0,2055207
1781	1	353	144	4,05	1,836	1,842	1,839	-0,2100659
1782	1	353	145	1,76	0,782	0,794	0,787	-0,2146112
1783	1	353	146	0,97	0,424	0,662	0,446	-0,2191564
1784	1	353	147	3,46	1,495	1,632	1,526	-0,2237017
1785	1	353	148	2,1	0,9	0,865	0,926	-0,228247
1786	1	353	149	2,31	0,987	1,104	1,008	-0,2327922
1787	1	353	150	2,45	1,047	1,019	1,043	-0,2373375
1788	1	353	151	2,67	1,148	1,151	1,151	-0,2418827
1789	1	353	152	4,16	1,806	1,869	1,827	-0,246428
1790	1	353	153	2,17	0,956	0,988	0,969	-0,2509732
1791	1	353	154	1,54	0,69	0,922	0,714	-0,2555185
1792	1	353	155	1,71	0,78	0,924	0,808	-0,2600637
1793	1	353	156	2,38	1,107	1,162	1,133	-0,264609
1794	1	353	157	1,1	0,521	0,524	0,542	-0,2691543
1795	1	353	158	2,43	1,17	1,147	1,163	-0,2736995
1796	1	353	159	2,56	1,251	1,111	1,241	-0,2782448
1797	1	353	160	0,7	0,347	0,321	0,346	-0,28279
1798	1	353	161	1,05	0,525	0,578	0,527	-0,2873353
1799	1	353	162	2,09	1,052	0,916	1,044	-0,2918805
1800	1	353	163	4,65	2,352	2,203	2,352	-0,2964258
1801	1	353	164	0,91	0,462	0,344	0,46	-0,300971
1802	1	353	165	0,57	0,29	0,503	0,286	-0,3055163
1803	1	353	166	3,36	1,711	1,746	1,723	-0,3100615
1804	1	353	167	2,39	1,216	1,144	1,244	-0,3146068
1805	1	353	168	1,34	0,68	0,833	0,709	-0,3191521
1806	1	353	169	1,49	0,752	0,776	0,742	-0,3236973
1807	1	353	170	2,08	1,042	1,031	1,047	-0,3282426
1808	1	353	171	1,72	0,853	0,865	0,877	-0,3327878
1809	1	353	172	2,6	1,274	1,247	1,275	-0,3373331
1810	1	353	173	1,25	0,604	0,523	0,598	-0,3418783
1811	1	353	174	1,39	0,662	0,701	0,664	-0,3464236

1812	1	353	175	1,54	0,723	0,668	0,726	-0,3509688
1813	1	353	176	3,42	1,583	1,478	1,58	-0,3555141
1814	1	353	177	1,39	0,636	0,505	0,634	-0,3600594
1815	1	353	178	3,63	1,648	1,675	1,638	-0,3646046
1816	1	353	179	3,09	1,397	1,324	1,4	-0,3691499
1817	1	353	180	3,26	1,476	1,622	1,497	-0,3736951
1818	1	353	181	1,88	0,855	1,06	0,892	-0,3782404
1819	1	353	182	2,31	1,059	1,283	1,088	-0,3827856
1820	1	353	183	2,3	1,064	1,233	1,108	-0,3873309
1821	1	353	184	1,43	0,668	0,783	0,697	-0,3918761
1822	1	353	185	0,59	0,278	0,364	0,295	-0,3964214
1823	1	353	186	1,69	0,8	0,756	0,798	-0,4009667
1824	1	353	187	3,1	1,473	1,294	1,466	-0,4055119
1825	1	353	188	2,32	1,106	0,933	1,093	-0,4100572
1826	1	353	189	0,73	0,349	0,317	0,333	-0,4146024
1827	1	353	190	2,08	0,995	0,999	0,986	0,03662813
1828	1	353	191	3,12	1,494	1,395	1,502	0,02884996
1829	1	353	192	2,36	1,133	1,1	1,147	0,26134667
1830	1	353	193	2,64	1,271	1,323	1,273	0,24593174
1831	1	353	194	2,66	1,286	1,324	1,289	0,05487149
1832	1	353	195	1,48	0,718	0,87	0,748	0,21107137
1833	1	353	196	1,26	0,614	0,804	0,647	0,51208673
1834	1	353	197	1,18	0,576	0,618	0,594	0,27287251
1835	1	353	198	3,07	1,498	1,456	1,508	0,63682037
1836	1	353	199	2,05	1	0,854	0,998	0,42631468
1837	1	353	200	2,27	1,106	1,105	1,096	0,08768124
1838	1	353	201	3,35	1,629	1,618	1,626	0,1357645
1839	1	353	202	2,09	1,013	1,056	1,028	0,00360624
1840	1	353	203	1,38	0,665	0,889	0,699	0,20852579
1841	1	353	204	1,16	0,553	0,672	0,575	0,64954829
1842	1	353	205	1,56	0,733	0,766	0,753	0,17309974
1843	1	353	206	1,76	0,812	0,748	0,823	0,03401184
1844	1	353	207	2,77	1,248	1,103	1,234	0,45283118
1845	1	353	208	1,94	0,852	0,694	0,833	0,65400306
1846	1	353	209	2,22	0,949	0,912	0,937	0,78064589
1847	1	353	210	2,23	0,925	0,88	0,924	0,5250975
1848	1	353	211	1,08	0,435	0,417	0,441	0,05932626
1849	1	353	212	2,63	1,029	1,023	1,035	0,1840599
1850	1	353	213	3,3	1,257	1,097	1,25	0,01159655
1851	1	353	214	4,87	1,813	1,732	1,809	0,6688523
1852	1	353	215	3,64	1,33	1,316	1,331	0,67224642
1853	1	353	216	2,3	0,828	1,005	0,841	0,20654589
1854	1	353	217	1,08	0,384	0,623	0,421	0,3085814
1855	1	353	218	4,81	1,696	1,847	1,733	0,67104434

1856	1	353	219	3,49	1,223	1,189	1,253	0,565544
1857	1	353	220	2,7	0,942	1,053	0,954	0,28659038
1858	1	353	221	1,07	0,372	0,453	0,376	0,27789297
1859	1	353	222	3,28	1,135	1,202	1,145	0,31692526
1860	1	353	223	0,89	0,307	0,267	0,331	0,64919474
1861	1	353	224	3,7	1,27	1,252	1,268	0,31006632
1862	1	353	225	3,08	1,054	0,837	1,038	0,26672068
1863	1	353	226	1,62	0,553	0,481	0,539	0,31084414
1864	1	353	227	3,72	1,272	1,264	1,27	0,4337393
1865	1	353	228	3,41	1,171	1,034	1,163	0,77124137
1866	1	353	229	4,73	1,639	1,679	1,653	0,08421642
1867	1	353	230	3,99	1,402	1,428	1,412	0,58916137
1868	1	353	231	3,49	1,25	1,416	1,268	0,56978664
1869	1	353	232	2,07	0,758	1,003	0,799	0,17168553
1870	1	353	233	1,6	0,601	0,831	0,641	0,20675802
1871	1	353	234	4,11	1,583	1,705	1,619	0,22945615
1872	1	353	235	2,6	1,027	0,99	1,045	0,07269058
1873	1	353	236	1,64	0,663	0,767	0,672	1,0648321
1874	1	353	237	1,22	0,502	0,543	0,504	0,25554839
1875	1	353	238	1,32	0,55	0,529	0,555	0,42094067
1876	1	353	239	1,2	0,503	0,422	0,511	0,369534
1877	1	353	240	2,5	1,046	0,847	1,027	0,48153972
1878	1	353	241	1,6	0,665	0,397	0,635	0,20301036
1879	1	353	242	2,22	0,914	0,755	0,886	0,24883088
1880	1	353	243	3,71	1,509	1,328	1,488	0,01697056
1881	1	353	244	2,94	1,181	1,058	1,172	0,6470027
1882	1	353	245	2	0,795	0,861	0,803	0,37236243
1883	1	353	246	2,51	0,988	1,057	0,996	0,33835059
1884	1	353	247	2,82	1,102	1,138	1,122	0,41790011
1885	1	353	248	3,7	1,441	1,494	1,465	0,12593572
1886	1	353	249	2,13	0,831	0,856	0,843	0,36097801
1887	1	353	250	3,51	1,377	1,492	1,387	0,18759543
1888	1	353	251	3,4	1,348	1,394	1,368	0,29656058
1889	1	353	252	0,7	0,282	0,425	0,309	0,48033764
1890	1	353	253	4,06	1,667	1,854	1,692	0,88041865
1891	1	353	254	3,41	1,434	1,352	1,447	0,08683271
1892	1	353	255	1,92	0,83	0,985	0,856	0,25010367
1893	1	353	256	1,99	0,885	1,051	0,903	0,02595082
1894	1	353	257	1,76	0,807	0,855	0,818	0,04970961
1895	1	353	258	1,7	0,803	0,898	0,835	0,59488894
1896	1	353	259	1,4	0,679	0,661	0,689	0,71509709
1897	1	353	260	2,27	1,129	1,046	1,121	0,03726453
1898	1	353	261	2,66	1,351	1,226	1,343	0,51724861
1899	1	353	262	1,96	1,013	0,961	1,009	0,49886383

1900	1	353	263	1,01	0,528	0,578	0,531	0,36981685
1901	1	353	264	1,04	0,547	0,593	0,555	0,42617326
1902	1	353	265	1,34	0,705	0,664	0,716	0,50070231
1903	1	353	266	1,8	0,94	0,817	0,941	0,0258094
1904	1	353	267	1,51	0,78	0,601	0,762	0,21347554
1905	1	353	268	0,86	0,438	0,289	0,413	0,26127596
1906	1	353	269	0,99	0,496	0,364	0,477	0,07650895
1907	1	353	270	5,74	2,838	2,643	2,822	1,12528973
1908	1	353	271	4,19	2,053	1,799	2,046	0,62133473
1909	1	353	272	1,46	0,712	0,971	0,724	0,6145465
1910	1	353	273	1,04	0,507	0,899	0,538	0,16935207
1911	1	353	274	0,84	0,41	0,677	0,466	0,23765859
1912	1	353	275	0,73	0,357	0,547	0,427	0,92821907
1913	1	353	276	2,56	1,259	1,157	1,266	0,30087394
1914	1	353	277	1,55	0,77	0,473	0,737	0,55734156
1915	1	353	278	2,04	1,03	0,904	0,999	0,43557778
1916	1	353	279	8,47	4,385	4,238	4,363	2,47734861
1917	1	353	280	1,59	0,853	0,758	0,866	0,03889087
1918	1	353	281	0,72	0,403	1,209	0,464	0,27923647
1919	1	353	282	0,49	0,287	0,72	0,352	0,17465537
1920	1	353	283	0,93	0,572	0,859	0,654	0,15839192
1921	1	353	284	1,24	0,799	0,922	0,871	0,11886465
1922	1	353	285	2,15	1,445	1,193	1,41	0,81465772
1923	1	353	286	0,75	0,523	0,303	0,487	0,93408806
1924	1	353	287	0,87	0,624	0,601	0,602	1,4250323
1925	1	353	288	0,65	0,474	0,368	0,466	0,12544074
1926	1	353	289	0,6	0,44	0,325	0,437	0,17295832
1927	1	353	290	1,34	0,979	0,793	0,968	0,11858181
1928	1	353	291	0,83	0,597	0,294	0,563	0,2032932
1929	1	353	292	1,31	0,921	0,739	0,891	0,26566002
1930	1	353	293	1,39	0,95	0,726	0,923	0,22295077
1931	1	353	294	1,55	1,028	0,887	1,011	0,37335238
1932	1	353	295	3,04	1,956	1,875	1,952	0,96739279
1933	1	353	296	2,02	1,264	1,195	1,264	0,62472884
1934	1	353	297	2,34	1,427	1,64	1,448	0,1973535
1935	1	353	298	0,68	0,405	0,6	0,438	0,44406306
1936	1	353	299	0,5	0,291	0,569	0,334	0,42893097
1937	1	353	300	2,29	1,307	1,386	1,344	0,36267507
1938	1	353	301	1,05	0,589	0,437	0,594	0,23051681
1939	1	353	302	2,7	1,493	1,469	1,486	0,19791919
1940	1	353	303	4	2,193	2,003	2,169	0,81960747
1941	1	353	304	1,9	1,039	1,062	1,042	0,08032733
1942	1	353	305	0,82	0,449	0,789	0,483	0,58124177
1943	1	353	306	1,7	0,934	1,141	0,965	0,4622357

1944	1	353	307	2,06	1,139	1,229	1,185	0,26191235
1945	1	353	308	1,26	0,703	0,757	0,734	0,0198697
1946	1	353	309	1,17	0,659	0,647	0,652	0,71721841
1947	1	353	310	1,12	0,638	0,55	0,626	0,05041671
1948	1	353	311	1,04	0,6	0,509	0,597	0,02588011
1949	1	353	312	1,78	1,044	0,904	1,034	0,19565645
1950	1	353	313	5,29	3,169	2,956	3,147	1,4521852
1951	1	353	314	1,63	1,005	0,857	1	0,13823938
1952	1	353	315	0,64	0,409	0,843	0,43	0,49419693
1953	1	353	316	1,13	0,751	1,031	0,789	0,28248916
1954	1	353	317	1,1	0,763	0,909	0,819	0,02998133
1955	1	353	318	2,02	1,468	1,577	1,52	0,8125364
1956	1	353	319	1,71	1,307	1,162	1,293	0,66227621
1957	1	353	320	0,97	0,781	0,793	0,771	0,25936677
1958	1	353	321	0,48	0,408	0,514	0,416	0,30426805
1959	1	353	322	0,45	0,403	0,448	0,417	0,03408255
1960	1	353	323	1,84	1,732	1,667	1,745	0,6873785
1961	1	353	324	0,62	0,613	0,394	0,607	1,45720565
1962	1	353	325	1,59	1,645	1,654	1,629	0,61023315
1963	1	353	326	0,54	0,583	0,461	0,572	0,22273864
1964	1	353	327	0,85	0,952	1,089	0,963	0,1509673
1965	1	353	328	0,88	1,015	1,043	1,041	0,24084057
1966	1	353	329	0,72	0,85	0,824	0,855	0,11709688
1967	1	353	330	0,42	0,502	0,531	0,516	0,12204663
1968	1	353	331	0,61	0,732	0,666	0,723	0,05437651
1969	1	353	332	0,71	0,849	0,725	0,844	0,23900209
1970	1	353	333	0,87	1,027	0,888	1,017	0,21312198
1971	1	353	334	0,34	0,394	0,25	0,378	0,37059466
1972	1	353	335	0,75	0,851	0,762	0,832	0,57975685
1973	1	353	336	0,59	0,654	0,471	0,642	0,2721654
1974	1	353	337	1,89	2,05	1,921	2,039	0,87957013
1975	1	353	338	1,22	1,301	1,115	1,292	0,33516861
1976	1	353	339	1,65	1,739	1,854	1,737	0,6688523
1977	1	353	340	0,95	0,996	1,151	1,021	0,02305168
1978	1	353	341	1,06	1,111	1,427	1,154	0,08414571
1979	1	353	342	0,86	0,906	1,169	0,966	0,18455487
1980	1	353	343	0,78	0,829	0,998	0,865	0,00417193
1981	1	353	344	1,23	1,323	1,425	1,351	0,38346401
1982	1	353	345	0,67	0,732	0,717	0,74	0,43529493
1983	1	353	346	1,07	1,189	1,273	1,198	0,11511698
1984	1	353	347	1,1	1,246	1,217	1,251	0,19530289
1985	1	353	348	0,52	0,601	0,644	0,612	0,31777379
1986	1	353	349	0,26	0,307	0,411	0,322	0,21778889
1987	1	353	350	0,74	0,889	0,844	0,889	0,03181981

1988	1	353	351	1,01	1,235	1,081	1,237	0,38417111
1989	1	353	352	1,22	1,52	1,382	1,511	0,27202398
1990	1	353	353	0,57	0,724	0,641	0,708	0,18285781
								8,0504107
								7,80886303
								7,53712189
								7,83410674
								7,42009572
								7,75222377
								7,72570727
								8,18419531
								7,73935443
								8,06356289
								7,73023275
								7,49794818
								7,52962656
								7,37413378
								7,58732647
								8,04489527
								7,56003215
								7,72436377
								8,22202552
								7,81282283

Table 2 Parameters calculated for the standardized dendrochronology of Sapelli

Characteristics	Ayous	Sapelli
Mean age ± SE	200±10	350±20
Mean EPS (standard)	0.89	0.98
Mean R bar(standard)	0.427	0.675
Mean Sensitivity (standard)	0.375	0.51
Standard Deviation (standard)	0.355	0.497
First-order partial autocorrelation (standard)	0.142	0.126

Table 3 main characteristics of species chronologies

The detrended TRW chronologies (TRWstandard) of both tree species were strongly correlated with one another ($r = 0.876$; $P < 0.01$) during their life trend. High EPS values (Table 3; greater than 0.85) in both species indicate that constructed chronologies from detrended individual TRW series were representative of radial growth variations of the whole population of trees (Wigley, Briffa & Jones 1984). There was also good coherence among individual growth series (high mean r-bar; Table 3). The r-bar and MS values were higher in the Sapelli than in the Ayous stands (Table 3), thus indicating that in Sapelli stands there is a stronger common

growth signal and greater year-to-year radial growth variability associated to inter-annual changes
in climatic conditions. Furthermore, the standard deviation of the chronology was larger in Sapelli species than in Ayous stands (Table 1), suggesting that radial growth responses to extreme environmental events are stronger in the former.

Preliminary conclusion

We show, as preliminary results, that the Sapele and Ayous species increased their growth trends during the last century (from 1900) possibly due to the effect of CO_2 fertilization coming from anthropogenic sources. Of course, this hypothesis should be verified on a significant sample of the populations of the tree. Further analyses will clarify this preliminary conclusion and move deeper inside in physiological explication. These first results suggest that it will be crucial to increase researches to find answers for the main questions on greenhouse-gasses emissions and the role of tropical forest dynamics (carbon intake/emissions/growth) in adapting to climate change.The authors believe that a comparison between pre- and post-industrial growth rates will require younger and older trees of the same species growing in the environment exposed to different CO_2 levels. This will eliminate any rate of growth introduced by the age of tree.

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Conclusions

Rainforests provide important services, now we call “ecosystem services”, including buffering against flood and drought, storing carbon from atmosphere, stabilizing soils, influencing rainfall patterns and providing habitats to wildlife and indigenous people. While rainforests are fundamental to human beings, they are rapidly being destroyed by activities of civilizations. The first cause of deforestation is conversion of forest land for agriculture. If in the past subsistence agriculture was the primary driver of rainforest conversion, today industrial agriculture — especially monoculture and livestock production — is the dominant driver of rainforest loss worldwide. As I show in the Chapter 1 logging, even if selective, represents the biggest cause of forest degradation and usually proceeds deforestation for agriculture.

Findings in Chapter 1 suggests that selective logging has several important negative effects on forest structure, dynamics, biodiversity and ecosystem services and that these effects can be truly evaluated only in the long term by analysing the evolving dynamics of repeated logging and not the mean structural values but the normalized indices.

I suggest that the attention should be paid not just to totally destructive practices such as deforestation (clearcutting) for alternative land uses (crops or grazing, commonly in the Amazon, or the palm oil plantations that are typical of South-east Asia), but also to the selective logging of the last virgin forests of Africa, which may be a more serious cause of forest degradation than what has been thought to date. The question rose in these last years and confirmed from the analyses of paper results suggest that it will be crucial to increase research about the key issues for forest management and conservation and particularly if selective logging is really sustainable for primary tropical forests.

In the Chapter 2 I continued the researches on the alteration of forest dynamics due to selective logging and I proposed a model for localized disturbances. From the data collected to validate the equilibrium model of canopy height and plant diversity, I found the evidences of a decreasing of plants diversity in tropical forest subject to selective logging respect to the same but untouched forest. This seems due to the local disturbance which involve the invasion of open space left by logged trees by weed, vines and climbers at the expense of the late-successional state cenosis. Although up to now there is not a well defined correlation between canopy height and biodiversity (which is discussed in Chapter 3) it is clear that the highest levels of biodiversity reside in the untouched forests. This finding calls for an urgent adaptation and mitigation response aimed at protecting and enhancing the forest conservation through specific interventions, both in terms of policy and management and regulatory mechanisms, to prevent human pressure on tropical areas. My work confirms the importance of

using dynamic, deterministic models for identifying vulnerabilities and thresholds while assessing the impacts of anthropogenic activities.

Moving forward, in Chapter 3, I combined data derived from the new global canopy map developed by NASA through the LiDAR survey of Earth and the global map of vascular plant produced by the Nees-Institut für Biodiversität der Pflanzen to show that there is a global positive correlation between forest canopy height and biodiversity and that it follows a latitudinal gradient. The combination of stratification (height/biodiversity relation), climatic factors (humidity and temperature) and productivity and evolutionary history allows species to fill the ecosystem niche in a fractal way and could be the key to understand why tropics are so diverse as discussed in Chapter 4.

I combined the species pool size and the fractal nature of ecosystems to clarify some general patterns of latitudinal gradient of biodiversity. The patterns described in this chapter, can be synthesized as the "cauliflower hypothesis of biological diversity" and although they could appear oversimplified, they can be also extended to altitudinal gradients and shed more light on ecological and evolutionary processes which shape biodiversity on Earth.

Finally, looking behind in climatic history in Chapter 5 I tried to understand the effects of greenhouse-gasses (GHG) emissions after the Industrial Age and their effects on growth trends of tropical trees born in the 17^{th} century .

I show, as preliminary results, that the Sapele and Ayous species studied in tropical forests of Africa increased their growth trends during the last century (from 1900) possibly due to the effect of CO_2 fertilization coming from anthropogenic sources. Further analyses will clarify this preliminary conclusion and move deeper inside in physiological explication. These first results suggest that it will be crucial to increase researches to find answers for the main questions on greenhouse-gasses emissions and the role of tropical forest dynamics (carbon intake/emissions/growth) in adapting to climate change.

In conclusions, I need to say that forests are worldwide often seen as resources providers and even if it is true for an economical point of view, the science of ecology should move beyond this mechanistic consideration and see them as not only ecosystems but as fundamental and indissoluble parts of the bigger system we call Earth. As organs of who the two science outsider James Lovelock and Lynn Margulis called "Gaia". Being nominated Doctor in Philosophy we have the moral imperative to be outsiders and to merge science with ethical issues, because one without the other is a mere speculation on mechanical parts and ecology is all but the study of distinct elements. Ecology is the study of life, nothing else that a long evolution of associations.

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