Spatial patterns of West-African plant diversity along a climatic gradient from coast to Sahel

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1. General introduction

Biodiversity comprises the variety of life on Earth at all its levels, from genes to ecosystems, through species, populations and communities including the ecological and evolutionary processes that sustain it (Gaston 1996; Williams & Humphires 1996). Within the last decades biodiversity became a central topic of social, political and scientific discussion. The currently most recurrent issues relative to biodiversity are its conservation and sustainable use. The increasing interest to biodiversity is mainly due to the increasing public awareness of its essential role to assure human well-being and survival by providing food, medicine and other important products (Chapin *et al.* 2000; Loreau *et al.* 2001; Millenium Ecosystems Assessment 2005b; Díaz *et al.* 2007; Hector & Bagchi 2007). The reason of this increasing interest in biodiversity is the overall threat to its maintaining, leading to its loss, caused by different factors such as climate change, strong demographic growth of the world and different destructive land used types (Baillie *et al.* 2004; Millenium Ecosystem Assessment 2005a). This threat is more accentuated in areas with high population density and growth, which has as direct consequences the increasing need for resources leading to an overexploitation, overgrazing and deforestation.

There is thus a general consensus that biodiversity is under assault on a global basis and that species are being lost at a pronouncedly enhanced level (Lawton & May 1995; Royal Society 2003). In response to that, over the last two decades, several prominent international organizations as well as the scientific community have engaged in developing regional, continental, and global schemes (UNCBD 1992; Dinerstein *et al.* 1995; UNEP 2002b; UNEP 2003c) to capture and prioritize substantial new flows of conservation investment (Dalton 2000; Myers & Mittermeier 2003; Whittaker *et al.* 2005).

An important component of biodiversity is its spatial patterning. The structure of communities and ecosystems (e.g. the number of individuals and species present) can vary in different parts of the world. Similarly, the function of these communities and ecosystems (i.e the interactions between the organisms present) can vary from one place to another. Different assemblages of ecosystems can characterize quite diverse landscapes that cover large areas. These spatial patterns of biodiversity are affected by climate, geology, and physiography (Redford & Richter 1990). Understanding plant species distribution patterns and the underlying factors is hence a crucial step for the conservation and management of plant communities and ecosystems.

Thus, to achieve an effective conservation of biodiversity, a central prerequisite is the biogeographic and macroecologic analysis of the factors and processes that determine the contemporary, and potentially also the future geographic distribution of species (Porembski 2003; Balmford *et al.* 2005; Brooks *et al.* 2006). These analyses include, for example, the identification of centers of species richness and centers of endemism (Barthlott *et al.* 1999; Kier & Barthlott 2001; Jetz *et al*. 2004; Lennon *et al.* 2004, Küper *et al.* 2004), the influence of different historical processes and biotic factors on biodiversity, the delineation of biogeographical regions from national to global scale (Wallace 1876; Engler 1879; Williams *et al.* 1999; Houinato 2001; Linder 2005) and the analysis of the impact of climate change on species distribution and biogeographic regions (Iverson 2001; Morin 2006; Sommer 2008).

In the present thesis we are interested in the analysis of species richness and the delineation of biogeographical regions, as well as the analysis of the potential impact of climate change on species distributions and on the phytogeographical regions in West Africa.

1.1 Spatial patterns of biodiversity

There are general, perhaps universal, patterns of biodiversity that have led to a plethora of hypotheses concerning their underlying processes. Species richness increases with the area sampled commonly known as species-area relationship (Arrhenius 1921; Preston 1962; Williams 1964; Connor & McCoy 1979; Rosenzweig 1995; Lomolino 2000; Williamson *et al.* 2001; Kreft *et al.* 2008). Moreover a well-documented and most general pattern in macroecology is the decrease in species richness (for most taxonomic groups) from the equator towards the poles, and generally high species richness in hot and humid places (Fischer 1960; Pianka 1966; Stevens 1989; Gaston 1996a; Rohde

1998; Field 2002; Mutke & Barthlott 2005; Lomolino 2005). However, other factors such as elevation gradients, changes of temperature, humidity, productivity, strongly affect the distribution patterns of species richness (Rahbek 1995; Rahbek 1997; Lomolino 2001; Braun *et al.* 2002; Grytnes & Vetaas 2002)

Biodiversity mapping: Biodiversity maps are useful for several reasons (Gaston 1998a). First, biodiversity maps provide concise, primary information about a highly complex phenomenon, i.e., the spatial distribution of biological diversity. Second, species richness (e.g. Barthlott *et al.* 1996; Barthlott *et al.* 1999a; Barthlott *et al.* 2005) can be much better illustrated than for instance depictions of latitudinal gradients (see Ruggiero & Hawkins 2006 and Kier *et al.* 2006 for a more detailed discussion). Biodiversity maps may thus be helpful to explore putative mechanisms and environmental factors contributing to these patterns. Spatial information on biodiversity distribution may also be important for conservationists and decision makers or may be useful for educational purposes (Brooks *et al.* 2006; Kier *et al.* 2006).

An obvious strategy to conserve plant biodiversity is to map distributional patterns and look for concentrations of diversity and endemism (Gentry 1992). Further, the management of forest requires understanding of its composition in relation to other forests, the effects of past impacts on the present status and the present relationship of the forest with surrounding land uses.

Biodiversity mapping approaches: Two basics approaches are used to map patterns of species richness at a broad scale (Barthlott *et al.* 1999a): the taxon-based approach and the inventory based-approach.

In the inventory based biodiversity mapping approach (Barthlott *et al.* 1999a), the data used are derived from species inventories within geographical units which can be represented by a variety of political boundaries (i.g., countries, provinces) or natural geographical areas (i.e. deserts or mountain ranges). These are, for example the total number of species or families, but also the taxon numbers of selected groups in a given region. The inventory based approach has been frequently applied to map the global richness pattern of vascular plants (Barthlott *et al.* 1996; Barthlott *et al.* 1999a; Barthlott *et al.* 2005; Mutke & Barthlott 2005) and for geo-statistical analyses of relationships between species richness and environmental variables (Mutke 2000; Mutke & Barthlott 2000; Mutke 2002a; Mutke 2002b; Mutke *et al.* 2002; Mutke & Barthlott 2005). Major constraints of this approach are related to complications with the data used and to some methodological issues in the analyses: inventory-based data do not provide any information on the taxonomy, ecology, or range-size related aspects of the diversity of an area. Given the low resolution of the data used, diversity maps are produced with a coarse spatial precision. Moreover, the geographical units involved in this approach are of different size, making comparisons between units difficult.

The taxon-based approach refers to information on the distribution of individual taxa (Barthlott *et al.* 1999a). In this approach, distribution maps of individual species are superimposed and the number of species is given per standard geographic units (e.g., grid cell) by simply counting the number of intersections between the range maps of all single species. The main sources of information on species occurrences worldwide stem from expert knowledge, museums, herbaria or other natural history collections (Graham *et al.* 2004). At the continental scale of Africa, data from natural history collections have been extensively used for analyzing plant richness (Linder 1998; Lovett *et al.* 2000; Linder 2001; Küper *et al.* 2004b; Küper *et al.* 2006). The main advantage of taxon-based diversity mapping is that measures of species richness can be reassigned to certain species pools, which allows the analysis of range size and endemism patterns as well as the complementarity of the species composition across different areas. Moreover, expert range maps have been frequently used to guide broad-scale conservation strategies, because they contain information on complementarity (Stuart *et al.* 2004; Ceballos *et al.* 2005; Ceballos & Ehrlich 2006; Grenyer *et al.* 2006). A major drawback of this approach is the frequent shortfall of reliable species distribution data. Furthermore, depending on the degree of knowledge and generalization, this approach may produce overestimated distribution ranges as compared to their real occurrences.

In this study we use the taxon-based approach to analyze the diversity patterns of vascular plants in West Africa based on a multi-sources database (Chatelain *et al.* 2002; Schmidt *et al.* 2005) with a relatively high spatial resolution of approximately 10km x 10km grid size.

***Species distribution modeling*: A great constraint in biodiversity mapping is the availability of sufficient data on species distribution ranges. Indeed, it is unrealistic to completely explore a large area (i.e. from national to global scale) to compile extensive data on the distribution of individual species from a given taxonomic group. A surrogate is to apply predictive species distribution models which are empirical models relating field observations and environmental variables based on statistically or theoretically derived response surfaces (Guisan & Zimmermann 2000; Guisan & Thuiller 2005) in order to fill gaps in data availability on a species in a given area. Maps of potential species distribution ranges are derived on the assumption that species distribution areas are more determined by different environmental factors (Guisan & Zimmermann 2000; Scott *et al.* 2002). Many previous studies have shown at different spatial scales good correlation between species richness and different climatic factors such as annual precipitation, actual and potential evapotranspiration and temperature (i.e. Wright *et al.* 1993; Jetz & Rahbek 2002; Mutke *et al.* 2002; Francis & Currie 2003; Hawkins *et al.* 2003a; Currie *et al.* 2004; Field *et al.* 2005; Mutke & Barthlott 2005). Species distribution models constitute a valuable tool for decision-makers in biodiversity conservation, invasive species monitoring and other natural resources management fields. A great range of algorithms developed within the last decade allow to predicting the potential distribution ranges of species. In this study, distribution ranges of the investigated species have been predicted by the mean of one of the most commonly used and most powerful algorithm, the Maximum Entropy approach (MaxEnt; Phillips *et al.* 2004; Phillips *et al.* 2006).

1.2 Delineation of biogeographical regions

The delineation of biogeographical regions based on floras and/or faunas is one of the most important features in ecological biogeography (Dufrêne & Legendre 1991). Moreover, knowledge about spatial patterns and location of ecologically homogenic entities is a major precondition for priority setting and representative area selection approaches in conservation biology and policy (Olson *et al.* 2001; Kier *et al.* 2005).

The delineation of biogeographical regions has a long history; since 1876 biogeographers started dividing the world into floral kingdoms and fauna regions (Wallace 1876; Engler 1879). From continental to regional extent in Africa, several authors in earlier studies defined biogeographical regions (Chevalier 1933; Lebrun 1947; Aubréville 1949a; Aubréville 1949b; Monod 1957; Trochain 1970; White 1979; White 1983; Guinko 1983; Adjanohoun *et al.* 1989). All these studies are solely based on the knowledge of the authors, and that of people, who much like them, had travelled broadly and had noted the composition of floras and faunas. Later, analytical approaches have worked their way into biogeography, and clustering procedures are now commonly employed (e.g. Williams *et al.* 1999; Qians 2001; Kingston *et al.* 2003).

The delineation of homogeneous areas based on present-day floras is one of the typical challenges in ecological biogeography. Clustering methods represent one of the interesting approaches to solve this problem (Birks 1987; Legendre 1990). These methods can also be applied on our datasets to search for geographically homogeneous areas.

A set of criteria, which could be summarized in four main categories are used to distinguish biogeographical regions (see Senterre 2005 for a detailed review): (1) floristic criteria generally used when dealing with large areas (global to continental scale) are based on species distributions and floristic or faunistic composition of the regions concerned; (2) physiognomic criteria used to delineate regions based on the physiognomy of the different types of vegetations present in the investigated area (Trochain 1970; Aubréville1962; Olson *et al.* 2001); (3) phytosociological criteria used (generally at a relatively small scale) to classify vegetation types are based on the analysis of plant communities; (4) ecological criteria used in the definition of regions (known as bioclimatic regions) take into account different climatic parameters such as rainfall, temperature, potential evapotranspiration and soil type.

In this study we based our analysis on species composition of standard geographical units and on different environmental parameters to redefine potential phytogeographical regions in the area.

1.3 Biodiversity and climate change

Emissions scenarios and projection of future climate change: The world’s climate is continuing to change at rates that are projected to be unprecedented in recent human history. The forth assessment report of the 2007 International Panel on Climate Change (IPCC 2007) indicates that the global average surface temperature increased by about 0.6 °C during the twentieth century, and that most of the warming observed over the last 50 years is attributable to human activities. The IPCC climate model projections for the period between 2000 and 2100 suggest an increase in global average surface temperature of between 1.4 and 5.8 °C. Some works have even indicated that the temperature increases to 2100 may be larger than those estimated in 2001 (Stainforth *et al.* 2005; Lovelock 2006). According to the IPCC Special Report on Emissions Scenarios (SRES, 2000), there are four groups of scenario families (A1, A2, B1 and B2) that explore alternative development pathways, covering a wide range of demographic, economic and technological driving forces and resulting greenhouse gas (GHG) emissions:

The **A1** storyline assumes a world of very rapid economic growth, a global population that peaks in mid-century and rapid introduction of new and more efficient technologies. A1 is divided into three groups that describe alternative directions of technological change: fossil intensive (**A1FI**), non-fossil energy resources (**A1T**) and a balance across all sources (**A1B**).

A2 describes a very heterogeneous world with high population growth, slow economic development and slow technological change. No likelihood has been attached to any of the SRES scenarios.

B1 describes a convergent world, with the same global population as A1, but with more rapid changes in economic structures toward a service and information economy.

B2 describes a world with intermediate population and economic growth, emphasising local solutions to economic, social, and environmental sustainability.

Projected warming in the 21st century shows scenario-independent geographical patterns similar to those observed over the past several decades. Warming is expected to be greatest over land and at most high northern latitudes, and least over the Southern Ocean (near Antarctica) and northern North Atlantic, continuing recent observed trends (Figure 1.1).

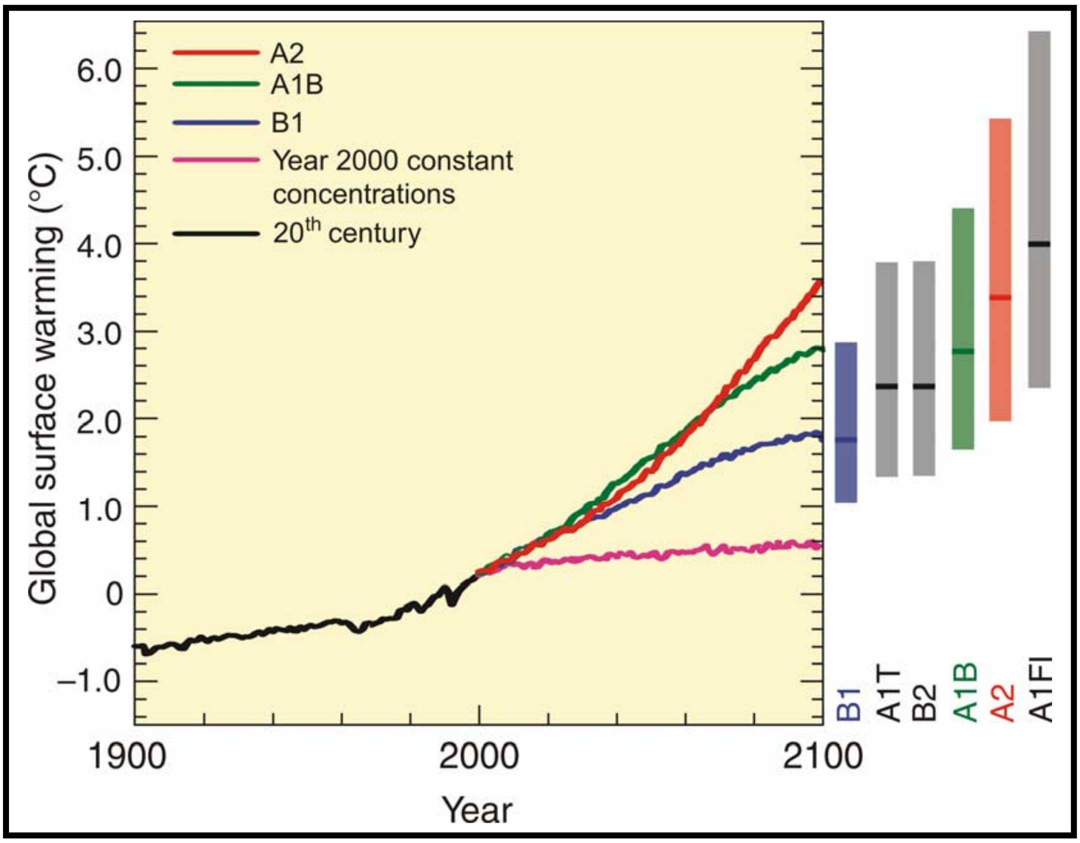


Figure 1.1: Modelled global mean surface temperature rise according to IPCC – SRES scenarios A1T, A1B, A1F1, A2, B1 and B2 (multimodel averages). Solid lines show the predicted continuations of the 20th century simulations. The bars in the middle of the Figure indicate the best estimate (solid line within each bar) and the range amongst the different scenarios for 2090 – 2099. *Source: IPCC Fourth assessment Report 2007*

Impact of climate change on ecosystems: According to the IPCC fourth assessment report, the resilience of many ecosystems is likely to be exceeded within this century by an unprecedented combination of climate, associated disturbances (e.g. flooding, drought, wildfire, insects) and other global change drivers (e.g. land-use change, pollution, fragmentation of natural systems, overexploitation of ressources). Approximately 20 to 30% of plant and animal species assessed might be at increased risk of extinction if increases in global average temperature exceed 1.5 to 2.5 ° C. According to the increases in temperature there are projected to be major changes in ecosystem structure and function (e.g., vegetation types or biogeographical regions), species' ecological interactions and shifts in species geographical ranges, with predominantly negative consequences for biodiversity and ecosystem goods and services.

This study investigates the potential impacts of climate change on vascular plant species richness at the regional scale across West Africa. This area is also known for its variety of phytogeographical regions; in the present work potential impacts of climate change on these regions are also evaluated.

1.4 General features of West African plant biodiversity

The wide range of ecosystems (forests, savannas, Sahel, rivers, mountains, mangroves) due to the variety in environments in West Africa, including topographical variation, a range of soil types, and sometimes very steep climatic gradient, makes the region rich in biodiversity.

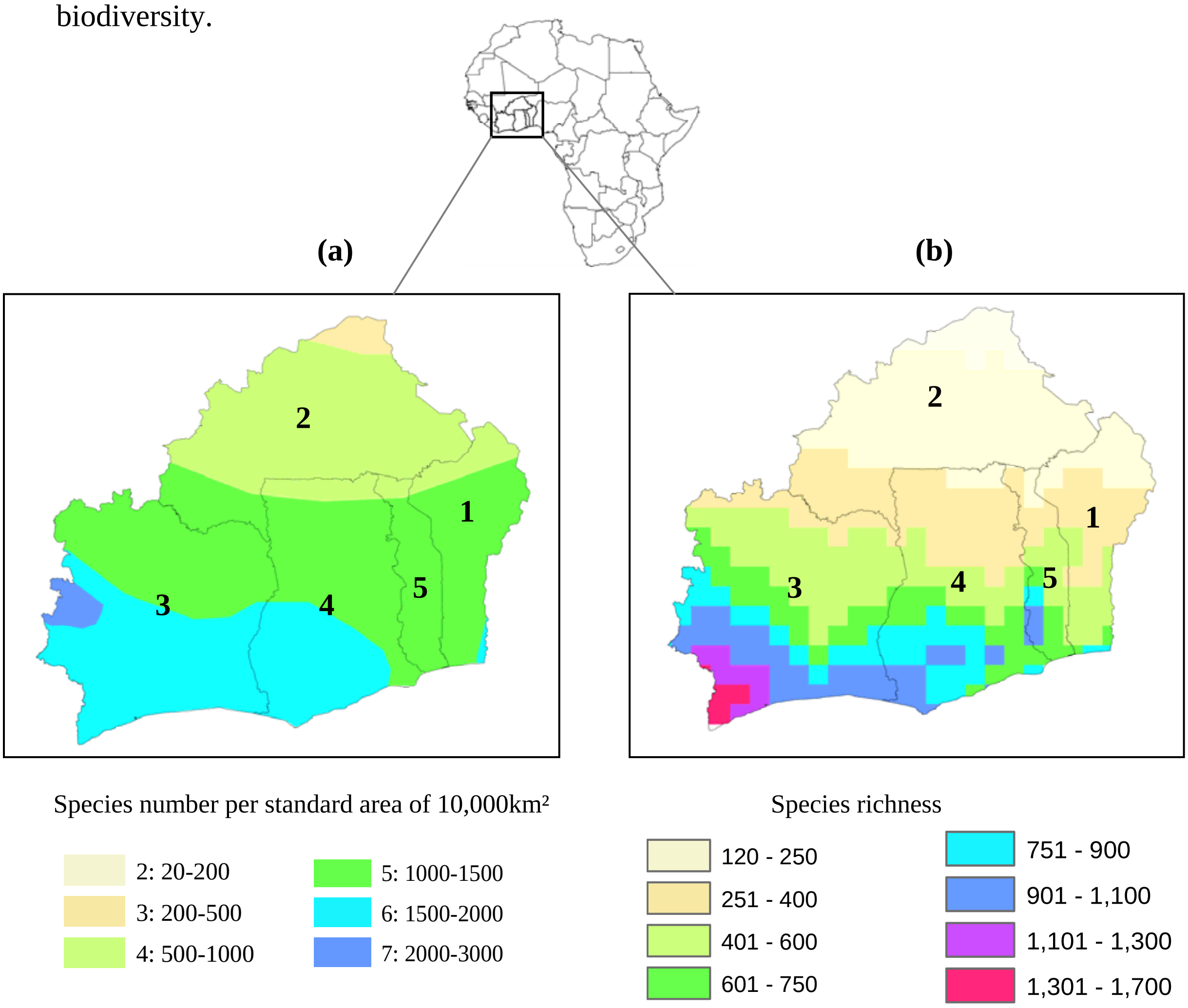


Figure 1.2: Plant species richness patterns in West Africa according to: (a) Barthlott *et al.* 2005; (b) Sommer, 2008. **1:** Benin; 2: Burkina Faso; **3**: Côte d'Ivoire; **4**: Ghana; **5**: Togo

This great variation induces an uneven distribution of biodiversity in general and vascular plant species in particular across the area (Figure 1.2, Barthlott 2005; Sommer 2008).

The rainforests of West Africa have been marked as one of the world's hotspots of biodiversity where exceptional concentrations of species with high levels of endemism face exceptional threats of destruction (Myers *et al.* 2000, revised by Küper *et al.* 2004b): Indeed it is estimated that this region contains 2800 vascular plant species, of which 650 species (c. 23 %) are endemic, and c. 400 species are considered to be rare (Poorter 2004). But these endemic species are threatened by deforestation, habitat fragmentation, and over-exploitation. The process of deforestation in Africa, which is mainly due to shifting cultivation and timber exploitation, is proceeding at an alarming rate. From 1990 to 2000, 12 millions hectares of forest have been cleared in West Africa (FAO 2001b). According to the FAO's study conducted from 1990 to 1995 (FAO 1995), the highest annual rate of African forest and woodland destruction occurred in West African countries such as Togo (1.44%), Ghana (1.26%), Bénin (1.25%), Guinea (1.12 %), Côte d'Ivoire and Nigeria (0.86%).

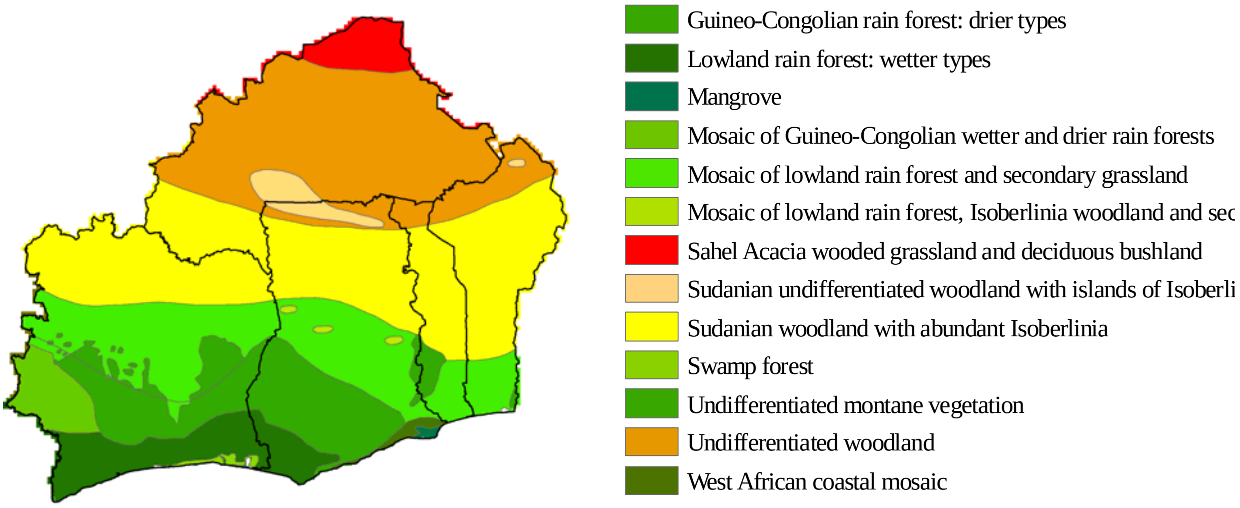


Figure 1.3: Vegetation zones of West Africa according to White (1983)

1.5 Institutional background of the thesis

This thesis has been conducted at the Nees Institute for Biodiversity of Plants (formerly the Department of Systematics and Biodiversity of the Botanical Institute) at the Rheinische Friedrich-Wilhelms Universität Bonn. Since 1995, the BIOMAPS working group (Biodiversity Mapping for Protection and Sustainable Use of Natural Resources, www.nees.uni-bonn.de/biomaps) focuses on the mapping and macroecological analysis of broad-scale of biodiversity (Barthlott *et al.* 1996; Barthlott & Winiger 1998; Barthlott *et al.* 1999a; Mutke *et al.* 2001; Barthlott *et al.* 2003; Barthlott *et al.* 2005; Kier *et al.* 2005; Mutke & Barthlott 2005; Barthlott *et al.* 2007; Kreft & Jetz 2007; Kreft *et al.* 2008).

The Nees Institute of Biodiversity of Plants, through its BIOMAPS working group is one of the numerous institutions working in the frame of the BIOLOG-BIOTA Africa research network supported, since its foundation in 2001, by the German Federal Ministry of Education and Research. The overall aims of BIOTA ("Biodiversity Monitoring Transect Analysis in Africa", www.biota-africa.org) are, among others, "to assess zoological and botanical biodiversity, its structural features and spatial patterns at various spatial scales, to assess the effects of anthropogenic land use and climate change, and to develop analytical and predictive tools for decision-making in the context of environmental and development policy" (BMBF 2003).

2. Aims of the study

The present study analyzes the spatial patterns of plant species diversity, the structure of phytogeographical regions on the basis of species composition and their possible change in the future under the effect of the climate change.
The study is divided in three main chapters:

Chapter 3: Patterns of vascular plant species richness along a climatic gradient and across protected areas in West Africa. Here, we model the potential distribution of species richness in West Africa at a relatively high spatial resolution (10km x 10km grid cell) on the basis of the distribution of 3,393 individual vascular plant species. We determine potential areas of species richness in the area of West Africa covering five countries (Bénin, Burkina Faso, Côte d’Ivoire, Ghana and Togo). We also investigated the effectiveness of the existing network of protected areas at regional and national scale by determining the proportion of covered species.

Chapter 4: Quantitative delineation of phytogeographical regions based on modeled plant species distributions in West Africa. In this chapter, we analyze the variation in species composition among sites (grid cells) across the region in order to identify and spatially represent areas with similar species composition. Clustering techniques are applied to define potential phytogeographical regions in West Africa, and the resulting patterns are compared to classical approaches (White 1983).
Finally, the importance of each defined phytogeographical region in terms of species richness and their value of sheltering range-restricted or endemic species are evaluated.

Chapter 5: Prediction of species richness and shift in phytogeographic regions under climate change in West Africa. In this chapter we evaluate the potential effect of climate change on the distribution range of species and the species richness pattern according to the A2 and B2 - IPCC climate scenario from two different models at different periods of time until 2080. We also estimate potential shift in phytogeographical regions induced by future climate change.

3. Patterns of vascular plant species richness along a climatic gradient and across protected areas in West Africa

3.1 Abstract

Knowledge on spatial patterns of biological diversity is fundamental for ecological and biogeographical analyses and for priority setting approaches in nature conservation.

Here we present a map of vascular plant species richness in West Africa (for the countries of Benin, Burkina Faso, Côte d’Ivoire, Ghana and Togo) based on the potential distribution of 3,393 species derived from natural history collections and field collections databases. We used the maximum entropy approach (MaxEnt) to model the geographic distribution of each species at a fine spatial resolution of 10km by 10km grid cell size and produced a species richness map by superimposing the distribution ranges of all species. Species richness decreases along the major temperature and precipitation gradient with high species number in the south and lower number towards the north. Our results show a very strong positive correlation ($r^2 = 0.93$ and $r^2 = 0.94$) between patterns of species and family richness supporting the feasibility of using higher taxa to dentify priority sites for conserving biodiversity in the region.

We identified regional centers of plants species diversity and additionally denominated national centers of species richness by considering the 25% and 50% most species rich areas per country. All centers of plant species diversity are confined to humid areas in concordance to the high positive correlation between species richness patterns and rainfall which appears to be the most important delimiter for the distribution ranges of many species in the area.

We also investigated the effectiveness of the existing network of protected areas at regional and national level by calculating the proportion of species they cover. While at regional scale 95% of all species are adequately represented by protected areas according to their potential distribution ranges, this proportion is considerably lower for some countries when considered separately.

Keywords: Species and Family richness, Vascular plant, Centers of species richness, Species distribution modeling, Protected Areas, West Africa.

3.2 Introduction

Describing and understanding the geographic patterns of species distributions and biodiversity are a major goal in ecology (Schall & Pianka 1978; Wright 1983; Rohde 1992; Gaston 2000a; Jetz & Rahbek 2002; Hawkins *et al.* 2003a; Currie *et al.* 2004; Ricklefs 2004). Knowledge on the spatial distribution of biodiversity is crucial for its further exploration, sustainable use and conservation (Mutke & Barthlott 2005). Among many principles used to guide conservation and management, an effective way to conserve biodiversity and sustain key ecological functions at different spatial scales from global to local extent, is the protection of locations with high species numbers (Scott *et al.* 1987; Pressey & Nichols 1989; Myers *et al.* 2000; Howard *et al.* 1998). In other words species richness is assumed to be one important indicator of conservation value (e.g., Meir *et al.* 2004) and identification of geographic centers of species richness and endemism constitute a central prerequisite in any conservation plan (Davis *et al.* 1994; Heywood *et al.* 1995; Gaston 2000; Purvis & Hector 2000; Mutke & Barthlott 2005).

Because of the respective importance of investigating species richness, ecologists have put considerable effort into documenting species richness and developing methods to identify potential predictors of species richness for different taxonomic groups. One of the most concerned taxonomic group are vascular plants which are considered as indicator group for overall biodiversity investigation given their central role as primary producers and providers of habitat space and structure in terrestrial ecosystems. Moreover, the distribution of plant species is relatively well known as compared to many other taxa as most animal groups, i.e. insects and arthropods (Barthlott *et al.* 1999; Meyers *et al.* 2000).

The investigation of spatial patterns of biodiversity at a sufficient accuracy is strongly hampered by the availability of qualitatively and quantitatively comprehensive data on species distributions. This is the case because it is practically not possible to explore a relative large area (i.e. regional and national extent) to collect distributional data of species in each cell in order to determine the number of species it contains. Yet, the more accurate the spatial information, the more effective can conservation actions be. One way to deal with this shortage is to apply predictive species distribution models which are empirical models relating field observations and environmental variables based on statistically or theoretically derived response surfaces (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). This allows filling gaps in data availability on a species in a given area. Maps of potential species distribution ranges are derived on the assumption that species distribution areas are determined by different climatic factors (Guisan & Zimmermann 2000; Scott *et al.* 2002) such as parameters related to annual precipitation and temperature which have been shown as most important factors shaping species geographic ranges in many previous studies (i.e. Wright *et al.* 1993; Jetz & Rahbek 2002; Mutke *et al.* 2002; Francis & Currie 2003; Hawkins *et al.* 2003a; Currie *et al.* 2004; Field *et al.* 2005; Mutke & Barthlott 2005; Kreft & Jetz 2007).

The use of numbers of higher taxa as estimators concords with several definitions of biodiversity, which explicitly recognize that the diversity of taxa in general, and not solely of species, are appropriate measures of biodiversity (Wilson 1992; Gaston 1994; Harper & Hawksworth 1994; Gastom & Blackburn 1995; Balmford *et al.* 1999).

In addition to the identification of geographic centers of species richness, a complementary step to evaluate the sustainable use and conservation of biodiversity is to test the efficiency of the existing protected areas (Fjeldså *et al.* 2004; Burgess *et al.* 2005). As a key component to maintain biodiversity (Rodrigues *et al.* 2004b; Chape *et al.* 2005), protected areas build the basis for comprehensive conservation efforts.

In West Africa, assessing biodiversity and understanding mechanisms of its change are difficult in many areas because of scarcity of qualitative and quantitative field data (Schmidt *et al.* 2005). And yet spatial information on biodiversity, in particular on vascular plants, is urgently needed because of the increasingly threat to biodiversity in the region due to deforestation, habitat fragmentation, over-exploitation and the currently observed climate change. Many previous studies have investigated spatial patterns of vascular plants diversity at the continental scale of Africa (Barthlott *et al.* 2005; Küper *et al.* 2005; Mutke *et al.* 2001; Linder 2001; Sommer 2008) using different approaches. While these studies have a continental extent, they are conducted at a relatively coarse spatial resolution and are based on only a fraction of the overall species occurring all over Africa. Studies at national scale in West Africa have investigated vascular plant diversity with relatively coarse spatial resolution (Schmidt *et al.* 2005) or are limited only to some families (Chatelain *et al.* 2002; Thiombiano *et al.* 2006). There is a wide range of protected areas in the region, according to the World Database on

Protected Areas (IUCN & UNEP, 2007), but very few of them are internationally recognized, the other being nationally designated. There is also no specific information on how well is the coverage of vascular plant species by the network of protected areas in the region.

In this chapter we modeled the potential distribution of species richness in West Africa, for the first time at a relatively high spatial resolution (10km x 10km grid cell) on the basis of the distribution of 3,393 vascular plant species (approx. 65% of all species estimated in the region). We determined potential areas of species richness in the area of West Africa covering five countries (Bénin, Burkina Faso, Côte d'Ivoire, Ghana and Togo). We also used modeled data at the family level to map in the region of West Africa the diversity of vascular plants. We then investigated the relationship between species richness and the most important environmental variables. We also evaluated the effectiveness of the existing network of protected areas at regional and national scales.

3.3 Data and Methods

Study area: We analyzed plant diversity patterns in the area located in West Africa between the latitudes 4°30’ and 15°05’N and the longitudes 8°30’ W and 3°55’E extending from the Atlantic coast to the Sahel area and covering five countries: Bénin, Burkina Faso, Côte d’Ivoire, Ghana and Togo. The study area has been partitioned into a grid of 12,152 pixels of ca. 10km x 10km (approx. 0.0833°) size each.

Species distribution data: We established a multi-sources database on vascular plant species distribution in the study area comprising 180,987 distribution records for 5,397 species in 576 genera and 224 families. The data originate mainly from herbarium specimens, as well as from taxonomic revisions and digitized distribution maps. This database is a combination of a set of autonomous data sources: the BISAP (Biogeographical Information System on African Plant Diversity, see Küper *et al.* 2004) database, the SIG-IVOIRE database (Gautier *et al.* 1999; Chatelain *et al.* 2002) and the OUA/VegDa database (Schmidt *et al.* 2005). The established database represents the best documented dataset on plant species distribution in the region. However, as we can notice on Figure 3.1 no collections are included for two countries (Ghana and Togo).

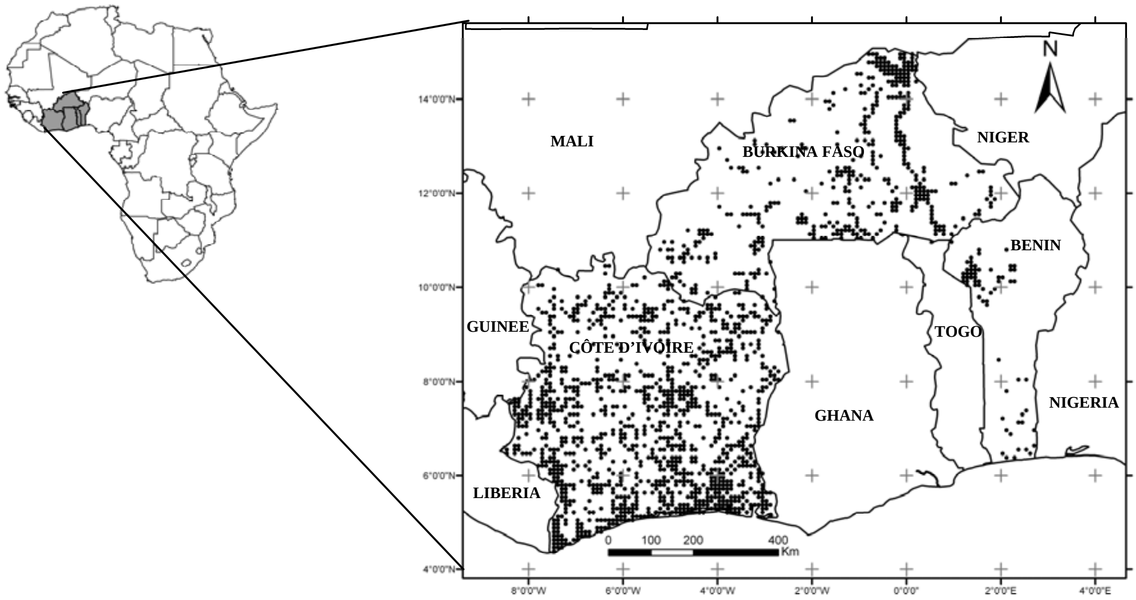


Figure 3.1: Data set comprising localities of 129,333 distribution records of 4,887 species across Bénin, Burkina Faso, Côte d’Ivoire. Each black dot represents at least one specimen at a spatial resolution of 10km grid cell size. As shown on Figure no data are available for Ghana and Togo.

Each occurrence locality is simply a latitude-longitude pair denoting a site where the species has been observed. Combining different data sources induces some inconsistencies in the final database to be used. First of all we proceeded to a pre-processing of the distribution data. The precision at which each species has been collected differ inside and between the databases, varying from 100 square meters to ca. 10,000 square kilometers. More than 90 % of all species (4,887 species in 129,333 distribution records) comprised in the common database have been collected with a spatial resolution of at least 100 square kilometers. We thus decided to use this resolution for the analyses. Duplicated records in each grid cell per species were excluded, as well as species with less than five collection points in the whole study area. Moreover, some taxonomic inconsistencies have been observed in the databases (taxonomic errors in the species names, presence of synonyms, presence of subspecies or varieties, species not completely identified and referred to as their genus followed by two or more coded letters given by the collector). These inconsistencies altogether induce an erroneous increase of the species number in the database by about 12%. “Cleaning” the database was hence a first and required step in order to avoid major artifacts in the results, though it appears to be time consuming.

Environmental data: The environmental variables used in this study fall into three categories: climate, elevation and land-cover. The climate variables are derived from data provided by the WorldClim database (Global Climate Data downloadable at *www.worldclim.org,* see Hijmans *et al.* 2005, for the documentation on the data). The climate variables are provided with an original spatial resolution of one square kilometer and comprise minimum, maximum and mean annual of precipitation and temperature. Data on the elevation are also available at the WorldClim database. In addition to climate parameters we used land-cover variables comprising among others, percentage of tree and herbaceous cover, percentage of bare ground cover and the annual average of spectral response values, downloaded from the Global Landcover website (GLC 2000, *http://glcf.umiacs.umd.edu/data/*). We rescaled all the environmental variables to a common resolution of 10km x 10km pixel size. Altogether, 16 environmental variables have been used in this study. A detailed list of all these variables is given in the Appendix 1.

Protected areas: We extracted data on protected areas for the study area from the 2007 Annual Release of the World Database on Protected Areas (IUCN & UNEP 2007; *http://www.wdpa.org/*). This database includes a set of 664 nationally designated (i.e. classified forests) and internationally recognized (IUCN categories I-IV) protected areas in our study area.

Niche-based models from presence-only data: The task of the modeling method is to predict environmental suitability for the species as a function of the given environmental variables. Geographic ranges for 3,393 species (approx. 63 % of all species comprised in the database) with more than five records have been modeled using MaxEnt (Philips *et al.* 2006). MaxEnt is one of the many available niche-based species distribution models, or environmental niche models (Segurado & Araújo 2004; Elith *et al.* 2006; Pearson *et al.* 2007; Tsoar *et al.* 2007; Costa *et al.* 2007), which currently play a central role in many areas of ecology, conservation and evolutionary biology, both because they can fill gaps in knowledge and because they allow a comprehensive estimate of multiple components of species diversity (Guisan & Zimmermann 2000; Araújo & Guisan 2006; Costa *et al.* 2007).

MaxEnt is a machine-learning method that estimates distributions of organisms by finding the probability distribution of maximum entropy (i.e., the most uniform) given the constraint that the expected value of each environmental predictor under this estimated distribution matches the empirical average of sample locations (Phillips et al. 2006). Different studies highlight the good quality of MaxEnt in predicting species distributions in comparison to other algorithms (see NCEAS: *http://www.nceas.ucsb.edu/*).

Dealing with the model transferability: Transferability is the possibility to predict a species' distribution in broad unsampled regions (Phillips *et al.* 2008; Peterson *et al.* 2007). As shown at Figure 3.1, we do not have any distributional data available for the region covering Ghana and Togo. However, the modeling approach allows filling the data gap in this region by extrapolating the distribution ranges of species over the entire study area, as long as the major environmental gradients for the entire study area is covered by distribution data elsewhere. We then proceeded to an "empirical validation" of the model output by simply comparing the modeled distribution ranges of some selected species with their overall documented distribution produced in a previous study (Poorter *et al.* 2004); see Appendix 2.

Species richness: For each species we recorded the area of occurrence predicted by the algorithm by transforming the probability value output of MaxEnt into a presence/absence value. We choose the 10 percentile training presence value as threshold, indicating that 90 percent of each species records with the highest predicted model values are counted as presence. One major problem in predicting species potential distribution range is the choice of an appropriate threshold. Because we are actually modeling richness and not individual ranges, we expect that problems of threshold estimates do not qualitatively affect the outcomes (Wisz *et al.* 2007). We produced the species richness map by superimposing the presence/absence distribution ranges of all 3,393 species and counting the number of intersections between these maps per grid cell.

For the purposes of providing more applicable tools for decision-makers, we decided to present the richness maps at the national scale of each country, by simply extracting the corresponding area (see Appendix 3).

Geographic centers of species richness: We looked for centers of species richness with a high concentration of species for the entire study area, and also at the level of each single country by selecting the 25 % and 50% of all grid cells with the highest species number.

Family diversity: The use of numbers of higher taxa as estimator concords with several definitions of biodiversity, which explicitly recognize that the diversity of taxa in general, and not solely of species, is an appropriate measure of biodiversity (Gaston & Williams 1993; Harper & Hawksworth 1994; Gaston *et al.* 1995). Justifying the use of higher taxa as surrogates requires good evidence that spatial differences in species richness are mirrored at other taxonomic levels (Prance 1994). We investigated the distribution pattern of species family richness based on species modeled distribution ranges.

Species richness and the distribution of protected areas: The purpose of this step of analysis is to highlight the proportion of vascular plant species covered by the network of the existing protected areas in the region. We overlaid the distribution of the existing protected areas on the species richness maps and extracted the number of species falling at least once inside any protected area (compare Sommer 2008). Because we are working at a spatial resolution of 100 km² (10,000 ha) grid cell size, we removed from the analysis all protected areas with a size of less than 10,000 ha. We also selected only grid cells overlapping at least by 50 % with protected areas (compare Sommer 2008).

Importance of environmental variables on species distributions: Among the outputs of MaxEnt a table giving the contribution of each environmental variable in predicting the distribution range of each species is provided. To know which variables contribute most to the distribution of all species in the area, we calculated the average contribution of each environmental variable over the all species that have been modeled.

3.4 Results

Plant diversity and spatial patterns of species richness: With its 4,887 species distribution records available at a spatial resolution of at least 100 square kilometer, 512 genera and 224 families, the database we established is the best available for the region. Figure 3.2 shows the most represented plant species families in the region.

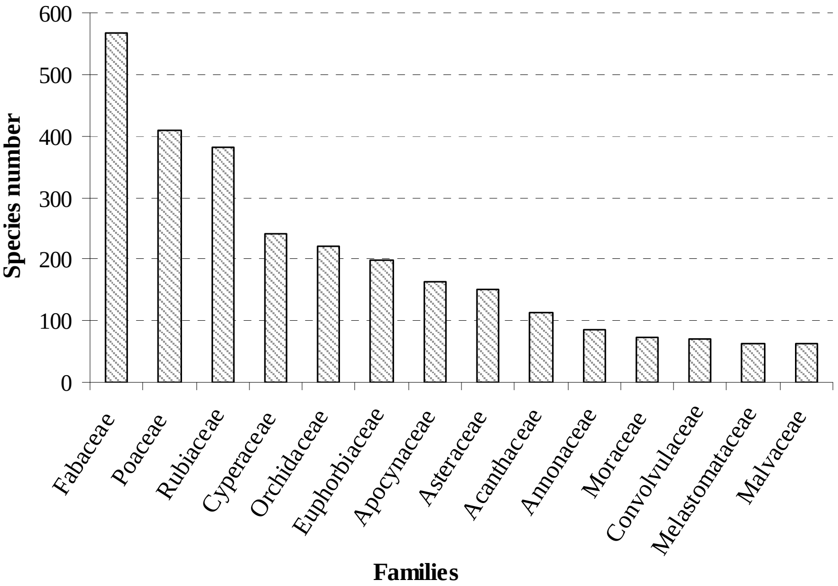


Figure 3.2: Floristic composition at family level – representation of the most speciose families from the database.

The frequency distribution of the geographic range sizes of species tends to be unimodal with a strong right-skew. That means, most species have relatively small range sizes, and very few have relatively large ones according to the documented database (Figure 3.3). The average number of collections per species is 11.55. The same tendency is also observed with the modeled data, but with an increase in the proportion of species having their range extended.

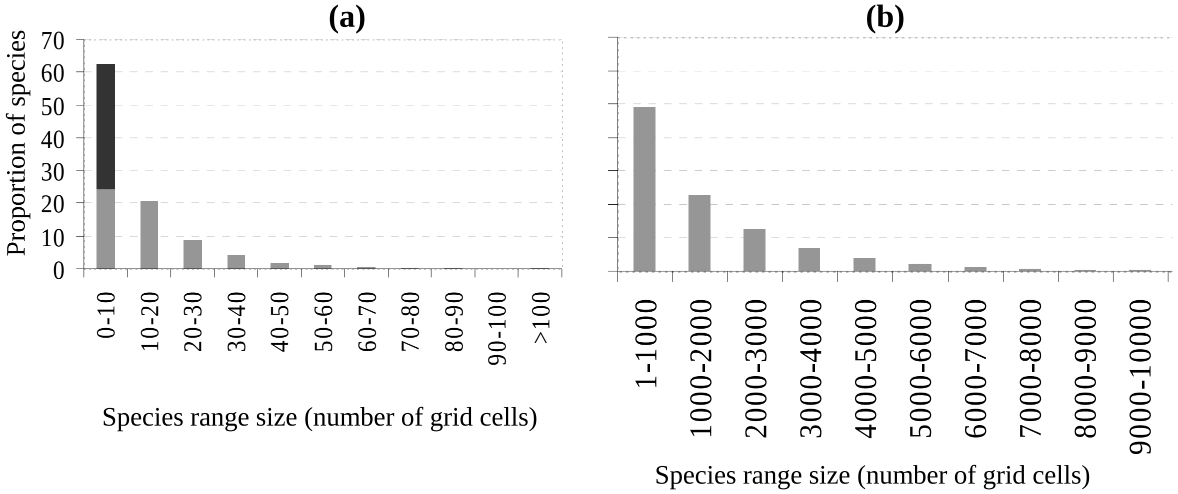


Figure 3.3: Species-range distribution in the study area of West Africa:
(a) based on documented data; dark bar indicates percentage of species with less than five collection points; (b) based on modeled data

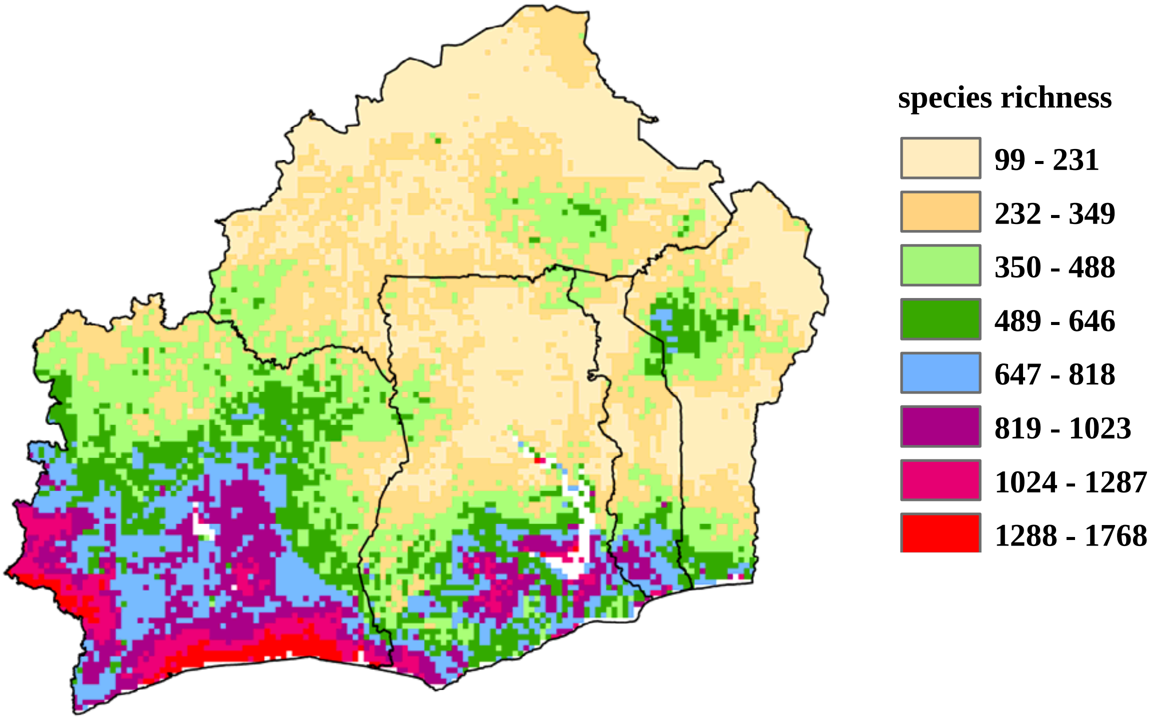
The general patterns of vascular plant species diversity in the region of West Africa are relatively well known (Barthlott *et al.* 2005; Sommer 2008). However, for the first time in the region, pattern of vascular plants diversity is depicted at relatively high spatial resolution with a grid cell size of about 10km x 10km (Figure 3.4). A remarkable observation is that this pattern follows a latitudinal gradient with high species number in the southern part and progressively decreasesing species numbers towards the north as already noticed by others authors at continental, regional and local scale (Barthlott *et al.* 2005; Sommer 2008; Poorter *et al.* 2004; Schmidt *et al.* 2005). However some spatial discontinuities in the diversity gradient are observed in some areas. For example in the extreme northern part of the Sahel zone, we noticed species richness values higher than expected, as well as in south-east and the south-west of the study area. Also in the north-western part of Benin corresponding to the region of Atacora mountain ranges extending to the north-east of Togo. Compared to other regions at the same latitude, we notice high species richness in the middle of Côte d'Ivoire corresponding to the so-called "V-Baoulé" region.

In the entire study area, the most prominent centers of species richness are located in the southern part, and particularly close to the coastline and also in the south-eastern part of Côte d'Ivoire, corresponding to the rainforest region. We can clearly distinguish for example the shape of one of the last remaining primary rainforests corresponding to the Tai National park protected area in the western part of Côte d'Ivoire.

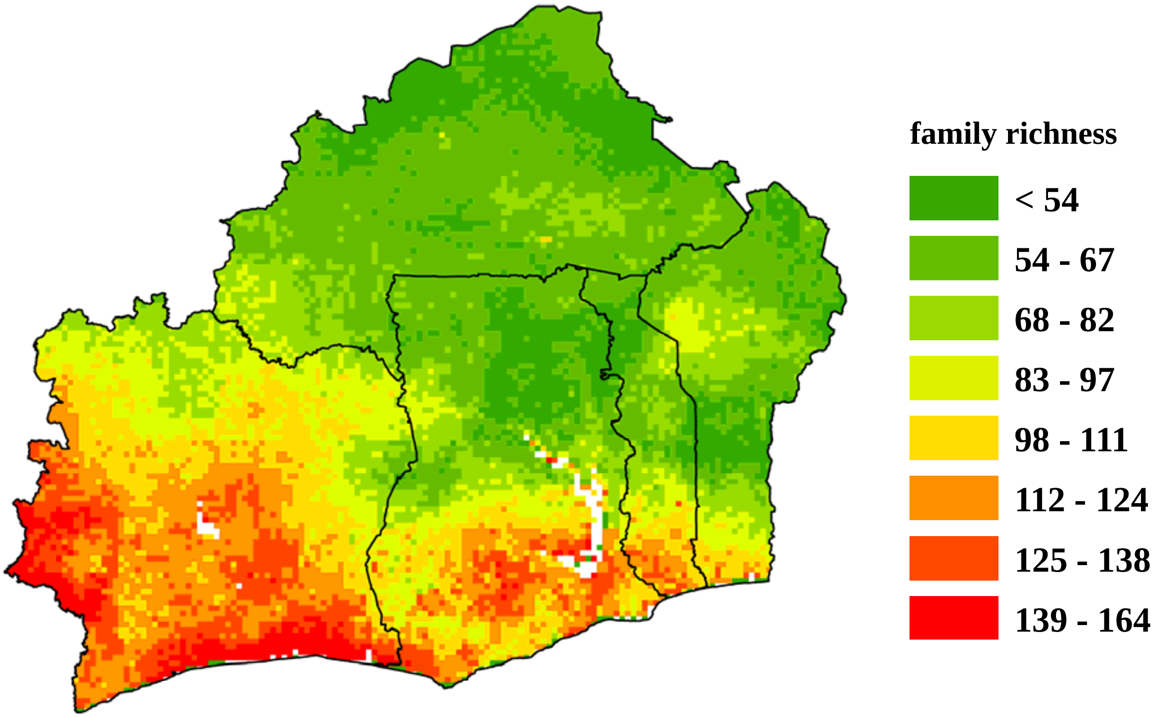
Moreover, this pattern follows the gradient of precipitation. In general the richest regions are located in the most humid areas, as highlighted by the determination of the geographic centers of species richness at different levels. There is a higher correlation between species richness and rainfall gradient than to other environmental variables. According to the MaxEnt output the variable contributing most to the distribution range of many species is the minimum value of annual precipitation followed by the maximum value of precipitation over the year and the standard deviation of the maximum of temperature. Two land cover variables, namely the percentage of tree and bare ground cover, are also highlighted as important in predicting species distribution ranges in the region.

The east-west variation in species richness within the region indicates major differences at the same latitude. For example at the southernmost border of Ghana, relatively low species richness is observed as compared to other areas at the same latitude.

The species family richness map, produced for the first time in the region, shows a great similarity between patterns of species richness and family richness. Likewise species richness patterns, family richness show the classic latitudinal gradient existing in the region. There is a significant positive correlation ($r^2 = 0.93$ for documented data and $r^2 = 0.94$ for the modeled data) between the numbers of families and the numbers of species in each grid square when considered at log/log scale (Figure 3.5). This correlation shows that it is possible to use higher taxa as a surrogate for species in survey of richness.



(A) species richness



(B) species family richness

Figure 3.4: Patterns of vascular plant diversity in West Africa at a spatial resolution of 10km x 10km. (A) species richness; (B) family richness. The family richness map shows a very similar pattern with the richness map of species. White areas are those with no environmental data and generally correspond to water body.

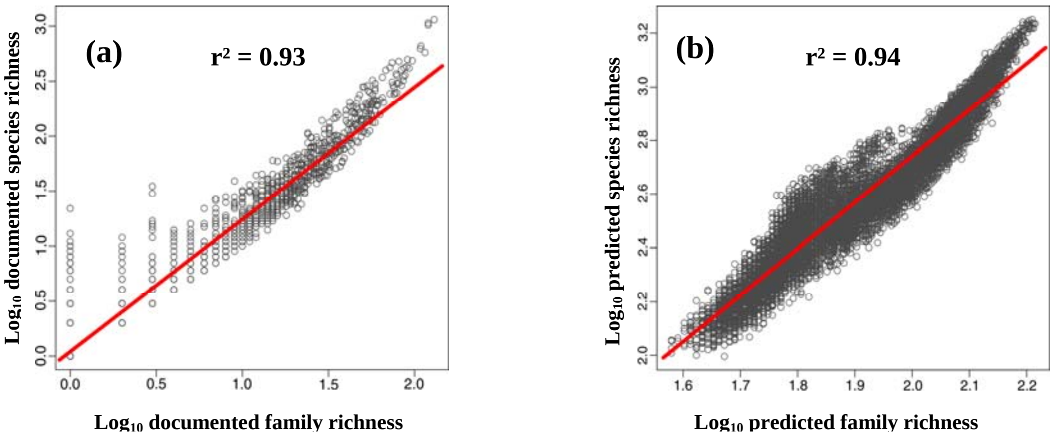


Figure 3.5: Relationship between numbers of families and numbers of species among grid cells of size 10km x 10km. (a) based on documented data; (b) based on modeled data. The documented data comprises 4,887 species in 224 families, and the modeled data contains 3,393 species in the same number of families.

The number of vascular plant species based on the modeling results for each surveyed country, except Côte d’Ivoire, falls between the range of estimated numbers of species comprised in the checklist of the corresponding country in concordance to the existing literature (see Appendix 4 for details).

Table 3.1: Modeled species number and percentage of species covered at least once by the existing network of Protected Areas (PAs) per surveyed country. Results are given for all types of PAs, only for PAs internationally recognized and only for national designated PAs.

Area extent	**Modelled total species number**	**Percentage of species covered by**		
		All PAs	IUCN recognized PAs	National designated PAs
Whole study area	3393	95.87%	94.08%	90.36%
Benin	2726	54.99%	48.86%	44.06%
Burkina Faso	1875	77.12%	62.45%	60.27%
Côte d'Ivoire	3107	93.11%	89.18%	91.02%
Ghana	3117	83.64%	79.79%	77.61%
Togo	2771	53.84%	47.92%	35.29%

Considering the entire study area at once, the existing network of all protected areas (nationally designated and internationally recognized) of at least 10,000 ha size cover up to 95.87% of species included in the analysis, according to their potential distribution range (Table 3.1). However if we consider each country separately, the percentage of species covered decrease considerably for some countries like Togo (approx. 54% of species covered), Benin (approx. 55%) and Burkina Faso (approx. 77%), Table 3.1.

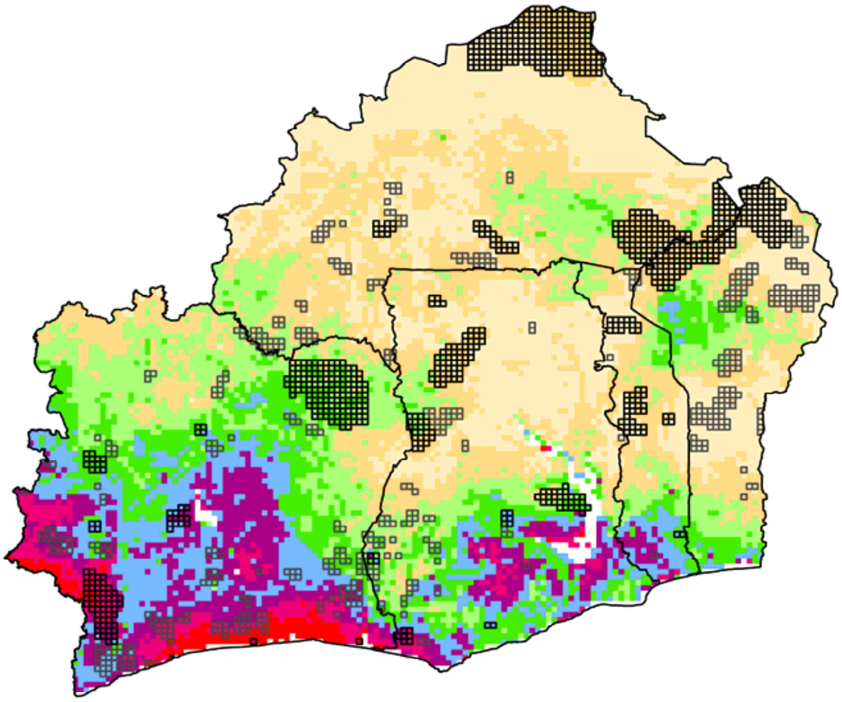


Figure 3.6: Spatial distribution of the network of protected areas (internationally recognized, in black color and national designated, in grey) and the modeled plant species richness in the study area. Only protected areas with more than 10,000 ha size are shown

3.5 Discussion

Geographic patterns of richness: In accordance with the well-known patterns of plant species richness in general, species number increase along the latitudinal gradient from the south to the northern part of the study area. The observed discontinuity in the species richness gradient in the upper border of the Sahel zone can be explained by the presence of an uncommon vegetation type in this area, usually known as the tiger bush. The tiger bush formation is a vegetation complex of striped thickets, occurring under special climatic and edaphic conditions on the slightly inclined pediplain (Lebrun 1999; Müller 2003), constituting an appropriate habitat for many species. For instance, some species known to be completely absent from other parts of the Sahel zone occur in this vegetation type.

Other notable discontinuities are observed in mountainous areas like the north-west of Benin and north-east of Togo, corresponding to the Atacora Chain having a high species number as already noticed by Adomou (2005). The same applies for the southwest of Burkina Faso in the sandstone massif area, as well as the western border of Côte d'Ivoire where the highest altitudes of the respective country are found. Our results therewith support the observation made by Barthlott *et al.* (2005) indicating that mountain regions constitute suitable habitats for many species because of the existence of variable climatic conditions due to the high geodiversity. Geodiversity, the diversity of abiotic factors, is an important factor which favors high species richness of vascular plants (Barthlott *et al.* 1996; Faith & Walker 1996; Barthlott *et al.* 1999, 2000; Jedicke 2001; Braun *et al.* 2002). Especially, mountainous regions are characterized by steep climatic gradients within short distances, heterogeneous geology and a diversity of different soil conditions. These mountainous regions in the study area are also known to shelter some highly endemic plant species (Akoègninou & Lisowski 2004; Adomou 2005; Poorter *et al.* 2004).

Moreover, the outstanding plant diversity observed in the middle of Côte d'Ivoire is due to the presence of the so called "V-Baoulé" a transition area where forest tends to take over the savanna (Spichiger & Blanc-Pamard 1973; Gautier 1992b, Poorter et al. 2004). The presence of different ecosystem types in this area provides suitable conditions for many species. In addition, a belt of high richness of rare and endemic species richness was found about 50-100 km inland, starting in Sierra leone, running through Liberia to southwest Côte d'Ivoire.

The patterns observed in the extreme southwest of Côte d'Ivoire showing an unexpected low number of plant species can be related to the climate variables used in the model as data on the importance of the seasonality of rainfall were not included into the model. In an earlier study for southeast Liberia and southwest Côte d'Ivoire, Bongers *et al.* (1999) showed that water availability, rather than rainfall alone was the most important parameter determining the abundance or the number of species. Length of the dry period and the intensity of that period (calculated as the cumulative water deficit) also had an effect, but were weaker than the amount of rainfall (Bongers *et al.* 1999). The lack of not including these parameters in our modeling approach could be overcome by using more parameters related to water availability, like soil water holding capacity. However, Poorter *et al.* (2004) indicate that the amount of rainfall alone accounts for 74% of the variation in species composition at the vegetation level.

Due to their insufficient representation in the data base, all species with less than 5 collection points had to be removed from the analysis. The amount of the removed species could concern a high number of the rare or endemic species, thus resulting in an underestimation of the grade of endemism in some regions. Also, most of the data for Côte d'Ivoire had been collected during the period corresponding to the civil war in Liberia; thus people avoided traveling into the southwestern part of the country, resulting in a higher grade of under-representation of this area in the data base.

Given the great similarity between species and family richness, an alternative to species based assessments can be the description of biodiversity at family level in the area, since it is sometimes difficult to collect exhaustive information on each species distributions. Many species had to be excluded from the analysis because of a lack of sufficient data. A surrogate could be to use higher taxonomic level data, i.e. family affiliation to look for areas with high biodiversity in the region, in order to overcome the insurmountable resource demands in obtaining equivalent data on species numbers more directly (Wiliams & Gaston 1994; Gaston *et al.* 1995). The advantage is that it is substantially easier and cheaper to identify specimens from survey samples to the level of higher taxa than to the level of species (Wiliams & Gaston 1994). However, the obvious difficulty with this approach is how to combine information on numbers of higher taxa, when these may in effect be defined in rather different ways (Gaston *et al.* 1995).

Protected areas: The network of protected areas in the region covers the distribution of vascular plant species relatively well, as already noticed in previous studies for the whole continent of Africa (Burgess *et al.* 2005; Sommer 2008). However, at more restricted spatial scale (national extent) the proportion of species covered by the national network of protected areas is much lower in some countries. This is due to the fact that a given species could be covered by protected areas in a given country, and is completely outside the network of protected areas elsewhere.

More and larger protected areas are required to adequately cover the maximum number of species at national level. For example in north-west and southern part of Benin as well as in north-east of Togo where a transboundary protected area covering both countries is of high conservation value. More protected areas in the south-west of Burkina Faso are also strongly required.

In comparison to previous studies, the spatial resolution used in this study is relatively high, thus allowing assessing with more accuracy the proportion of species covered by the protected areas. However, this spatial resolution remains more or less rough, given the method of analysis and also the size of protected areas comprised in the data base. We removed from the data all protected areas with less than 10,000 ha (corresponding to the spatial resolution). Yet, in the data, there are a great number of protected areas of very small size and are thus excluded. This leads undoubtedly to an underestimation of the amount of species falling inside the protected areas, which could explain the lower proportion of covered species at national scale.

Modeling approach: The goal of species distribution modeling is to predict the potential distribution of species which describes where conditions are suitable for survival of the species, which is in turn of great importance for conservation (Anderson & Martínez-Meyer 2004; Phillips *et al.* 2004). Some areas have been identified to being suitable to a higher number of species than primarily observed. One advantage of the modeling is to look for potentially suitable areas for many species, if there is no human disturbance. Thus, these areas could be set as priority areas for conservation. However, this approach has the weaknesses of sometimes overestimating the distribution ranges of species. This weakness can be corrected, for example by removing areas where the species is known to be absent because of deforestation or other habitat destruction. The model thus remains very unreliable if based on climate variables alone. It is therefore important to include different categories of environmental parameters if available, such as land cover data (see Appendix 5 for a visual comparison between patterns of species richness with and without the land cover variables). The latter seems to result in an overestimation of species richness, because of the absence of any kind of disturbance factors. This is not the case if some land cover factors are included into the model. Other ecological and historical factors are also important drivers of species richness patterns and must be taken into account both in theoretical modeling and data analysis.

Biotic interactions, and more particularly competition, represent a challenge for the future development of species distribution modeling. Further improvements of the distribution models can be expected from detailed soil data. Moreover, it is a key challenge to make empirical and correlative species models meet process-based community models. A way of integrating biotic interactions into static distribution models might be the use of integrated systems of simultaneous regression equations or generalized linear models.

3.6 Conclusion

Altogether, our results indicate that species distribution models are valuable tools to improve the understanding on species richness gradients also in areas with heterogeneous availability of distribution data. The link between species occurrence data, climatic maps and modeling algorithms offers important advantages for the documentation, assessment and conservation of biodiversity. However, the reliability of the model output strongly depends on the quality, resolution and spatial heterogeneity of the available documented occurrence data. Further improvement of the distribution models can be expected from detailed soil data. A principal issue for the future will be linking biodiversity data with measures characterizing human impact, e.g. human population and cattle density.

4. Quantitative delineation of phytogeographical regions based on modeled plant species distributions in West Africa

4.1. Abstract

The delineation of biogeographical regions is one of the major challenges in biogeography. Classical approaches are mainly based on expert knowledge on features of macroclimate, species distributions and vegetation structure. Here, we use a novel approach to identify fundamental phytogeographical regions for Sub-Saharan West Africa based on modeled potential species distributions for 3,393 plant species in combination with agglomerative hierarchical clustering and indicator species analyses across 12,152 grid cells at a spatial resolution of 10km x 10km. We found that patterns of plant species composition in the region are closely related to the steep north-south environmental gradient existing in the region. The clustering resulted in a phytogeographic regionalization consisting of seven clearly distinguishable groups of grid cells. We then allocated ecological information of these quantitatively defined regions by identifying character species for certain vegetation types. The identified phytogeographical regions broadly reflect the vegetation zones as defined in the seminal work of White (1983). Refering to their spatial distribution, notable differences occur at the margins of some regions that are shifted southwards resulting in a decline of the area covered by the rainforest region close to the Atlantic Coast. The introduced approach represents a repeatable and objective approach to discern and characterize biogeographical regions based on species data and hence is a major improvement to classical subjective approaches.

Keywords: Species distribution modeling, Cluster analysis, Indicator species, Phytogeographical regions, West Africa, White’s vegetation zones.

4.2. Introduction

The delineation of biogeographical regions based on floras and/or faunas is a central issue in ecological biogeography (Dufrêne & Legendre 1991; Williams *et al.* 1999). Moreover, knowledge about spatial patterns and location of ecologically homogeneous entities is a major precondition for priority setting and representative area selection approaches in conservation biology and policy (Olson *et al.* 2001; Leathwick *et al.* 2003; Kier *et al.* 2005).

Already in the 19th century biogeographers started delineating biogeographical regions (from regional to global scale) based only on their own estimates and that of people who had comprehensive knowledge about composition of flora or fauna (Wallace 1876 in Cox & Moore 1993; Cox 2001; Heikinheimo *et al.* 2007; Engler 1879; Chevalier 1933; Lebrun 1947; Aubréville 1949a; Aubréville 1949b). A major drawback of these classical approaches is that they are not repeatable and different studies provide very different results for same area (Cox & Moore 1993).

Following these early seminal works, studies based on more analytical approaches have been conducted using clustering methods (Williams *et al.* 1999; Qian 2001; Kingston *et al.* 2003; McLaughlin 1992; Linder *et al.* 2005).

Clustering methods represent a useful approach that can be applied to a given biological dataset to search for regions with a homogenous taxonomic composition (Birks 1987; Legendre 1990). In a geographical context, regions are delineated based on dissimilarities according to their specific and inherent features. In biogeography, clustering techniques to delineate biogeographical regions can be based on information of species occurrences within defined sub-units of the area of investigation (Linder *et al.* 2005). Hence, biogeographical regions in this sense represent areas of a certain minimum size with a largely homogenous species composition that differs from that of other biogeographical areas.

A major constraint for delineating biogeographic regions by clustering techniques across large areas (e.g. at regional to continental extents) is the availability of sufficient species distribution data. One option to deal with this data shortage is to apply species distribution models for individual species as a function of environmental variables at their known collection sites, thereby extrapolating the potential distribution of species to all suitable sites within the entire region of interest (see Guisan & Zimmermann 2000 for a review of different modeling approaches) before applying clustering methods. This “predict first, assemble later”-approach (Ferrier & Guisan 2006), appears appropriate and legitimate in cases of insufficient distribution data availability.

Early contributions to the phytogeographical division of continental Africa into a number of chorological units such as regions, domains and sectors mainly used intuitive approaches (e.g. Chevalier 1933; Monod 1957; Trochain 1970; White 1979 & 1983). A first and unique attempt to subdivide the entire Sub-Saharan Africa into phytogeographical regions based on clustering approach at a rather coarse resolution is the work of Linder *et al.* 2005.

For West Africa, the existing studies on subdivision of phytogeograhical regions are mostly based on expert knowledge using observations on vegetation physiognomy **(**Lebrun 1947; Aubréville 1949a & 1949b; White 1983; Adjanohoun *et al*. 1989; Guinko 1983). Studies at local or national level have used phytosociological approaches (Adomou 2005; Poorter *et al.* 2004), some of them referring to particular taxonomic groups (Thiombiano *et al.* 2006) to delimit phytogeographical regions.

Recently, comprehensive floristic datasets became available for the countries of Benin, Burkina Faso, Côte d’Ivoire and adjacent areas, collected within the frame of the BIOTA Africa research project and from other institutions (Küper 2005; Schmidt *et al.* 2005; Chatelain *et al.* 2002). These data for the first time allow a comprehensive quantitative analysis of species compositions and the delineation of phytogeographic regions across this area and at a high spatial resolution.

Here, we analyzed the variation in species composition among sites (grid cells) across the region in order to identify and map areas with similar species composition. Clustering techniques are applied to define potential phytogeographical regions in West Africa, and the resulting patterns are compared to classical approaches (e.g. White 1983). Finally, the importance of each defined phytogeographical region in terms of species richness and their value of sheltering range-restricted or endemic species have been evaluated.

4.3. Data and Methods

Study area: The study area is located in West Africa between the latitudes 4° 30’ N and 15° 05’ N and longitudes 8°30’ W and 3° 55’ E extending from the Atlantic coast to the Sahel area and covering five countries: Bénin, Burkina Faso, Côte d’Ivoire, Ghana and Togo. It is a region with a considerable variation in temperature, precipitation and vegetation types from north to south.

The study area has been divided into 12,152 regular grid cells of approximately 10km x 10km (approx. 0.0833°). Grid cells falling inside the coastal areas (corresponding to mangrove vegetation type) have been removed from the analysis because species of this type of vegetation are not included in the raw database.

Modeling of species distribution ranges: We used a database of Natural History Collections of plant species and environmental data (see below) to perform species distribution models. The potential distribution of all 3,393 species comprising at least 5 collection points was modeled using the Maximum Entropy approach (MaxEnt, Phillips *et al.* 2006). As output we obtained the potential distribution of each species as probability values per grid cell. These probability values were transformed into a binary (presence/absence) dataset by choosing the 10 percentile training presence value as threshold, indicating that 90 percent of each species records with the highest predicted model values are counted as presence (Cameron *et al.* 2008). Moreover, we set up a presence/absence matrix containing all modeled species and all grid cells.

Environmental data: As environmental predictor variables for the species distribution models, a set of 16 environmental parameters was selected. These data include climate variables obtained from the WorldClim website (Hijmans *et al.* 2005; *www.worldclim.org*), and land-cover variables downloaded from the Global Landcover (GLC 2000, *www.glcf.umiacs.umd.edu/data/*) website. A detailed list of all these variables is given in Appendix 1.

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Dissimilarity matrix: From the modeled species distribution database (species presence/absence matrix) we computed a dissimilarity matrix between all possible pairs of grid cells using the Bray-Curtis dissimilarity index with values ranging from 0 to 1. The smaller the value, the more similar is the species composition in the respective grid cell. The Bray-Curtis dissimilarity in its presence/absence form corresponds to the Sørensen index.

The formula of the presence–absence version of the Bray-Curtis dissimilarity index is:

$$D_{ij} = 1 - \frac{2A}{2A + B + C} \qquad (1)$$

(Ferrier *et al.* 2007) where A is the number of species common to both sites i and j (here grid cells); B is the number of species present only at site i; and C is the number of species present at site j.

In contrast to other indices, the Bray-Curtis dissimilarity index has many advantages for the integration of ecological data, including independence from scale of measurement and from joint absence (Su *et al*. 2004; Clarke 1993; Clarke & Warwick 1994*).*

Cluster analysis - Analyzing the variation in species composition: After computing the dissimilarity matrix between all possible pairs of locations we performed a cluster analysis in order to identify grid cells with similar species composition. We used the complete linkage of the agglomerative clustering method (see Legendre & Legendre 1998 for a review of different clustering methods). The output of the clustering is a dendrogram from which we classified the sites into groups by choosing a dissimilarity level (h). Varying this dissimilarity level, we obtained different groups of cells with similar species composition and visualized these groups as maps. A major difficulty of cluster analysis is to identify the level of abstraction where the clustering has to be stopped. Here, at the dissimilarity level of h=0.8, we obtained 24 clusters. A dissimilarity analysis between these 24 clusters was performed in order to merge some similar “subgroups” into one with the purpose to get clusters that better correspond to phytogeographical regions (Zhou et al. 2003).

The dissimilarity matrix establishment and the cluster analysis were conducted using the “vegan” library (Oksanen *et al.* 2008) of the R statistical language (R Development Core Team, 2008).

Delineation of phytogeographic regions and searching for character species of each region: Beyond portraying resemblance between locations, the spatial patterns that emerge when groups of sites with similar species composition are mapped should be ecologically meaningful. Therefore in the next step we looked for clusters that species composition could be used to derive ecological information, by identifying indicator or characteristic species for each groups of sites. Indicator species were defined as the most characteristic species of each group, found mostly in a single of typology and present in the majority of the sites belonging to that group (Dufrêne & Legendre 1997). This index is at maximum when all individuals of a species are found in a single group of sites and when the same species occurs in all sites of that group.

We used the “labdsv” library (Roberts 2006) to perform the indicator species analysis: for each species i in each cluster of sites j, the product of two values, A_{ij} and B_{ij} is calculated. A_{ij} is a measure of specificity whereas B_{ij} is a measure of fidelity:

$$IndVal_{ij} = A_{ij} * B_{ij} * 100 \qquad (2)$$

$$A_{ij} = N_{individuals\ (ij)} / N_{individuals\ (i)} \qquad B_{ij} = N_{sites\ (ij)} / N_{site\ (j)}$$

$N_{individuals\ (ij)}$ is the mean number of individuals of species i across sites of group j, while $N_{individuals\ (i)}$ is the sum of the mean numbers of individuals of species i over all groups. $N_{sites\ (ij)}$ is the number of sites in cluster j where species i is present, while $N_{sites\ (j)}$ is the total number of sites in that cluster.

For presence/absence data, $A_{ij} = (N_{sites\ (ij)} / N_{sites\ (i)})$ where $N_{sites\ (i)}$ is the total number of sites occupied by species i.

The indicator value of species i for a group of sites is the largest value of $IndVal_{ij}$ observed over all clusters i of that partition:

$$IndVal_i = max\ [IndVal_{ij}] \qquad (3)$$

Relative richness of each defined phytogeographical region: After delineating the potential phytogeographical zones of the region we estimated the importance of each zone in terms of species richness by counting the number of species which fall inside the given area.

Range-restricted species / Species restricted to each phytogeographical region: We identified range restricted species from the results of the indicator value calculation. The indicator value is the product of the specificity and the fidelity, see Formula (2). A species exclusively restricted to a region has its specificity equal to 1 for that region (*IndVal* different to 0) while 0 in others regions (*IndVal* = 0 in these regions).

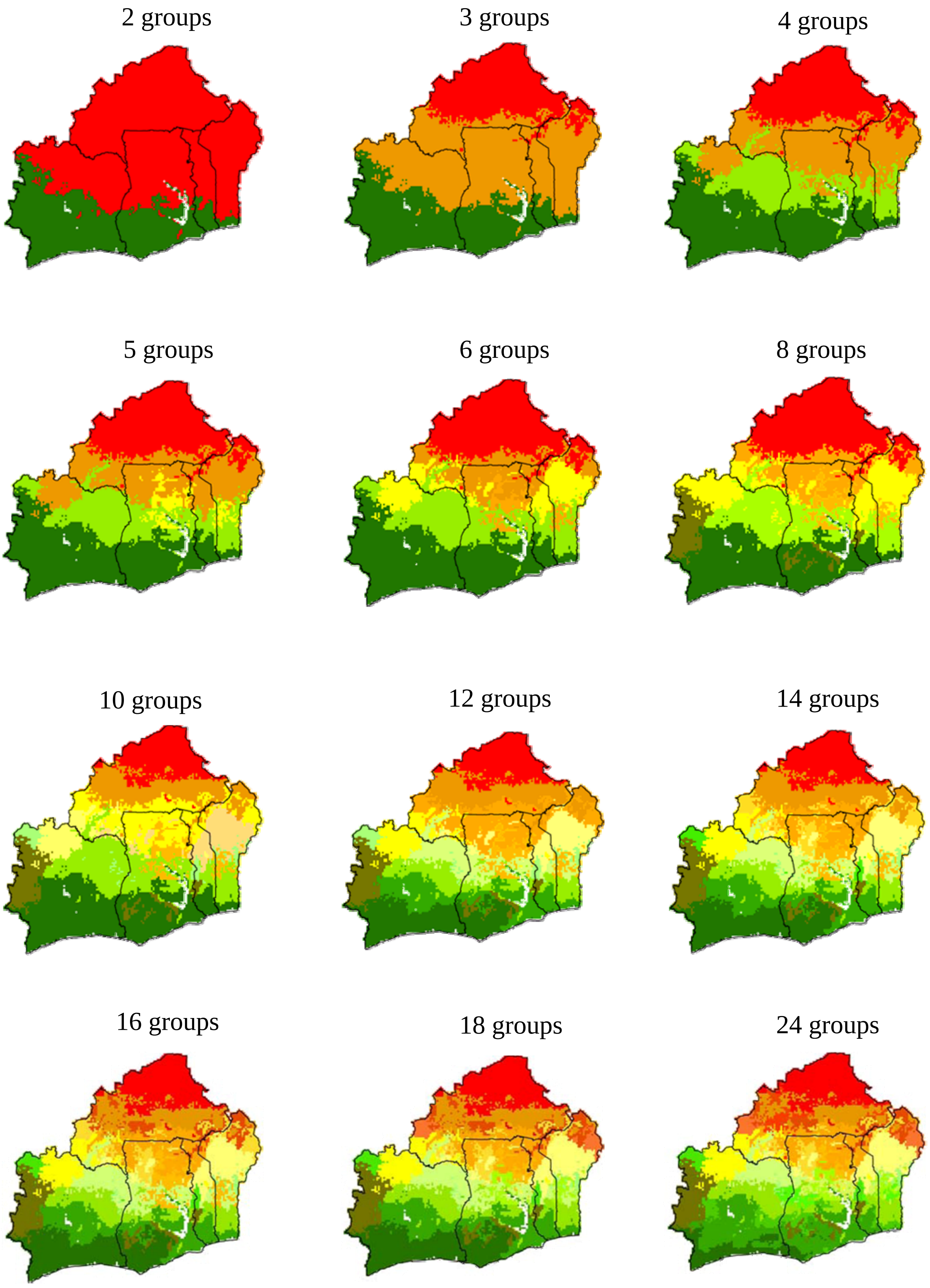
4.4. Results

Spatial Clusters: A first illustration of the clustering results is presented in form of a dendrogram showing different groups of cells with similar species composition according to the level of similarity/dissimilarity.

At the dissimilarity level of $h = 0.98$ (similarity equal 0.02), all grid cells are grouped into two different clusters, latitudinally dividing the study area in two parts with the northern part almost two times larger than the southern part.

Decreasing the level of dissimilarity (increasing similarity level) between grid cells we got different groups of cells with similar species composition. The different spatial patterns obtained are presented below (Figure 4.1).

At the dissimilarity value of 0.96, three major patterns of groups of cells with similar species composition emerged. These follow major environmental features along the north-south gradient. We distinguished a first group in the south extending from the coast to about 7° N (i.e. the wettest part in the region), an adjacent group of cells laying between 7 ° and 11 ° N separating the southern one from the northern one which cover the driest part of the study area. These 3 major groups correspond to the subdivision of the study area into 3 climatic zones: the Guineo-Congolian and Sahelian regions linked by the Soudanian zone.



2 groups
3 groups
4 groups
5 groups
6 groups
8 groups
10 groups
12 groups
14 groups
16 groups
18 groups
24 groups

Figure 4.1: Groups of locations (grid cells of 10 km x 10km size) with similar species composition, according to the level of dissimilarity between pairs of sites: the color is used to distinguish the clusters within each image, and we also tried as close as possible to imply a one-to-one matching of clusters between images: at different levels of dissimilarity, the unchanged clusters are plotted using the same color as previously. New appearing groups from a level to another are plotted using new colors.

Beyond this level of dissimilarity, many different groups of very small size emerged and we obtained different patterns difficult to distinguish.

At a dissimilarity level from h = 0.96 to h = 0.91, we successively obtained 4, 5, 6, 7 clusters only deriving from the previously intermediate group (the Soudanian zone), whereas the two other groups (in the north and the south) remained unchanged. This means that at this level of dissimilarity, the three groups have very little species in common; there are species with their range limited only to one of the region. The rapid change in the Sudanian region is due to the heterogeneity in environmental attributes of this region. Indeed, it is a region of a variety of habitat types with different assemblage of species (from very small to large assemblage of species).

First changes in the southern group are observed at the dissimilarity level of h = 0.90, dividing the whole area into eight clusters, the northern cluster still remaining constant.

At the dissimilarity value of h = 0.8, we got 24 different clusters; among which some previous cluster remain unchanged. However the southernmost cluster is split into two important groups. Most of the new formed groups are derived from a subdivision of clusters located between 7° and 11° N.

Beyond this level of dissimilarity, many different groups of very small size emerged and we obtained different patterns difficult to distinguish. Therefore, we stopped any further splitting at this point and used the 24 regions to delineate potential phytogeographic regions in the study area.

Delineation of potential phytogeographical regions: From the 24 groups of grid cells with similar species composition at the dissimilarity level of h = 0.8, groups of different size emerged, but only few of them were large enough to match our definition of a phytogeographical region (at least 10.000 km^2), the others had a very small size and could not be interpreted ecologically. We then merged some spatially contiguous subgroups into one group referring to: (1) their resemblance in terms of species composition by performing a dissimilarity and cluster analysis between the 24 groups; (2) the relevance of the borders between homogeneous areas. Most of the groups between 7° and 11° N are sunnarized into one when we cut the dendrogramm at a given level (given the nature of the data, the dissimilarity index used here is the Euclidian distance).

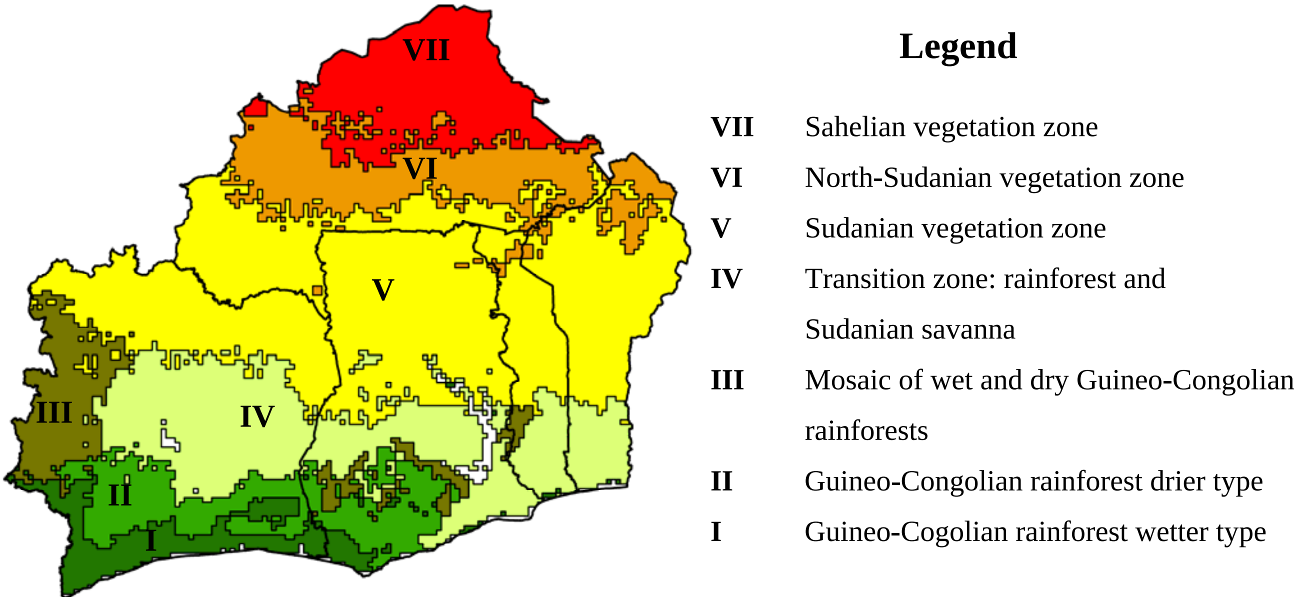


Figure 4.2: The proposed new potential phytogeographical regions in West Africa

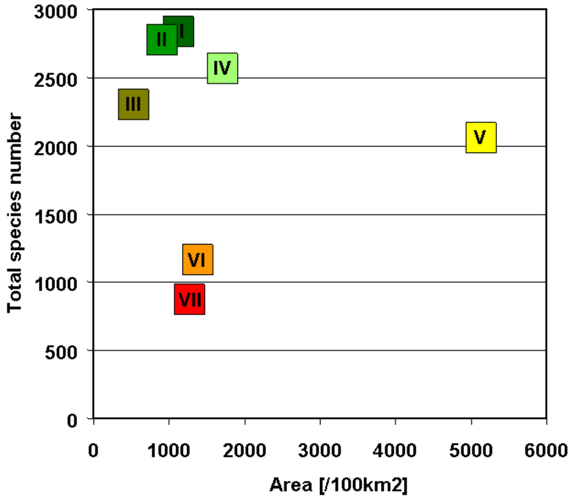


Figure 4.3: Species – area relationship per region. The richest regions in species are the rainforests though they have a small extent as compared to other phytogeogrphic regions. The total species number and the percentage of range restricted species in this study are based on modeled potential distributions and not on documented species richness of these phytogeographic regions.

This step allowed us to divide the study area into 7 major and homogenous distinguished groups here refered as groups I to VII, running in roughly parallel bands from the southern Guinean coast with high and well distributed rainfall throughout the year to increasingly drier zones in the Sahel. In the following step we determined the ecological significance of these groups by looking for indicator species which characterize each group. We decided to use the nomenclature of White to distinguish our new delimited phytogeographic areas.

Indicator species per phytogeographic region: For each region we derived a list of characteristic species; for some regions this list comprises a great number of species. As an example, we showed a list of 10 selected indicator species per region with their indicator value over all the defined phytogeographic regions (Table 4.1). We chose these species according to the existing literature, if possible, presenting them as indicator species of the corresponding region. According to the maximum of the indicator value of the species, an exhaustive list of all possible indicator species (with *IndVal* > 50%) of each region is presented in Appendix 6.

Species distribution ranges and commonness over the phytogeographic regions: We classified the species into different distribution types based on their range size (proportion of species restricted to one pytogeographic region) and their commonness (proportion of species belonging to different regions simultaneously). The classification was based on the value of the specificity of the species to each region. The results are summarized in Figure 4.5. In the diagram we distinguish three main types of regions having the highest number of species restricted to them: the rainforest (I), the soudanian (V) and the Sahelian (VII) vegetation types (Figure 4.4). On the basis of the total species number used for the analysis, the percentage of species restricted to each region is also shown in Figure 4.4. The rainforest is the region having the highest species richness but only 67 (ca. 2% of all species used in this study) have been identified as restricted to this region.

Table 4.1: List of 10 selected indicator species per potential phytogeographical regions (group I – VII) with their indicator value (bold numbers). The indicator value of a species for a group is the maximum value observed over all groups.

Species	Family	I	II	III	IV	V	VI	VII
Tabernaemontana glandulosa	APOCYNACEAE	**63.19**	1.94	0.04				
Combretum grandiflorum	COMBRETACEAE	**57.70**	2.23	1.64				
Xylopia staudtii	ANNONACEAE	**55.22**	0.15	0.04	0.02			
Salacia cerasifera	CELASTRACEAE	**52.15**	7.22	0.05	0.12			
Vitex phaeotricha	VERBENACEAE	**50.09**	1.92	0.27				
Cola nitida	STERCULIACEAE	**47.05**	7.01	2.99				
Palisota bracteosa	COMMELINACEAE	**43.67**	14.70	0.79				
Bulbophyllum saltatorium	ORCHIDACEAE	**41.49**	3.47	7.85	0.03			
Leptaspis zeylanica	POACEAE	**33.26**	4.72	3.71				
Streblus usambarensis	MORACEAE	9.48	**44.59**	1.87	0.58			
Irvingia robur	IRVINGIACEAE	28.08	**42.12**	2.75	0.90			
Uvaria anonoides	ANNONACEAE	32.14	**41.56**	2.77	1.31			
Psychotria kitsonii	RUBIACEAE	1.01	**39.49**	0.02	1.10			
Alafia barteri	APOCYNACEAE	25.51	**38.09**	4.83	2.98			
Ficus sagittifolia	MORACEAE	25.52	**32.10**	0.12	10.94			
Bulbophyllum phaeopogon	ORCHIDACEAE	13.30	**31.54**	0.02	1.04			
Acroceras gabunense	POACEAE	3.65	**29.56**	0.24	8.53			
Dicliptera elliotii	ACANTHACEAE	6.90	**29.53**	0.31	7.32			
Combretum racemosum	COMBRETACEAE	19.32	**29.16**	4.05	21.84			
Asplenium megalura	ASPLENIACEAE	4.79	0.27	**40.58**	0.02	0.38		
Nervilia fuerstenbergiana	ORCHIDACEAE	6.54	1.74	**35.15**	0.04	0.24		
Dicranolepis pubescens	THYMELAEACEAE	3.81	5.04	**34.76**	0.71			
Vernonia doniana	ASTERACEAE	14.81	14.82	**31.22**	0.81	0.07		
Melinis minutiflora	POACEAE	1.19		**31.12**	0.21			
Zanthoxylum viride	RUTACEAE	3.06	2.88	**29.73**	16.99	0.34		
Drypetes inaequalis	EUPHORBIACEAE	6.88	17.35	**27.49**	3.49	1.04		
Dissotis thollonii	MELASTOMATACEAE	0.99	1.24	**27.45**	2.00	10.50		
Dissotis grandiflora	MELASTOMATACEAE			**25.97**	0.64	13.00		
Salacia pyriformis	CELASTRACEAE	23.04	3.86	**24.72**	0.11	0.20		
Cordia guineensis	BORAGINACEAE		9.55	0.07	**55.15**	1.11		
Utricularia reflexa	LENTIBULARIACEAE			0.26	**51.02**	0.42		
Albizia coriaria	FABACEAE	0.57	13.99	0.33	**50.23**	2.50		
Eulophia angolensis	ORCHIDACEAE	0.20	4.70	3.70	**49.51**	1.31		
Pycreus nuerensis	CYPERACEAE		0.66	3.55	**49.28**	6.21		
Commelina bracteosa	COMMELINACEAE		12.02	0.17	**48.82**	0.05		
Physalis pubescens	SOLANACEAE	0.47	21.97	0.02	**47.66**			
Indigofera congesta	FABACEAE	0.08	0.35	1.11	**47.14**	1.81		0.04
Cola millenii	STERCULIACEAE		1.77	1.01	**45.24**	0.58		
Sabicea solitaria	RUBIACEAE	11.49	19.29	15.71	**40.17**	0.91		
Digitaria exilis	POACEAE	1.82	0.10	3.89	1.15	**58.05**	5.22	
Schizachyrium rupestre	POACEAE			0.57	5.02	**52.21**	8.33	1.98
Celtis integrifolia	ULMACEAE				0.76	**47.83**	20.50	17.60
Bambusa vulgaris	POACEAE	3.90	5.31	6.47	19.72	**47.74**	6.29	0.11
Vernonia purpurea	ASTERACEAE			0.15	0.39	**47.22**	0.14	0.06
Landolphia heudelotii	APOCYNACEAE			3.72	8.10	**42.33**	0.11	
Indigofera macrocalyx	FABACEAE			4.93	2.96	**40.56**	19.94	0.77
Xeroderris stuhlmannii	FABACEAE			1.33	0.03	**37.40**	6.74	0.35
Fagara zanthoxyloides	RUTACEAE				0.03	**18.79**	0.02	
Capparis tomentosa	CAPPARACEAE			0.16	0.92	**17.58**	30.32	0.16
Bulbostylis scabricaulis	CYPERACEAE					8.67	**48.43**	1.54
Cassia singueana	FABACEAE					1.20	**44.51**	0.16
Crotalaria vogelii	FABACEAE					10.15	**43.63**	1.92
Hyparrhenia rudis	POACEAE					1.85	**41.20**	1.74
Ficus iteophylla	MORACEAE					4.43	**39.75**	12.13
Lippia chevalieri	VERBENACEAE					0.26	**32.81**	0.83
Capparis tomentosa	CAPPARACEAE			0.16	0.92	17.58	**30.32**	0.16
Blepharis maderaspatensis	ACANTHACEAE					1.98	**28.25**	12.29
Loudetia annua	POACEAE					3.51	**28.03**	0.30
Caralluma decaisneana	APOCYNACEAE					0.05	11.47	**66.22**
Capparis rothii	CAPPARACEAE					0.06	1.41	**63.57**
Eragrostis cilianensis	POACEAE					0.05	11.35	**59.39**
Caralluma dalzielii	APOCYNACEAE						0.45	**52.27**
Acacia nilotica	FABACEAE				0.04	0.51	28.48	**46.95**
Bauhinia rufescens	FABACEAE				0.93	0.14	4.59	**45.06**
Colocynthis vulgaris	CUCURBITACEAE					0.50	15.90	**42.11**
Leptadenia hastata	APOCYNACEAE					0.03	3.89	**41.63**
Euphorbia balsamifera	EUPHORBIACEAE					7.14	6.01	**30.53**
Ziziphus spina-christi	RHAMNACEAE					5.54	23.44	**30**

Among these species are for instance: *Anthonotha vignei; Tapinanthus praetexta; Dichapetalum dictyospermum; Albertisia cordifolia; Dorstenia embergeri; Xylopia rubescens.*

Species solely present in the Sudanian region, are for example: *Saba florida; Vernonia glaberrima; Ficus capensis; Laggera pterodonta; Borreria scandens.* Despite its low species richness, the Sahel zone shelters a high number of species exclusively restricted to it (55 species). Among these species the most well-known are for example: *Acacia laeta; Acacia raddiana; Aristida mutabilis; Carraluma retropiciens; Cenchrus prieurii; Grewia tenax; Leptadenia pyrotechnica.*

See Appendix 7 for an exhaustive list of all species restricted to one phytogeographical region according to our results. Figure 4.4, shows the number and proportion of species common to at least two different phytogeographic regions.

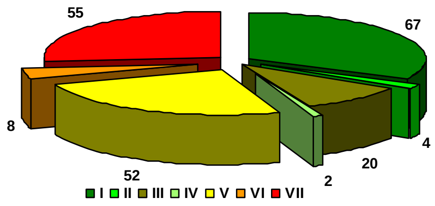


Figure 4.4: Number of range-restricted species per phyto-geographical region: from I to VII; refer to the Figure 4.2 for the identification of each region

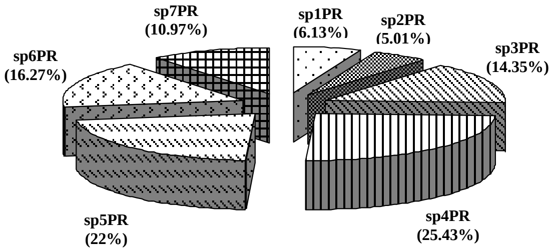


Figure 4.5: Proportion of species present in the 7 phytogeographic regions (PR): sp2PR: species common to: 2 phytogeographic regions; sp3PR: 3 regions; sp4PR: 4 regions; sp5PR: 5 regions; sp6PR: 6 regions; sp7PR: all the 7 regions

Comparison with the classic approach- phytogeographic regions of White (1983): The selected 7 clusters correspond fairly well with the vegetation zones defined by White (1983). However, some differences exist: White distinguished, including the regions delineated through our study, three other important phytogeographical regions: the mangrove, swamp forest and the West African coastal mosaic, which are not identified in our study, because our database does not contain species of this type of vegetation. Moreover notable differences in the extent of some areas are observed (Figure 4.6). The similarity and differences are discussed below.

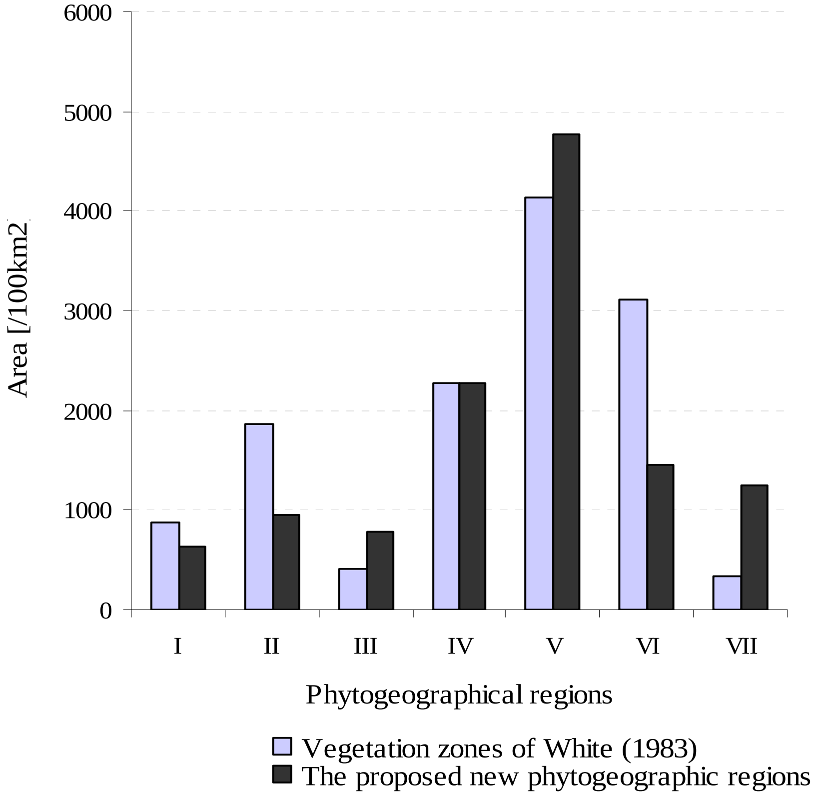


Figure 4.6: Comparison of area extent between our delineated phytogeographic regions and the vegetation zones of White (1983)

4.5. Discussion

Phytogeographical regions: Our delimited potential phytogeographic regions based on species composition of standard sites (grid cells) are closely similar to the vegetation zones defined by White (1983) in West Africa. Seven clear phytogeographic regions have been distinguished and are disposed along a climatic gradient from the south to the north, with different vegetation types corresponding to those of White (1983). However, White distinguished nine main types of vegetation zones including the mangrove and swamp vegetation area. These vegetation types were not included in our analysis because data on the distribution of species characterizing these types of vegetation are not included in the database we used.

The rainforest regions cover the southern part of the study area, extending from the south-west of Côte d'Ivoire to the south-west of Ghana where it ends due to the Dahomey gap effect. The Dahomey gap, covering the south-eastern part of Ghana and the southern part of Togo and Bénin, is a savanna vegetation zone or transition zone between savanna and rainforest splitting the rainforest zone into two parts commonly known as the Upper Guinea and Lower Guinea/Congolian Forest Blocks and was already highlighted in several previous studies (for example Aubréville 1938, White 1983, Poorter *et al.* 2004).

The Sudanian zone is a region of high heterogeneity due to the presence of many different habitat types. This induced notable artifacts during the clustering procedure. Our analyses retrieved broadly two regions: the north sudanian vegetation zone includes many species that can also be found in the Sahelian region and the south sudanian zone.

Opposed to previous studies which subdivided the Sahelian zone into two different phytogeographic regions (Guinko 1983; Fontès & Guinko 1995; Thiombiano *et al.* 2006), this region in our analysis is indentified as one phytogeographic zone and remained unchanged during the clustering procedure, also at a low level of dissimilarity (Figure 4.1). This could be due to the southward spread of the distribution of many Sahelian species, as already observed in the area for some species of the genera *Combretum* (Thiombiano *et al.* 2006), and *Acacia* (Wittig *et al*. 2004).

The delineated phytogeographic zones largely reflect the basic climatic zones. Previous studies in the region at a more restricted spatial scale have already shown a good correlation between the climatic zones and phytogeographical areas (Adjanohoun 1989) and indicated that rainfall constitutes the major factor determining vegetation pattern and largely explains the variation in species composition (Aubréville 1962, Newbery & Garlan 1996; Adomou 2005; Thiombiano *et al.* 2006). One reason for changing phytogeographic regions boundaries is the observed decrease of the mean annual rainfall in the region from north to south (Le Houérou 2009). Indeed climatic fluctuations require plants to be able to shift their distribution range by spreading into areas with good representation of their ecological niche.

Other notable differences between our new pattern of vegetation zones and the phytochoria of White are observed in the spatial extent of some areas (Figure 4.6). Beside the ecological factors (such as climate, geology, landform, soil), the observed phytogeographic patterns could be described as a result of historical human activities and climate fluctuations. For instance, we notice a southward shift in the margins of the rainforest zones (drier and wetter types) induced by the transformation of one vegetation type into an other one. Given the decrease of precipitation over the last decades at the northern edges of the most humid zone, the wetter rainforest type is progressively transformed into the drier type by its upper border, while a part of the drier rainforest type is becoming a zone of transitional vegetation between rainforest and savanna. The transformation is more accentuated in the Sudanian and Sahelian areas which are extended due to the conversion of the northern border of the rainforest/savanna transition zone and the southward spread of Sahelian species into the northern sudannian vegetation zone. These observations could be explained by the high degradation of vegetation in the area. Indeed in the last two decades, the vegetation of West Africa was subject to strong changes induced mainly by deforestation with a percentage of deforestation up to 90%, habitat fragmentation and over-exploitation (Collins 1990; Sayer *et al*. 1992; Hawthorne 1996; Fairhead & Leach 1998; FAO 1993; FAO 2001 b). The steady increase in human population leads to an extension of agricultural land. The same tendency is observed in the drier areas, causing an extension of the Sahelian vegetation zone. In semi-arid regions tree cover decreased (Anhuf *et al.* 1990; Breman & Kessler 1995) due to firewood cutting, overgrazing and droughts of the 1970s. Many former tree savannas were changed to shrubs/grass savannas or ended up in bare land.

Also, changes in vegetation cover are mostly followed by micro and meso scale climatic changes. Together with the aspect of global changes, this may lead undoubtedly to shifts of vegetation zones.

Indicator species analysis: The search for indicator species was conducted in order to determine the ecological meaningful and the floristic characteristics of each phytogeographical region. Among the great number of indicator species characterizing some regions, two different groups of species can be distinguished: rare species that characterize a given region and are present in a few sites of this region, and widespread or common species that characterize a given region and are found in almost all the sites of this region. The labels rare or common species depend on the level of the sampling patch size (Nee *et al.* 1991). Species that are rare at a higher level may be common at the lower levels. The issue here is to deal with the ability to assess the spatial and temporal consistency of indicator status. The consistency of indicator status may depend on the spatial scale of the analysis and the ecological amplitude of a species (Bakker 2008). On a broad spatial scale, rare species will have a small indicator value while common species will have a high indicator value. Based on the indicator value of each species and according to the results of previous studies (i.e. Guinko 1984; Poorter *et al.* 2004; Adomou 2005) in which some species have been identified as indicators of a given vegetation type in the area, we drew up a list of indicator species per potential phytogeographical region. For example in our analysis, the species *Acacia raddiana* (*IndVal* = 2.18%), *Aristida mutabilis* (*IndVal* = 3.30%), *Leptadenia pyrotechnica* (*IndVal* = 1.69%) have a very low indicator value, but they are well-known as characteristic species of the Sahel vegetation type (Guinko 1984; Lebrun *et al.*1991). Likewise rare indicator species for other regions have been identified. If we set a threshold of the *IndVal* > 25 %, to identify indicator species, as suggested by Dufrêne & Lengendre (1997), many interesting species would have been ignored, though they are known to be characteristic of a given vegetation type.

The indicator value analysis also allows identifying species that contribute to the specificity of each group. Indeed, most of the rare species are exclusively restricted to one phytogeographic region and have the highest specificity value for this region.

Range-restricted species or endemic species: According to the literature, the rainforest region (drier and wetter type), has been identified to harbor almost one third of the total estimated number of all species in this region (; Hall & Swaine 1981, White 1983, Poorter *et al.* 2004). However our results bring out only 67 species (ca. 2% of the species used in this study) to exclusively occur in the rainforest (Figure 4.4). This could be explained by the exclusion of many endemic species during data processing for the modeling. Indeed, we only considered species that are well represented in the area in terms of the number of collection localities. The other species, which may contain a great number of range restricted species to a given region, have been removed from the list (about 63% of all species comprised in the raw database have been modelled).

Strengths and weaknesses of our approach: One major issue in delineating biogeographical regions is whether it can be based on quantitative statistical methods or on human expertise alone (McMahon *et al.* 2001). Quantitative approaches are more explicit, repeatable, transferable and defensible than subjective approach based on human expertise. Moreover, the applied approach allows overcoming issues related to data shortage. However, some weaknesses remain at different levels of the analysis. Despite the advantages of this approach it still requires subjective ecological expertise to adjust the border of some regions. Indeed, in descriptive multivariate data analysis in general, it is always a challenge to assess the reality of the clusters that have been identified. The difficulty comes from the fact that borders cannot be statistically tested through analysis of variance for instance, since the data necessary to perform this test are the very same that gave birth to the borders to be tested (Dufrêne & Legendre 2003); see Perruchet (1983) for a review of this question. Thus, after defining our regions we manually reshaped borders of some regions based on expert-knowledge (compare Dufrêne & Legendre 2003).

Uncertainties induced by setting a threshold: the output of the model used to predict species' potential distribution ranges is given in the form of probabilities of occurrence which have to be translated into a presence/absence form by setting a threshold for cluster analysis. However, a great issue to deal with in species distribution modeling is the choice of an appropriate threshold, which constitutes an important level of uncertainty. For each species, the right threshold should be found to avoid an over- or under-prediction of its distribution range. This step may also need the help of experts who know the ecology of the given species. But dealing with big data sets (i.e. database comprising more than 1000 species) it is too time consuming and unrealistic to go through the distribution map of each species in order to estimate their distribution range as close as possible to their real distribution.

Technical issues: in this study, the analyses were based only on one clustering method; attempts to apply others techniques have been strongly hampered because of the limited power of the computer (because of the size of the database, we used species presence/absence matrix of 3,393 species by 12,152 grid cells). As different clustering algorithms may produce markedly different results because clustering methods impose different models onto the data (Legendre & Legendre 1998; Williams *et al.* 1999), it is worthwhile and strongly recommended to apply different methods for comparison in order to validate the obtained patterns. With an increase in processing power of computers, different methods could be applied for comparison between the results produced easily in the future.

4.6 Conclusion and perspectives

This study shows that similarity analysis between sites (here grid cells) based on their species composition in combination with the application of indicator value approaches can contribute to delineate biogeographical regions more accurately than by expert estimation alone. The major constraints are related to the availability of representative data on species distributions, an issue that was tackled by the modeling of species distribution ranges.

The considerably high similarity between our phytogeographical regions and those delineated by White (1983) indicates a good relationship between our method of analysis and the perception of the phytogeographers.

It would be also very interesting to apply kind of studies to other taxonomic groups such as Bats and Amphibians, since quantitative and qualitative data on these groups are now available, as comparable studies do not exist for this region to date.

5. Prediction of species richness and shift in phytogeographic regions under climate change in West Africa

5.1 Abstract

Analyzing the possible impact of projected future climate changes on biodiversity is a crucial step towards the development of suitable adaptation and mitigation strategies.

Here we used two IPCC climate change scenarios from two different climate models to evaluate the potential impact of climate change on plant species richness and also assessed the possible shift in potential phytogeographical regions in West Africa.

We modeled potential current and future distributions of 3,393 vascular plant species at a spatial resolution of 10km x 10km grid cell size based on species distribution modeling techniques (MaxEnt). Summing up the potential distribution ranges of all modeled species per grid cell, we produced species richness maps for each climate scenario (global average increase in temperature of 2.4°C and 3.4°C) and each climate model for 2020, 2050, and 2080. Based on the distribution ranges of species, current and future potential phytogeographic regions were defined by the mean of cluster analyses and indicator species analyses.

The results of our analysis show a generally negative impact of climate change on biodiversity in the area, with a severe loss of suitable habitats for many plant species, particularly in the rainforest region, with losses of up to 50% of species per grid cell by 2080. Moreover, these changes also affect the potential future distribution of phytogeographic regions: in general, there is a southward shift in the potential location of phytogeographic regions, with a considerable increase of the drought-adapted Sahel region, contrasted by a severe decline of the rainforest region. The rainforest area in West Africa must be set as high priority area for biodiversity conservation.

Keywords: Species distribution modeling, Species diversity patterns, Vegetation zones, Climate change scenarios

5.2 Introduction

Understanding the impact of projected climate change on plant species diversity and vegetations zones is a required precondition to develop effective strategies for conservation (Schroter *et al.* 2005, Araújo and Rahbek 2006, Engler *et al.* 2009).

Climate is a strong regulator for the distribution, productivity and many other aspects (i.e. abundance) of species, as well as diversity patterns (Holdridge 1947; Woodward 1987). The climate impact on species has been used to reconstitute paleoclimates from information on species past distributions (Guiot 1987). There is also a general agreement that climate (mainly temperature and precipitation) is the primary factor explaining the distribution of forest and savanna, at least at a continental scale (Adejuwon 1971, Swaine 1992, Cramer and Leemans 1993, Adams 2007).

According to the IPCC greenhouse gas emission scenarios projections (IPCC 2000) temperature and rainfall will change considerably in Africa within the next decades (Mitchell *et al.* 2004; de Wit & Stankiewiecz 2006; Alley *et al.* 2007; IPCC 2007; Richardson *et al.* 2009) due to anthropogenic actions (Karl & Trenberth 2003; Raupach *et al.* 2007). Increase in temperature of about 1.5 to 2.5°C and decrease in precipitation ranging from 100 to 400 mm/yr may be possible (Dietz *et al.* 2004).

The increasing anthropogenic climate change will undoubtedly have a high impact on plant species distribution and diversity (Parmesan & Yohe 2003; Root *et al.* 2003; Thuiller *et al.* 2008; Sommer 2008). The consequence of this influence at species level may be expansions, contractions or shifts of their ranges (Walther *et al.* 2002, Parmesan 2006). The extreme situation may be extinction of some species at regional or local scale (Thomas *et al.* 2004; Thuiller *et al.* 2005).

Moreover, species composition of assemblage and vegetation will be strongly influenced by climate change (Pamesan & Yohe 2003, Baselga & Araújo 2009, Sommer *et al.* 2010). Several studies have suggested that species turnover may be high in some regions under climate, potentially resulting in modifications of community structure strong enough to lead to ecosystem disruption (Bakkenes *et al.* 2002; Erasmus *et al.* 2002; Peterson *et al.* 2002).

Evidence of accelerating climate change (IPCC 2007) highlights the urgency of obtaining accurate estimations of species range shifts in coming decades so that effective mitigation strategies can be developed to sustain ecosystem services and function (MEA 2005, Rosenzweig *et al.* 2008). To achieve this goal, species distribution modeling tools are commonly used in an effective way.

The relationship between climate and species distributions has been a basis for numerous models in ecology and especially in biogeography (Austin 1985; Prentice *et al.* 1992; Neilson 1995; Kleidon & Mooney 2000; Thuiller *et al.* 2003, Kreft & Jetz 2007). A widespread method to assess the impact of future climate change on plants has been the utilization of species distribution models (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). The models commonly used to assess climate impacts, indicate that climate may result in substantial shifts in species distributions. The models make a number of assumptions, the most fundamental being that climate ultimately limits species distributions.

In Africa, some studies have already been carried out to estimate future plant species distributions, at large geographical scales (continent-wide), but they remain at a relatively coarse spatial resolution (Sommer 2008); or at regional extent, focusing mainly on southern Africa (Midgley *et al.* 2002, Bomhard *et al.* 2005, Erasmus *et al.* 2002, Simmons *et al.* 2004, Thuiller *et al.* 2006, Broennimann 2006).

To our knowledge, there are no published assessments of potential impacts of climate change on regional plant species diversity of West Africa. Only very few investigations exist on vegetation dynamic under climate changes in this area (Wittig *et al.* 2007). These studies are only limited at local or national scale.

Here, we used documented data on 3,393 vascular plant species distributions and present-day climate variables to build contemporary bioclimatic models. We then apply these models to project changes in species diversity under future climate scenarios. By comparing current versus future potential distributions, we assess whether suitable climate space for plant species is projected to increase or decrease with projected climate change in West Africa.

Based on today and future distribution of plant species, we assessed possible shifts in phytogeographic regions in the study area.

5.3 Data and Methods

Study area: Extending from the Atlantic coast to the Sahel zone, the study area is located in West Africa between the latitudes 4°30’ and 15°05’N and the longitudes 8°30’W and 3°55’E and cover five countries: Bénin, Burkina Faso, Côte d’Ivoire, Ghana and Togo. It is a region of contrasts with a great variation in temperature, precipitation, and vegetation types along a gradient from north to south.

The study area has been divided into 12,152 regular grid cells of approximately 10km x 10km each (approx. 0.0833°). Grid cells falling inside the coastal areas (corresponding to mangrove vegetation type) have been removed from the analysis because species of this type of vegetation are not included in the documented database we established.

Species distribution data: We compiled a database on the distribution of 4,887 vascular plant species of which 3,393 have sufficient geographic records were used in this study. The database consists of a combination of three main sources of data on plant species distribution: the BISAP database (Biogeographical Information System on African Plant Diversity, see Küper et al. 2004), the SIG-IVOIRE database (Gautier et al. 1999; Chatelain et al.2002) and the OUA/VegDa database (Schmidt et al. 2005). Each occurrence locality is a latitude-longitude pair denoting a site where the species has been observed. The spatial resolution is approximately 10km.

Environmental variables: We assembled eleven environmental variables relating to three principal traits: temperature, precipitation and topography (Table 5.1). All these variables were extracted from the Worldclim database (Hijmans et al., 2005; *http://www.worldclim.org/*), which provides a set of global climate layers generated through interpolation of climate data from weather stations at a original resolution of 30” grid (c. 1km²). The dataset comprises monthly averages of each climate variable for the period from 1950 to 2000, here referred to as today. The same variables are available for the future derived from the IPCC 3rd Assessment data downloadable from http://www.worldclim.org/futdown.htm. These future climate data have been simulated using different General Circulation Models (GCMs) and based on different IPCC climate-change scenarios. In this study, we concentrate on HadCM3 (Hadley Center for Climate Prediction and Research) and CSIRO (Australia’s Commonwealth Scientific and Industrial Research Organisation) models and the IPCC A2 and B2 climate-change scenarios, referring to an average global warming of +3.4 °C and 2.4 °C, respectively. For the analysis we rescaled all the environmental variables to a common resolution of 10km x 10km pixel size to match species data.

Table 5.1: Environmental variables used in MaxEnt to predict current and projected potential distribution ranges of species. These variables have been downloaded from the WorldClim website with an original resolution of approx. 1 km that has been rescaled to approximately 10km grid cell size. *Source*: *http://www.worldclim.org*

Abbreviation	**Variables description**
Alt	Altitude
prec_30_max	Maximum value (“wettest month”) of the 12 monthly precipitation
prec_30_min	Minimum value (“driest month”) of the 12 monthly precipitation
prec_30_std	Standard deviation of the 12 monthly precipitation data
prec_30_sum	Total annual precipitation calculated as the sum of all 12 monthly rainfall
tmax30_max	Maximum of the mean monthly maximum temperature
tmax30_min	Minimum of the mean monthly maximum temperature
tmax30_std	Standard deviation of the mean monthly maximum temperature
tmin30_max	Maximum of the mean monthly minimum temperature
tmin30_min	Minimum of the mean monthly minimum temperature
tmin30_std	Standard deviation of the mean monthly minimum temperature

Species distribution modeling: Assuming that climate is the most important factor determining the distribution range of species, we modeled individual species niches from point observations and project these models into the future using different future climate scenarios. Historical factors, particularly species dispersion capacity have not been taken into account.

For each 3,393 investigated vascular plants species, we used MaxEnt (The Maximum Entropy approach, Phillips *et al.* 2006) to create contemporary (here referred to as today) niche-based distribution models based on locality points and climate surfaces.

We then projected these models for climatic conditions in 2020, 2050 and 2080 according to the IPCC A2 and B2 scenarios and the HadCM3 and CSIRO climate models.

The potential geographic ranges of species are given in form of probabilities for the presence of each species. At each time period and for each model and scenario, we transformed the probability value output of MaxEnt into a presence/absence matrix. We chose the ten percentile training thresholds from the MaxEnt logistic output, indicating that 90 percent of each species records with the highest predicted model values are counted as presence.

Potential species richness and change in species diversity: We produced potential species richness maps for today as well as for the future according to different scenarios and models by superimposing the presence/absence potential distribution ranges of all 3,393 species. The number of species falling inside each grid cell was counted.

We then estimated the possible potential gain and loss in species number per grid cell by 2080. Absolute values of species gained and lost have been calculated by simply making the difference between present and future values.

Current and projected potential phytogeographical regions: From the current potential species presence/absence matrix, we calculated Bray-Curtis dissimilarity between all possible pair of sites (here grid cells) according to the formula:

$$d_{ij} = 1 - 2A/2A + B + C$$

where A is the number of species common to both sites i and j (here grid cells); B is the number of species present only at site i; and C is the number of species present at site j.

We then clustered grid cells on the basis of the Bray-Curtis dissimilarity matrix by using the complete linkage of the agglomerative clustering method (see Legendre *et al.* 1998 for a review of different clustering methods). We defined current potential phytogeographic regions based on the indicator species analysis (Dufrêne and Legendre 1997); see chapter 4 for details. These steps have been repeated separately for each climate scenario and model and for each time period.

5.4 Results

Contemporary and projected future potential species richness: the pattern of contemporary species richness here presented (Figure 5.1) differs slightly by its smoothly structure from the richness pattern when we included landcover variable into the model (see Appendix 5 for visual comparison).

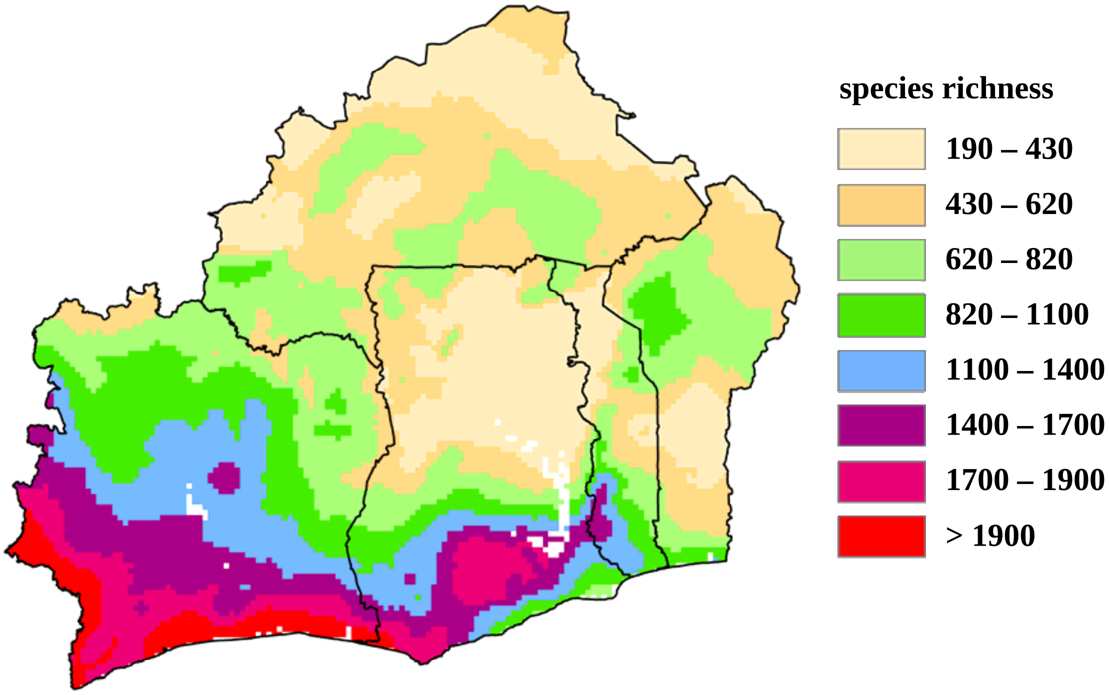


Figure 5.1: Contemporary potential vascular plant species richness based on the distribution records and superimposed modeled geographic range of 3,393 species in West Africa. Only precipitation, temperature and altitude have been used as prediction variables. Here land cover variables have been excluded from the model.

As already noticed (see chapter 4, for more detail), species richness patterns follows the steep environmental gradient in the region, with high species number in the south and decreases progressively toward the north (Figure 5.1). Similar altitudinal structures are observed in the future spatial patterns of species richness for all models and scenarios, but with gain or loss of species for some areas (Figure 5.2).

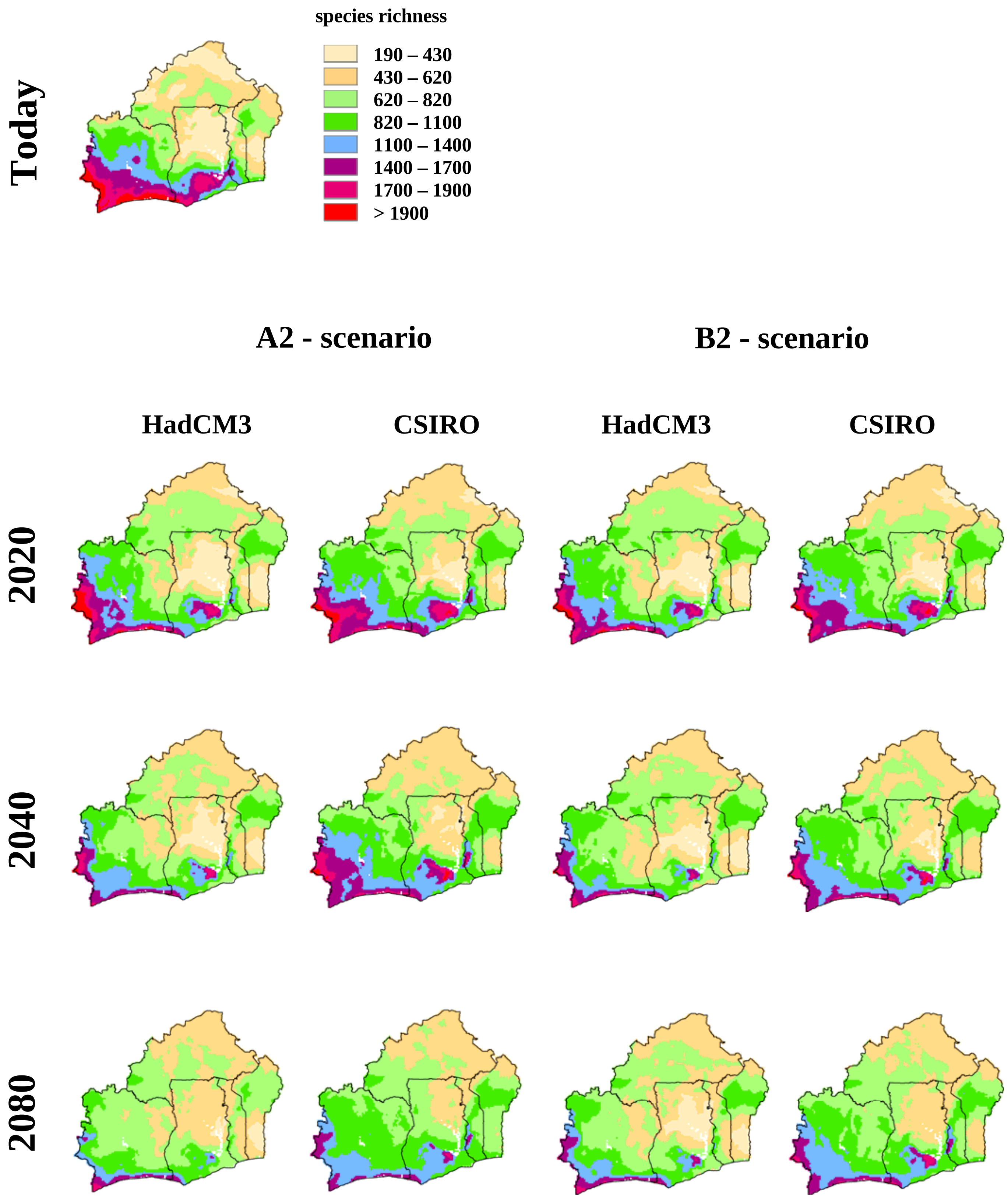


Figure 5.2: Projected potential species richness for IPCC A2 and B2 scenario according to two different models, at different periods of time. According to IPCC report (2007) an average increase in global temperature of +3.4 for A2 and +2.4 for B2 scenarios is expected.

In general high values of species richness are located in most humid areas, as well as in mountains areas for all diversity patterns (current and projected according to different scenarios and models). However between consecutive periods of time, there is a general decrease in species number per grid cell. This decrease reaches up to 50% per grid cell in some areas, in particular in the rainforest regions (Figure 5.3).

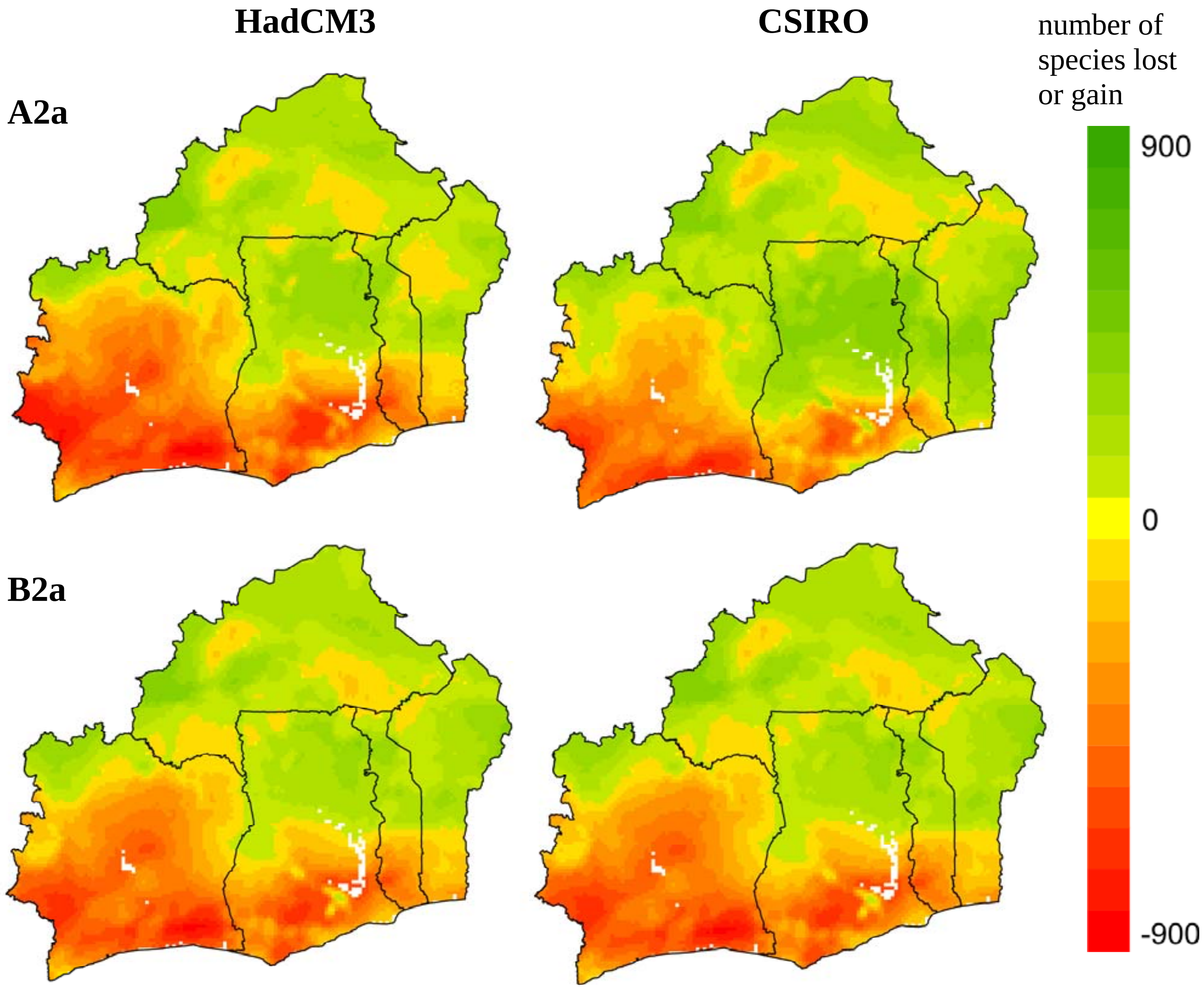


Figure 5.3: Change in species richness by 2080 according to A2 (+3.4 °C) and B2 (+2.4 °C) IPCC climate change scenarios for HadCM3 and CSIRO climate models showing the absolute number of species predicted to be lost or gained per grid cell. Severe impact of climate change occurred in the southern part with up to approx. 50 % of species loss per grid. White cells are no data areas.

The rate of decrease in species richness is very high in the extreme southern part of the study area, corresponding to the rainforest regions. In contrast, this rate is lower in the drier regions, as well as in the regions of high altitude: for instance, southwest of Burkina Faso around the Pic de Sindou; also in the region extending from northwest of Benin to southwest of Togo along the mountains ranges of Atacora.

Amongst all scenarios and models in average 9.5% of all species in the study area are committed to extinction by the end of the century under climate change. More than 95% of the species threatened by extinction have small contemporary ranges. Here we referred to as small range species, species present in less than 15 % of all grid cells comprised in the study area.

For all models and IPCC climate change scenarios there is negative impact on plant diversity in the study area. However, the B2 scenario appeared less harmful to vascular plant diversity than the A2 scenario (see Table 5.2).

Table 5.2: Summary of projections for investigated vascular plant species in the year 2080. This table shows the percentage of species subject to an increase or decrease in their potential range size; the percentage of species extinct and the average percentage of loss in range for all species by 2080.

IPCC scenario	A2		B2	
Climate model	CSIRO	HadCM3	CSIRO	HadCM3
Percent of species with area increase	35.53	28.82	33.19	30.86
Percent of species with area decrease	64.17	70.88	66.48	68.84
Percent range loss	34.76	41.39	30.80	35.18
Percent of species extinct	**10.27**	**13.44**	**6.70**	**7.87**

Potential phytogeographic regions: Based on the contemporary potential distribution of the investigated vascular plant species, we delineated seven potential phytogeographic regions, which structure and disposition reflect those of the vegetation zones defined by White (1983). By the mean of indicator species analysis the delineated regions are defined as (Figure 5.4): Guineo-Congolian rainforest wetter type (I); Guineo-Congolian rainforest drier type (II); Mosaic of Guineo-Congolian wetter and drie type (III); Transition zone between rainforest and Sudanian vegetation type (IV); Sudanian vegetation zone (V); North-sudanian vegetation zone (VI) and the Sahelian vegetation zone (VII).

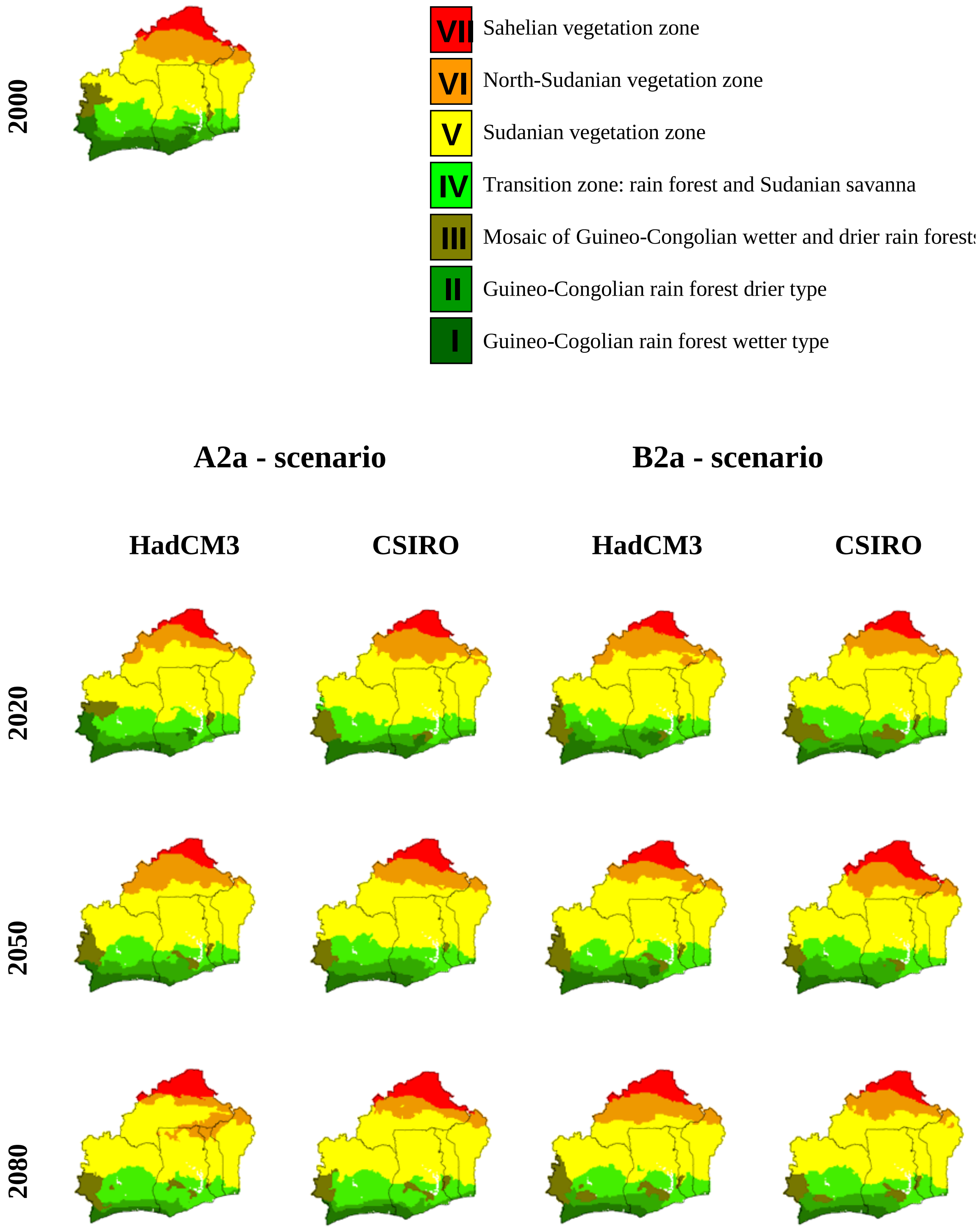


Figure 5.4: Potential shift in phytogeographical regions in West Africa for the IPCC A2 and B2 scenario according to two different global climate models. Maps are displayed at different period of times from the years 2000 to 2080. White cells are no data areas

Each region is characterized by a set of well known indicator species (according to the literature).

The same vegetation zones are delineated for the future under different climate scenarios and climate models. We identified corresponding possible future vegetation zones based on a set of indicator species for each region. For all groups delimited at different periods of time by cluster analysis a similar set indicator species are identified. As shown at Figure 5.5 notable changes are observed in future potential vegetation zones; the rainforest vegetation types decrease considerably; in contrast expansions in drier areas are observed (Figure 5.5).

Moreover southward slight expansion in the sudanian vegetation zone occurred, as well as in the transition zone between forest and sudanian savanna region. Figure 5.5 shows the future possible dynamic of vegetation zones under climate change, according to the used climate scenarios and models. We can clearly notice a general negative impact for all models and scenarios.

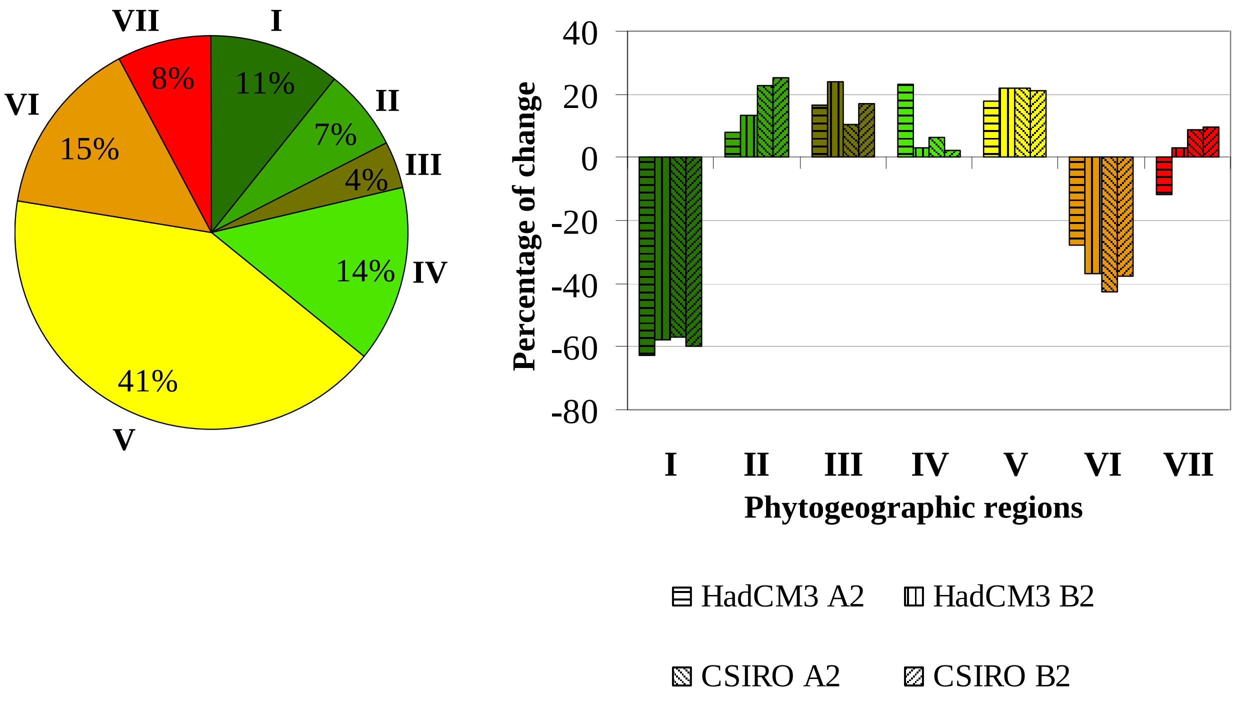


Figure 5.5: Potential change in phytogeographic regions by 2080 according to IPCC A2 and B2 scenarios and based on two climate models (HadCM3 and CSIRO). Here are presented: (a) the proportion of each contemporary potential phytogeographic region in the study area with a total size of 12,152 grids cell of 10 km resolution; (b) the percentage of possible change (reduction or expansion) in each region by 2080 under climate change.

5.5 Discussion

For the first time in West Africa, we modeled the distribution ranges of 3,393 vascular plants species and projected their future potential ranges under different climate scenarios and models at relatively fine spatial resolution of approximately 10km x 10km. For all scenarios, a negative impact of future climate on the size of species potential ranges change is expected. According to our results, the A2 scenario (with an projected average temperature increase of +3.4°C by 2080) appeared as being threatening plant diversity in the investigated area to a higher rate than the B2 scenario (average temperature increase of +2.4°C by 2080). According to the latest assessments on the rate of possible global warming that incorporate the rate of warming since the year 2000, the A2 scenario is considered as a realistic one that may even be pronouncedly exceeded (Richardson 2009).

According to our models, the major losses in species habitat suitability observed in the most humid areas could be explained by the rapid decrease in the rainfall amount in these areas. Indeed in several previous studies, rainfall has been described as the most important water factor determining the distribution of plant species, as well as vegetation patterns in West Africa (Hall & Swaine 1976; van Rompaey 1993, van Rompaey & Oldeman 1997, Bongers *et al.* 2004, Tchouto 2004). As species distributions are – apart from biotic interactions as competition – mostly constrained by their physiological level of tolerance (O’Brien 1998; Hawkins *et al.* 2003; Currie *et al.* 2004), a decrease in precipitation will possibly lead to local extinction events for plant species that are getting below their level of drought tolerance.

In contrary to what could be expected, the drier regions are projected to loss only very few species according to our results. Interestingly, the results indicate even considerable gains of species in some areas of these regions. Possible explications of this observation could be related to water availability in terms of precipitation. The applied General Circulation Models are characterized by a major discontinuity in terms of the estimated changes in the amount and variability of precipitation events, causing somewhat inconsistent responses in the species distribution models.

Our results support the general assumption that mountain areas seem to be less sensitive to climate change. This may be due to the structural complexity of habitats in mountain areas that facilitate the persistence of species in small pockets of suitable conditions, e.g. in gallery forests or in mountain areas with still suitable meso- and microscale conditions even when broad-scale climate conditions are getting harsh and unsuitable (Sommer *et al.* 2010).

According to our results, almost all species that lose their entire suitable habitats in future have presently small distribution ranges. This supports the paradigm of narrow ranged species that are more vulnerable to extinction (Pimm and Raven 2000, Broennimann *et al.* 2006) and they should be particularly in the focus of conservation (Gaston 1994; Purvis *et al.* 2000). However, the higher vulnerability of narrow ranging species in our models also has methodological reasons simply because it is more unlikely for a small environmental envelope to persist under changing climate conditions when distribution models are applied. In contrast to this, there is empirical evidence that narrow ranging species often occur in azonal systems where they are to a high degree adapted to, and that these species are less affected by broad scales climate conditions (Kreft *et al.* 2006). This effectuates that a severe threat or an extinction of these species is unlikely as long as their habitats are not actively destroyed.

It is well known that patterns of spatial and temporal change in vegetation are ultimately controlled by climate and its dynamics (Prentice & Solomon 1991, Printice 1992), that species distributions in the past have varied in accordance with changing climate conditions, and that we can accordingly expect plant species to continue to change their distribution ranges (Woodward 1987). The possible potential gain and loss in the climatic potential for species richness per grid cell may induce changes in species composition, and therefore on vegetation zones (Pamesan & Yohe 2003, Baselga & Araújo 2009).The pronounced decline of potential species richness observed in the forest regions due to deteriorating living conditions caused by a shift of the relation between temperature and rainfall towards more arid conditions may induce a conversion of forest habitats into other vegetation types. As the delineation of our vegetation zones is based only on their respective species composition, the expansions of the Sahel region and the reduction of the north Sudanian region could be due to the southward spread of the distribution of many Sahelian species. This was already observed in the area for some species (Wittig *et al.* 2004, Thiombiano *et al.* 2006). Also, the slight southward expansion of the Sudanian vegetation region could be a consequence of the migration of some of its species into adjacent regions. In concordance with the local extinction of some species formerly occurring in this transition area, this could trigger the conversion of the northern border of deciduous rainforest vegetation.

Identifying regions with high absolute numbers of species lost or gained is of prime importance for conservation planning, whereas regions with a high percentage turnover may experience a high reshuffling of biological assemblages, which may further lead to some ecosystems disruption (Bakkenes *et al.* 2002; Erasmus *et al.* 2002; Peterson *et al.* 2002). Therefore, the creation of reserves requires the consideration of the possible effects of climate change and these reserves should not be restricted to areas with a high probability of change. As many diverse systems are located in the transition zones between ecosystems or biomes (Leemans 1990), reserves have to be large enough to allow for spatial shifts of these areas within the protected areas, or at least provide corridors between them (Williams *et al.* 2005).

Our study does not include the impacts of land-use change, yet climate change is also predicted to interact with other drivers of biodiversity change such as habitat destruction and fragmentation due to human land use activities (Pearson & Dawson 2005). In general, vegetation in Africa faces an increasing pressure by human land use such as livestock production, deforestation and crop production (Williams *et al.* 2007). Many countries in West Africa have their economy based on agricultural production, therefore a large proportion of suitable areas were transformed into farmland areas resulting in major loss of species as well as vegetation coverage (FAO 1995, FAO 2001, Achard *et al*. 2002). Moreover the introduction of foreign species could cause possible changes in vegetations structure (Kriticos *et al.* 2003). However, a previous study carried out at coarser spatial resolution has shown that species turnover in the sense of supplementation or replacement of the indigenous flora of an area by other species is of minor importance in Africa (Sommer 2008). Altogether, these threats may possibly act in synergy to increase extinction risk.

Biotic interactions can affect the species’ ability to adapt to changes in their environment. For example Jordano (2000) suggests that >90% of tropical plant species rely on animals for the dispersal of their seeds. However, modifying individual species distribution models to account for complex biotic interactions is difficult (Araújo and

Luoto 2007, Heikkinen *et al.* 2007). Indeed, it requires information on the biology of organisms that is either unavailable or available for specific case studies alone.

Uncertainties in assessing impact of climate change: Different levels of uncertainties could be distinguished in assessing the potential impact of climate change on species distribution, as well as on vegetation zones dynamics. Uncertainties can be induced by the selection of climate variables that are used to predict the potential distribution range of each species. We used only environmental variables related to temperature, precipitation and elevation because of data availability. Yet, other important factors are known to shape considerably the distribution range of many species and vegetation structure such as biotic interaction. Moreover, fire is a major factor in structuring vegetation (Bond *et al.* 2005), and some biome shifts follow these changes in fire regime, whereas others are forced directly by climate**.**

Further uncertainties are induced by scarcity in climate data in regions and there is a notable lack of geographic balance in data and literature on observed changes in natural and managed systems, with marked scarcity in developing countries (IPCC 2007). Also the confidence in the projections derived from the General Circulation Models is higher for some variables (e.g. temperature) than for others (e.g. precipitation) and it is higher for larger spatial scales and longer time averaging periods (IPCC 2007).

Uncertainties appear additionally due to the cut-off methods used to determine species presence/absence ranges as part of the species distribution models. Here, we used the same threshold for all species over the time periods. Choosing an appropriate threshold is a crucial step for the quality of the model output. Different thresholds could lead to very different projected distributions, causing additional challenges for biodiversity risk assessment and conservation purposes (Manel *et al.*2001, Thuiller 2004). Furthermore, projections into the future with climatic conditions outside the current range necessarily involve uncertainties in the form of over- and underestimations of the respective consequences. Hence, predictions of current and future species distributions need to be interpreted in consideration of the related methodological uncertainties to ensure that results in relation to species range shifts, extinctions, colonizations and species turnover are adequately emphasized (Thuiller 2004).

5.6 Conclusion

Based on potential species distributions derived from natural history and field collections, future climate projections and species distribution modeling, our analysis show a generally negative impact of climate change on vascular plant species richness in West Africa, as well as on the maintenance of vegetation zones of the area.

The major losses in species habitat suitability observed in the most humid areas, while the drier regions are projected to loss only very few species according to our results, in contrary to what could be expected. Morevore, mountain areas seem to be less sensitive to climate change.

6. General conclusions

The present thesis investigated the spatial patterns of vascular plant species richness, the distribution of phytogeogaphical regions based on potential distribution of species, as well as the potential impact of projected future climate change on the observed patterns. Findings of the study can be used to support the sustainable monitoring and conservation of biodiversity in West Africa.

Our results indicate that species distribution models are valuable tools to improve the understanding on species richness gradients particularly in areas with a heterogeneous availability of distribution data (chapter 3). We applied a species distribution model (The Maximum Entropy approach, Phillips *et al.* 2006) to calculate the potential distribution ranges of individual plant species in relation with their environmental suitability. For the first time, a regional species richness map for all vascular plant species in the area of investigation has been produced at a relatively high spatial resolution. In accordance with the spatial distribution of global plant species richness (Barthlott *et al.* 1996; Mutke & Barthlott 2005, Barthlott *et al.* 2007) the patterns of plant species richness follow the steep climatic gradient existing in the region of West Africa. The main determinant of species distribution ranges appeared to be the amount of rainfall. Highly important areas in terms of plant species richness at regional scale as well as at national extent of each surveyed country have been identified in the most humid areas in concordance to many previous observations. As surrogate to data shortage on species distributions, this study confirmed the suitability of the use of higher taxa, such as plant family affiliation, to depict the distribution patterns of biodiversity. This has the advantage to be much more efficient in getting valuable information for the development of biodiversity conservation strategies. As a complementary step to analyse the conservation status of biodiversity, an investigation of the effectiveness of existing protected areas in the region shows an overall good coverage of species. However at national scale, the establishment of new protected areas is suggested, in particular in Burkina Faso, Benin and Togo.

Knowledge on the distribution of biogeographical regions is also an essential precondition for setting priorities in conservation biology and policy (Olson *et al.* 2001; Kier *et al.* 2005). The proposed potential phytogeographical regions (chapter 4) were delineated by using a newly developed methodological approach tha investigates the variation in species composition among standard sites. The results can be considered as a refinement of the well known vegetation zones, established on the basis of classical approaches (White 1983). An important aspect integrated in this study is the use of indicator species analysis (Dufrêne & Lengendre 1997). This allowed identifying groups of species that characterize each phytogeographical region. It further facilitates the analysis of range-restricted or endemic species, thus highlighting the qualitative importance of the corresponding regions. Moreover, an imperative finding from this study is the pronounced shift of the phytogeographical regions observed in comparison to the vegetation zones of White (1983) especially in the forest zones in the south and in the drier areas in the north. The spatial resolution used in this analysis seems to be, at the moment, the finest possible because of many limitations in the methodology due to the limited comprehensiveness of the database.

Accurate estimations of the likely future impacts of climate change on plant diversity are critical for the development of conservation strategies (Araújo and Rahbek 2006). An important tool for these estimations is species distribution modeling: the modeling of individual species, groups of species such as ‘functional types’, communities, ecosystems or biomes. The strong relation between species distributions, vegetation patterns, and climate indicates that plant species are sensitive to climate change. Our results showed a generally negative impact of climate change on species richness in the region according to two IPCC climate change scenarios based on the HadCM3 and CSIRO General Circulation Models (chapter 5). This impact is particularly accentuated in most humid areas, resulting in a loss of habitat suitability for up to 50% of species per grid cell. In the study area, an average of 9.5% of all investigated species is losing its entire potential suitable habitats by 2080.

Moreover, our results indicate a pronounced negative impact of climate change on the potential distribution of vegetation zones. While the Sudanian vegetation zone possibly enlarges, a considerable reduction of the forest zone is possible by the end of the century. The potential contemporary distribution of vegetation zones, as well as the respective projected future changes are in particular alarming as these types of vegetation is in West Africa already under heavy threat due to habitat conversion (FAO 1995, FAO 2001, Achard et al. 2002). One major advantage of the applied method to define phytogeographic regions is its repeatability, and therefore its applicability for the long term monitoring of vegetation, as well as for the assessment of the impact of future climate change on vegetation dynamics (chapter 5).

As the introduced approach is repeatable, it would be recommendable to apply this to other groups of organisms such as bats and amphibians, since quantitative and qualitative data on these groups are now gathered and available within the BIOTA project. Moreover, the impacts of climate change are predicted to amplify other drivers of biodiversity loss such as habitat destruction and fragmentation (Pearson & Dawson 2005), or the introduction of invasive species (Kriticos *et al.* 2003). Further, fire is a major factor in structuring vegetation (Bond *et al*. 2005), and some vegetation shifts due to changes in fire regime, whereas others are forced directly by climate. Including these aspects into the modeling algorithm would be highly recommendable in future studies, for a better understanding of biodiversity issues in the region.

The implementation of ecosystem-based approaches of biodiversity conservation and environmental management requires the availability of species richness maps, as well as maps depicting geographic areas with similar ecosystem characters. In the direction of achieving the overall goal of the Convention on Biological Diversity (UNCBD 1992), this thesis constitutes a contribution to provide decision-makers with spatial information for the development of sustainable conservation strategies of biodiversity at regional level of West Africa, as well as at the national scale of each investigated country. On top of identifying important areas in terms of their qualitative and quantitative features for biodiversity conservation, the study calls for an establishment of supplement protected areas, as well as for the reinforcement of the existing network of protected areas which are highly threatened by many factors such as uncontrolled logging and land conversion for agriculture (IUCN 2010). Moreover, the achieved results are helpful in elaborating effective strategies for mitigating the projective impact of future climate change on biodiversity in the region.

7. Summary

DA, Sié Sylvestre (2010). Spatial patterns of West-African plant diversity along a climatic gradient from coast to Sahel. Doctoral Thesis, Mathematisch-Naturwissenschaftliche Fakultät (Nees-Institut für Biodiversität der Pflanzen), Rheinische Friedrichs-Wilhems-Universität Bonn. 121 pp.

Understanding species distribution patterns and the corresponding environmental determinants is a crucial step in the development of effective strategies for the conservation and management of plant communities and ecosystems. Therefore, a central prerequisite is the biogeographical and macroecological analysis of factors and processes that determine contemporary, potential, as well as future geographic distribution of species. This thesis has been conducted in the framework of the BIOMAPS-BIOTA project at the Nees Institute of Biodiversity of Plants, which was funded by the German Federal Ministry of Education and Research (BMBF). The study investigated patterns of plants species richness and phytogeographic regions under contemporary environmental conditions and forecasted future climate change in the area of West Africa covering five countries: Benin, Burkina Faso, Côte d'Ivoire, Ghana and Togo.

Firstly, geographic patterns of vascular plant species richness have been depicted at a relatively fine spatial resolution based on the potential distribution of 3,393 species. Species richness is closely related to the steep climatic gradient existing in the region with a high concentration of species in the most humid areas in the south and decreases towards the northern drier areas. The investigation of the effectiveness of the existing network of protected areas shows an overall good coverage of species in the study area. However, the proportion of covered species is considerably lower at national extent for some countries, thus calling for more protected areas in order to cover adequately a maximum number of plants species in these countries.

Secondly, based on the potential distribution range of vascular plant species, seven phytogeographic regions have been delineated that broadly reflect the vegetation zones as defined by White (1983). However notable differences to the delineation of White (1983) occur at the margins of some regions. Corresponding to a general southward

shifted of all regions. And expansion of the Sahel vegetation zone is observed in the north, while the rainforest zone is decreased in the very south.This is alarming since the rainforest shelters a high number of species and a high proportion of range-restricted or endemic species, despite their relatively small extent compared to the other regions.

Finally, the evaluation of the potential impact of climate change on plant species richness in the study area, results in a severe loss of future suitable habitat for up to 50% of species per grid cell, particularly in the rainforest region. Moreover, the analysis of the possible shift of phytogeographic regions shows in general a strong deterioration of the West African rainforest. In contrast the drier areas are expanding continuously, although a slight gain in species number can be observed in some particular regions.

The overall lesson to retain from the results of this study is that the West African rainforest should be fixed as a high priority area for the conservation of biodiversity of plants, since it is subject to severe contemporary and projected future threats.

8. Zusammenfassung

DA, Sié Sylvestre (2010). Räumliche Muster der Pflanzendiversität entlang eines klimatischen Gradienten von der Küste Westafrikas bis in den Sahel. Dissertation, Mathematisch-Naturwissenschaftliche Fakultät (Nees-Institut für Biodiversität der Pflanzen), Rheinische Friedrichs-Wilhems-Universität Bonn. 121 Seiten.

Das Verständnis des Zusammenhangs zwischen räumlichen Verbreitungsmustern von Pflanzenarten und Umweltfaktoren ist ein entscheidender Schritt für die Entwicklung von effektiven Schutz- und Managementstrategien für Arten, Pflanzengemeinschaften und Ökosystemen. Biogeographische und makroökologische Untersuchungen ermöglichen die Analyse der bestimmenden Faktoren und Prozesse, welche die potentielle, die aktuelle wie auch die zukünftige geographische Verbreitung von Arten bestimmen. Die vorliegende Arbeit wurde am Nees-Institut für Biodiversität der Pflanzen im Rahmen des BIOMAPS-BIOTA Projekts durchgeführt, welches vom Bundesministerium für Bildung und Forschung (BMBF) gefördet wurde. Es werden Muster der pflanzlichen Artenvielfalt, sowie die Verbreitung der phytogeographischer Regionen unter heutigen und zukünftigen klimatischen Bedingungen untersucht. Das Untersuchungsgebiet liegt in Westafrika und besteht aus den fünf Staaten Benin, Burkina Faso, Elfenbeinküste, Ghana und Togo.

Zuerst wurden, basierend auf der potentiellen Verbreitung von 3393 Arten, geografische Muster der Artenvielfalt von Gefäßpflanzen auf einer hohen räumlichen Auflösung dargestellt und beschrieben. Die Zunahme der Artenvielfalt von Nord nach Süd korreliert mit der Zunahme des mittleren Jahresniederschlages. Somit finden sich hohe Artenzahlen in den Regionen feuchter Klimate im Süden und geringe Artenzahlen in den nördlichen trockenen Regionen.

Die Effizienz des des bestehenden Schutzgebietssystems Westafrikas wurde hinsichtlich der Repräsentierung der untersuchten Pflanzenarten ermittelt. Bei einer Betrachtung des gesamten Untersuchungsgebietes zeigte sich eine insgesamt gute Repräsentation aller Pflanzenarten. Auf nationaler Ebene besteht jedoch ein Defizit im Schutz einiger Arten. Daher ist in diesen Ländern die Einrichtung weiterer Schutzgebiete erforderlich, um eine maximale Anzahl von Pflanzenarten in den nationalen Schutzgebietssystemen zu repräsentieren.

Des Weiteren wurden basierend auf der potentiellen Verbreitung der Gefäßpflanzen sieben phytogeographische Regionen klassifiziert, welche hinsichtlich ihrer Verbreitung weitgehend mit denen nach White (1983) definierten Vegetationszonen übereinstimmen. Jedoch sind im Vergleich zu White (1983) alle Grenzen der phytogeographischen Regionen südwärts verschoben. Während die Sahel-Vegetationszone folglich eine ausgedehntere Fläche einnimmt ist die Größe der Regenwaldgebiete geringer. Dies ist besonders alarmierend, weil die Regenwaldflächen trotz ihrer vergleichsweise geringen Ausdehnung eine Vielzahl kleinräumig verbreiteter und endemischer Arten beherbergen.

Abschließend wurde eine Analyse des potenziellen Einflusses des Klimawandels auf die Vielfalt der Pflanzenarten im Untersuchungsgebiet durchgeführt. In den Regenwaldregionen betrafen diese Verluste bis zu 50% aller Arten pro Gridzelle. Bezogen auf eine mögliche Veränderung der phytogeografischen Regionen durch den Einfluss des Klimawandels ist generell eine starke Verringerung des Areals des westafrikanischen Regenwaldes zu erwarten, bei einer gleichzeitigen Ausdehnung von Regionen, die in trockenen Gebieten liegen. In diesen Regionen ist ebenso ein geringfügiger Anstieg der Artenzahlen möglich.

Die Ergebnisse dieser Studie heben die Bedeutung der westafrikanischen Regenwälder für den Schutz der pflanzlichen Biodiversität hervor. Da sie bereits heute und im Kontext des globalen Klimawandels in der Zukunft starken Bedrohungen ausgesetzt sind, bedarf es einer besonderen Schutzpriorität dieser Wälder.

9. Résumé

DA, Sié Sylvestre (2010). Les modèles spatiaux de la diversité des plantes le long d'un gradient climatique de la côte Ouest Africaine jusqu'au Sahel. Thèse de Doctorat Unique, Mathematisch-Naturwissenschaftliche Fakultät (Nees-Institut für Biodiversität der Pflanzen), Rheinische Friedrichs-Wilhems-Universität Bonn. 121 p.

Comprendre les modèles spatiaux de la distribution des espèces et les facteurs environnementaux déterminants, est une étape cruciale dans l'élaboration de stratégies efficaces pour la conservation et l'aménagement des communautés végétales et des écosystèmes. Par conséquent, l'analyse biogéographique et macroécologique des facteurs et processus déterminant la distribution géographique réelle, potentielle et future des espèces, constitue un préalable. Financièrement supportée par le Ministère Allemand de l'Éducation et de la Recherche (BMBF) à travers le projet BIOMAPS-BIOTA, cette étude a été conduite à l'Institut Nees pour la Biodiversité des Plantes. Elle examine les modèles spatiaux actuels et futures, sous l'effet des changements climatiques, de la richesse en espèces végétales ainsi que des régions phytogéographiques dans la zone de l'Afrique de l'ouest couvrant cinq pays dont le Bénin, le Burkina Faso, la Côte d'Ivoire, le Ghana et le Togo.

D'abord, les modèles géographiques de la richesse en espèces de plantes vasculaires ont été décrits à une résolution spatiale relativement fine sur la base de la distribution potentielle de 3393 espèces. La richesse en espèces est étroitement liée au fort gradient climatique qui existe dans la région, avec une forte concentration d'espèces dans les zones les plus humides au sud et décroit progressivement lorsque l'on se déplace vers les zones de plus en plus sèches au nord. L'analyse de l'efficacité du réseau des aires protégées montre une bonne couverture des espèces dans toute la zone. Cependant, la proportion d'espèces couvertes diminue considérablement pour certains pays lorsqu'on se limite à l'échelle nationale, faisant ainsi ressortir la nécessité d'aires protégées supplémentaires afin de parvenir à une couverture adéquate d'un nombre maximum d'espèces végétales dans ces pays.

Ensuite, sur la base de l'aire de distribution potentielle des espèces de plantes vasculaires, sept régions phytogéographiques ont été délimitées et dont la disposition et la structure reflètent largement celles des zones de végétation de White (1983), avec cependant des différences remarquables. Notamment au niveau de l'étendue de certaines zones telles que les zones de forêt dense humide et décidue qui voient leur superficie réduite considérablement, réduction se traduisant par un déplacement des limites nord de ces zones vers le sud. Tandis qu'une extension significative de la zone de végétation sahélienne est observée. Cependant, malgré leur superficie réduite, les régions de forêts demeurent les plus riches en espèces végétales et abritent un nombre considérable d'espèces endémiques, comparativement aux autres zones phytogéographiques.

Enfin, l'évaluation de l'impact des changements climatiques sur la richesse en espèces végétales de la zone d'étude, met en évidence une perte sévère des habitats favorables pour plusieurs espèces, et particulièrement dans la zone de forêt dense où plus de 50% des espèces par carré pourraient être touchées. De plus l'analyse des modifications possibles induites par les changements climatiques au niveau des zones de végétations révèle en générale une forte destruction des forêts Ouest-africaines. Par contre on assistera à une extension des zones plus arides, bien qu'un léger gain en espèces végétales y soit observé.

La leçon à retenir de l'ensemble des résultats de cette étude est de définir la zone de forêt dense Ouest-africaine comme zone de haute priorité pour la conservation de la biodiversité des plantes, du fait des menaces actuelles et futures auxquelles elle fait face.

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List of Abbreviations

BIOMAPS	: “Biodiversity Mapping for Protection and Sustainable Use of Natural Resources” – Working group at the Nees Institute for Biodiversity of Plants, University of Bonn
BIOLOG	: Research project “Biodiversity and Global Change” of the BMBF
BIOTA Africa	: BIOdiversity monitoring Transect Analysis in Africa, Project network within the BIOLOG-Programme
BISAP	: Biogeographic Information System on African Plant Diversity
BMBF	: German Federal Ministry of Education and Research
CSIRO	: Commonwealth Scientific Industrial Research Organisatin (Australia), specific GCM
GCM	: General Circulation Model
GLC	: Global Land Cover
HadCM	: specific GCM including future climate simulations
IPCC	: Intergovernmental Panel on Climate Change
MaxEnt	: Maximum Entropy probability distribution model

Appendix

Appendix 1: List of all environmental variables used in this study.

Appendix 2: Some illustrations of closing the „data gap“ in Ghana and Togo. Comparison between our potential distribution maps and the observed distribution according to Poorter *et al.* 2004 (chapter 3).

Appendix 3: Extracted vascular plant potential species richness maps for each surveyed country in West Africa (chapter 3).

Appendix 4: The number of vascular plant species based on the modeling result for each surveyed country compared to the estimated numbers of species comprised in the checklist of the corresponding country concordantly to the existing literature (chapter 3).

Appendix 5: Patterns of vascular plant potential species richness based on two different set of environmental variables (chapter 3 & 5).

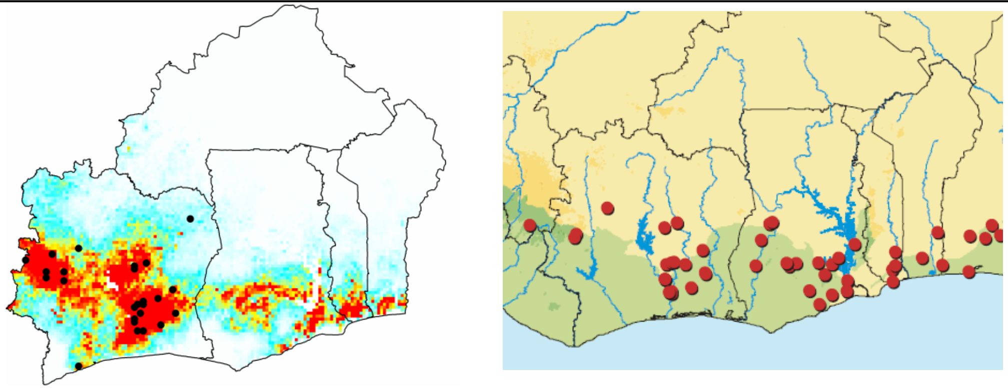
Appendix 6: List of all possible indicator species with an indicator value higher than 50% per phytogeographical region (chapter 4).

Appendix 7: List of species with their distribution ranges restricted to the corresponding phytogeographical region, according to our results (chapter 4).

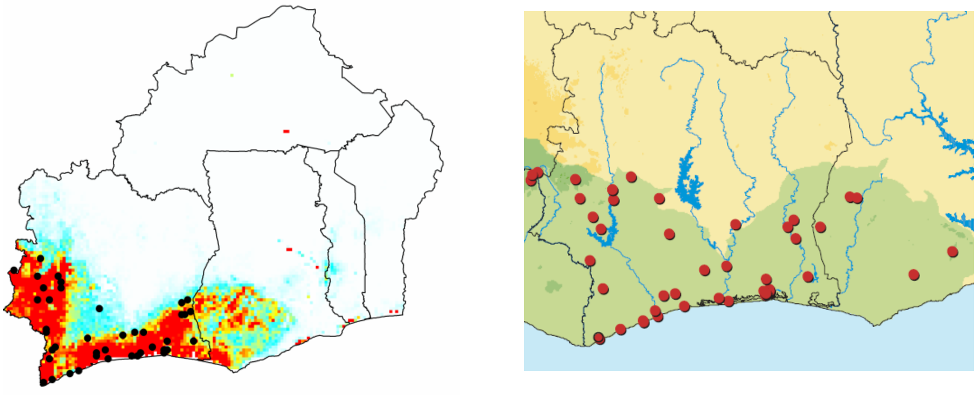
Appendix 1: List of 16 environmental variables (comprising climate and land cover data) used to model species potential distribution range (chapter 3). The environmental datasets were jointly selected and prepared in the frame of the BIOTA West project network under special contribution of the working groups from Ulm and Würzburg (remote sensing group).

Abbreviation	**Variables description**	**Sources**	**Original resolution**
alt	Altitude	WorldClim1.4	1km
prec_30_max	Maximum value (“wettest month”) of the 12 monthly precipitation	WorldClim1.4	1km
prec_30_min	Minimum value (“driest month”) of the 12 monthly precipitation	WorldClim1.4	1km
prec_30_std	Standard deviation of the 12 monthly precipitation data	WorldClim1.4	1km
prec_30_sum	Total annual precipitation calculated as the sum of all 12 monthly rainfall	WorldClim1.4	1km
tmax30_max	Maximum of the mean monthly maximum temperature	WorldClim1.4	1km
tmax30_min	Minimum of the mean monthly maximum temperature	WorldClim1.4	1km
tmax30_std	Standard deviation of the mean monthly maximum temperature	WorldClim1.4	1km
tmin30_max	Maximum of the mean monthly minimum temperature	WorldClim1.4	1km
tmin30_min	Minimum of the mean monthly minimum temperature	WorldClim1.4	1km
tmin30_std	Standard deviation of the mean monthly minimum temperature	WorldClim1.4	1km
glc_raw2	Annual average of spectral response values in the Near-Infrared, band2	SPOT-VEGETATION composite	-
glc_raw3	Annual average of spectral response values in the Red channel. Band3	SPOT-VEGETATION composite	-
bare	Percent of bare ground cover	MODIS	500m
herb	Percent of herbaceous ground cover	MODIS	500m
tree	Percent of tree ground cover	MODIS	500m

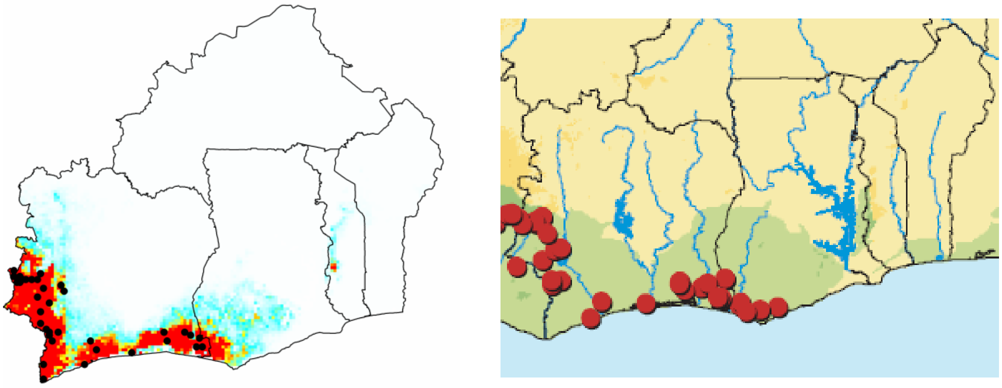
Appendix 2: Some illustration of closing the „data gap“ in Ghana and Togo. Comparison between our potential distribution maps (left side) and the observed distribution according to Poorter *et al.* 2004 (right side).



Combretum zenkeri. Engl. & Diels.
(Combretaceae)



Crossostemma laurifolium Planch. ex Benth.
(Passifloraceae)



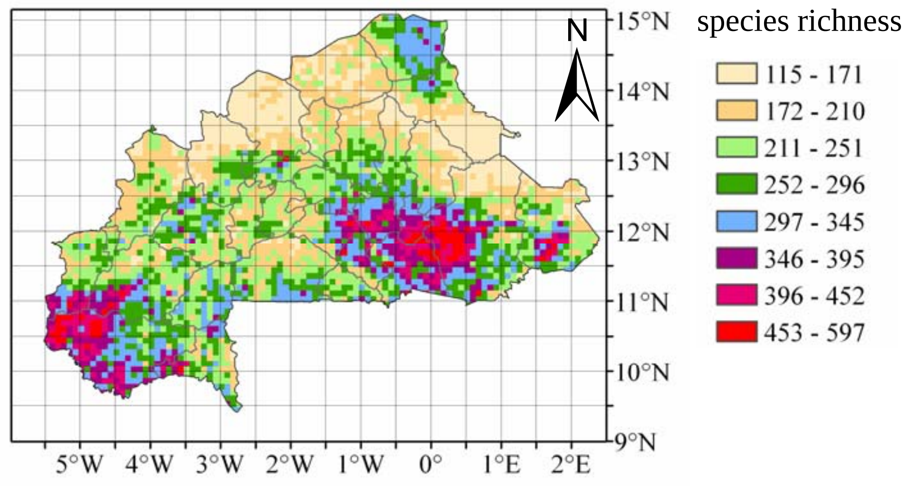
Dorstenia turbinata Engl.
(Moraceae)

● Collection points according to our documented data

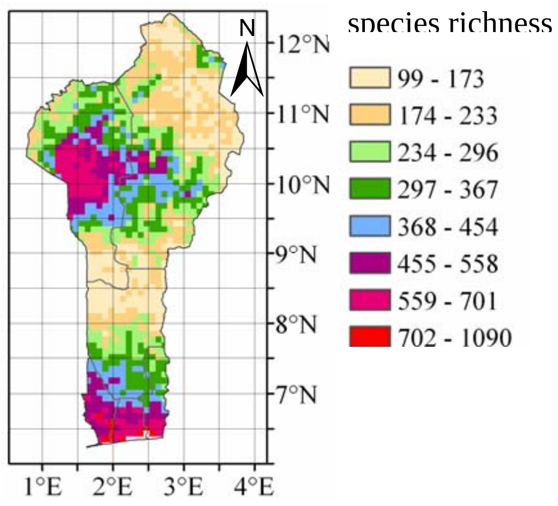
● Collection points according to Poorter et al. 2004

Probability of presence

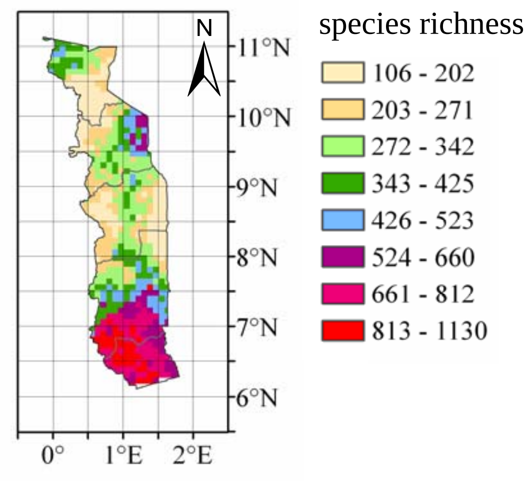
Appendix 3: Extracted vascular plant potential species richness maps for each surveyed country in West Africa. The same color scheme has been used to illustrate species richness for all countries, **but classes indicating species number per grid cell differ between countries**



BURKINA FASO

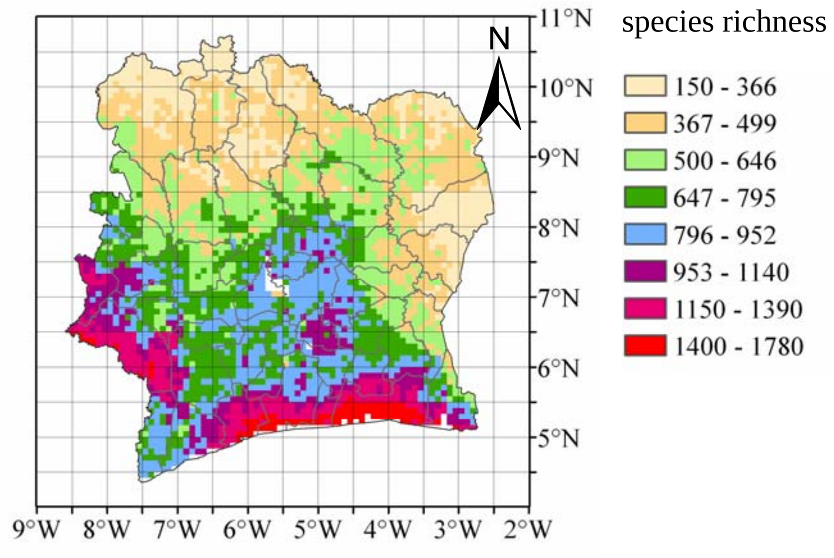


BENIN

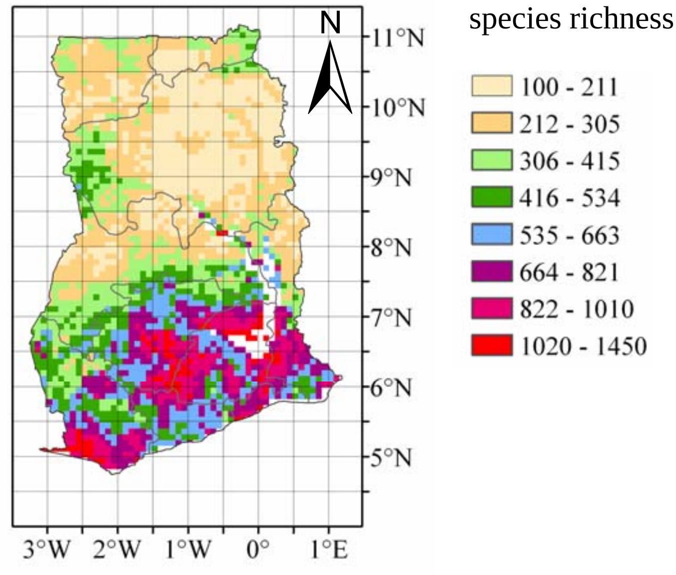


TOGO

Appendix 3: Extracted vascular plant potential species richness maps for each surveyed country in West Africa. The same color scheme has been used to illustrate species richness for all countries, **but classes indicating species number per grid cell differ between countries.**



COTE D'IVOIRE

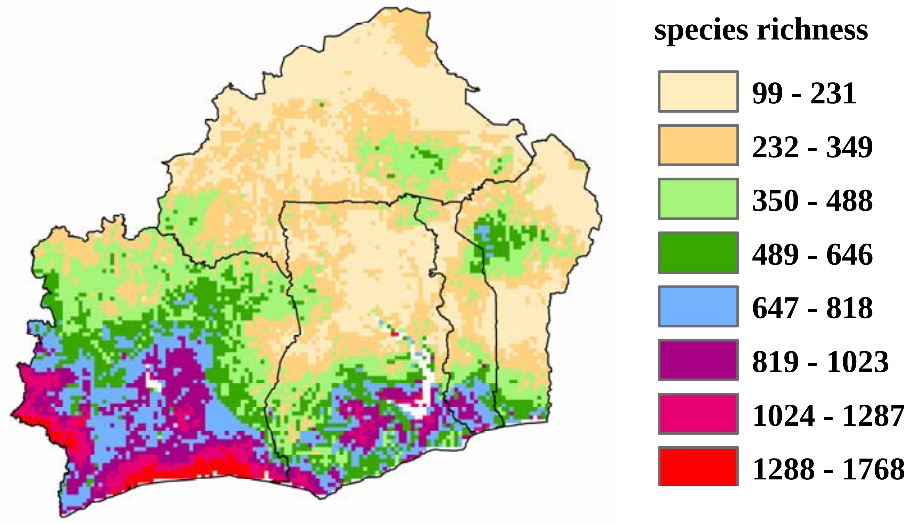


GHANA

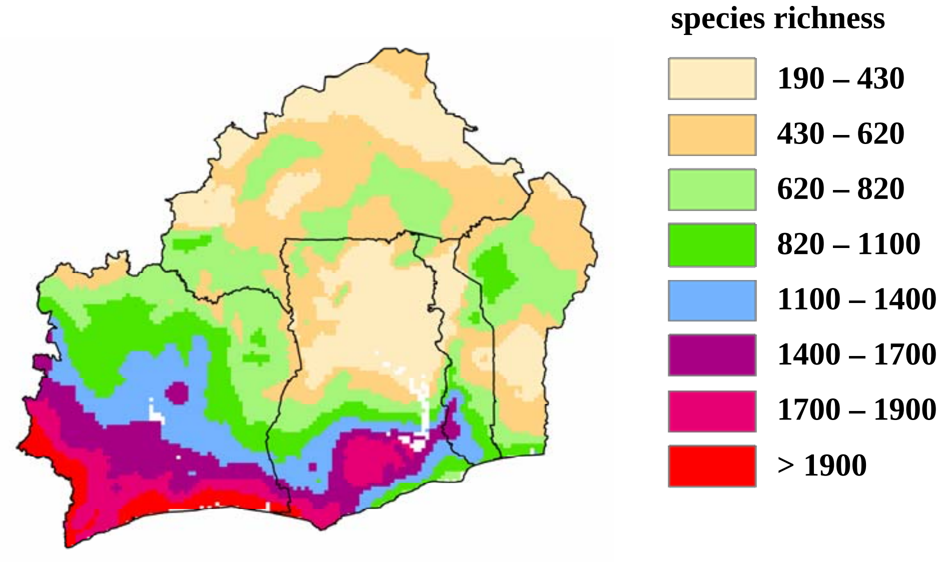
Appendix 4: The number of vascular plant species based on the modeling result for each surveyed country compared to the estimated numbers of species comprised in the checklist of the corresponding country concordantly to the existing literature Except for Côte d'Ivoire, there is general congruence between both estimated numbers for the surveyed countries

	According to our database (raw data)		**Species number according to the modelled data**	**From the literatur**	
	Based on a total number of 4876 species	**Based on a total number of 3399 species**		**Species number**	**Sources**
Bénin	1052	915	**2712**	3000	Project Flora of Benin 2001).
Burkina Faso	1509	1189	**1865**	1054	Guinko 1984;
Côte d'Ivoire	4171	3082	**3105**	?	
Ghana	No data	No data	**3093**	?	
Togo	No data	No data	**2734**	2000-3085	Akpagana 1994 Afidégnon et al. 2003, Earth Trends-Togo 2003)

Appendix 5: Patterns of vascular plant potential species richness based on two different set of environmental variables: (1) with land cover variables included into the model; (2) without land cover variables, only precipitation, temperature and altitude have been used as predictor variables.



(1) Potential species richness based on climate and landcover variables as predictors



(2) Potential species richness based only precipitation, temperature and altitude as predictors variables.

Appendix 6: List of all possible indicator species with an indicator value higher than 50% per phytogeographic region.

Species	Family	I	II	III	IV	V	VI	VII
Tabernaemontana glandulosa	APOCYNACEAE	**63.19**	1.94	0.04				
Dichapetalum oblongum	DICHAPETALACEAE	**62.84**	7.38	0.00	0.00			
Dichapetalum toxicarium	DICHAPETALACEAE	**60.39**	5.68	0.00				
Crotonogyne chevalieri	EUPHORBIACEAE	**57.76**	5.66	1.14	0.01		0.00	
Combretum grandiflorum	COMBRETACEAE	**57.70**	2.23	1.64				
Diospyros gabunensis	EBENACEAE	**57.57**	8.97	0.03	0.00			
Nephthytis afzelii	ARACEAE	**56.70**	2.10	0.06				
Cuviera acutiflora	RUBIACEAE	**56.69**	4.44	0.21	0.00			
Iodes liberica	ICACINACEAE	**55.61**	1.02	0.02				
Adenia dinklagei	PASSIFLORACEAE	**55.55**	4.40	2.19	0.01			
Xylopia staudtii	ANNONACEAE	**55.22**	0.15	0.04	0.02			
Cercestis dinklagei	ARACEAE	**54.51**	3.72	0.79	0.00			
Psychotria gabonica	RUBIACEAE	**54.14**	13.75	0.90	0.00			
Diospyros vignei	EBENACEAE	**53.79**	4.21	0.00	0.00			
Ostryocarpus riparius	FABACEAE	**53.70**	4.37	0.27	0.03			
Psychotria subobliqua	RUBIACEAE	**53.28**	1.93	0.53				
Anthonotha fragrans	FABACEAE	**53.10**	4.21	0.53				
Dictyophleba leonensis	APOCYNACEAE	**53.10**	5.98					
Scaphopetalum amoenum	STERCULIACEAE	**53.08**	5.89	0.00	0.00			
Uvariastrum insculptum	ANNONACEAE	**53.05**	5.36	0.00	0.00			
Diospyros sanza-minika	EBENACEAE	**52.96**	2.25	0.04				
Gilbertiodendron preussii	FABACEAE	**52.71**	5.21	0.11	0.00			
Landolphia incerta	APOCYNACEAE	**52.55**	20.36	0.07	0.02			
Spathandra blakeoides	MELASTOMATACEAE	**52.45**	6.61	0.99	0.02			
Salacia cerasifera	CELASTRACEAE	**52.15**	7.22	0.05	0.12			
Mapania ivorensis	CYPERACEAE	**51.81**	9.71	0.02	0.00			
Sabicea ferruginea	RUBIACEAE	**51.74**	4.00	0.36				
Axonopus flexuosus	POACEAE	**51.64**	9.30	0.28	0.20			
Rhigiocarya racemifera	MENISPERMACEAE	**51.37**	9.25	1.44	0.01		0.00	
Lasianthus batangensis	RUBIACEAE	**51.17**	2.88	0.02				
Campylospermum duparquetianum	OCHNACEAE	**50.35**	1.49	0.01				
Chrysophyllum pruniforme	SAPOTACEAE	**50.10**	10.32	0.34	0.05			
Vitex phaeotricha	VERBENACEAE	**50.09**	1.92	0.27				
Calpocalyx aubrevillei	FABACEAE	**50.05**	1.16	0.60	0.00			
Phyllanthus bancilhonae	EUPHORBIACEAE	0.14	0.59	**56.33**	0.22	0.11		
Cordia guineensis	BORAGINACEAE	0.00	9.55	0.07	**55.15**	1.11		
Utricularia reflexa	LENTIBULARIACEAE	0.01	0.00	0.26	**51.02**	0.42		
Albizia coriaria	FABACEAE	0.57	13.99	0.33	**50.23**	2.50		
Polysphaeria arbuscula	RUBIACEAE	0.00		0.32	6.00	**58.72**	1.90	
Digitaria exilis	POACEAE	1.82	0.10	3.89	1.15	**58.05**	5.22	0.00
Cissampelos mucronata	MENISPERMACEAE	0.00		1.21	3.48	**54.63**	1.66	5.22
Canscora diffusa	GENTIANACEAE			0.45	0.00	**54.14**	1.79	
Vigna luteola	FABACEAE	0.70	0.12	0.05	3.66	**53.63**	2.85	
Loudetiopsis scaettae	POACEAE	0.00		0.13	0.55	**52.32**	0.13	
Schizachyrium rupestre	POACEAE	0.00		0.57	5.02	**52.21**	8.33	1.98
Elephantopus mollis	ASTERACEAE	5.51	3.42	8.39	11.67	**51.55**	6.76	0.02
Ischaemum amethystinum	POACEAE			0.35	1.73	**50.60**	0.43	0.00
Indigofera oubanguiensis	FABACEAE		0.00	0.05	10.92	**50.24**	6.00	
Cyperus digitatus	CYPERACEAE	0.00		0.55	0.70	**50.11**	19.44	16.69
Abutilon pannosum	MALVACEAE					0.02	3.67	**74.55**
Hibiscus sidiformis	MALVACEAE					0.01	3.41	**71.96**
Cyperus pulchellus	CYPERACEAE						4.78	**70.25**
Alternanthera repens	AMARANTHACEAE	0.01				0.05	4.36	**68.86**
Caralluma decaisneana	APOCYNACEAE					0.05	11.47	**66.22**
Capparis rothii	CAPPARACEAE					0.06	1.41	**63.57**
Hibiscus esculentus	MALVACEAE	0.02					0.63	**63.12**
Marsilea polycarpa	MARSILEACEAE	0.00	0.04	0.21	0.84	0.05	1.27	**62.26**
Luffa aegyptiaca	CUCURBITACEAE					0.07	4.49	**61.39**
Tapinanthus globiferus	LORANTHACEAE	0.01			0.00	0.34	13.07	**59.85**
Eragrostis cilianensis	POACEAE	0.00			0.00	0.05	11.35	**59.39**
Solanum incanum	SOLANACEAE					0.00	3.22	**57.75**
Utricularia inflexa	LENTIBULARIACEAE					0.10	23.17	**54.34**
Hibiscus micranthus	MALVACEAE					0.07	0.55	**53.75**
Caralluma dalzielii	APOCYNACEAE					0.00	0.45	**52.27**

Appendix 7: List of species with their distribution ranges restricted to the corresponding phytogeographical region, according to our results.

Region	Species	Family	Fidelity
I	*Aframomum chrysanthum*	ZINGIBERACEAE	0.003
I	*Airyantha schweinfurthii*	FABACEAE	0.041
I	*Albertisia cordifolia*	MENISPERMACEAE	0.003
I	*Albertisia mangenotii*	MENISPERMACEAE	0.083
I	*Albertisia scandens*	MENISPERMACEAE	0.029
I	*Alternanthera littoralis*	AMARANTHACEAE	0.003
I	*Anisopus mannii*	APOCYNACEAE	0.003
I	*Anthonotha vignei*	FABACEAE	0.348
I	*Anthostema aubryanum*	EUPHORBIACEAE	0.052
I	*Avicennia germinans*	AVICENNIACEAE	0.005
I	*Berlinia confusa*	FABACEAE	0.076
I	*Brachystegia leonensis*	FABACEAE	0.132
I	*Calophyllum inophyllum*	HYPERICACEAE	0.105
I	*Catharanthus roseus*	APOCYNACEAE	0.027
I	*Coelocaryon preussii*	MYRISTICACEAE	0.006
I	*Conocarpus erectus*	COMBRETACEAE	0.022
I	*Crinum purpurascens*	AMARYLLIDACEAE	0.079
I	*Crudia klainei*	FABACEAE	0.033
I	*Cyperus crassipes*	CYPERACEAE	0.011
I	*Dalbergia ecastaphyllum*	FABACEAE	0.011
I	*Dasylepis racemosa*	FLACOURTIACEAE	0.087
I	*Dichapetalum dictyospermum*	DICHAPETALACEAE	0.006
I	*Didelotia brevipaniculata*	FABACEAE	0.033
I	*Diospyros tricolor*	EBENACEAE	0.003
I	*Dorstenia embergeri*	MORACEAE	0.057
I	*Dracaena praetermissa*	DRACAENACEAE	0.006
I	*Dramsenia grandiflora*	APOCYNACEAE	0.032
I	*Eugenia whytei*	MYRTACEAE	0.04
I	*Eulophia caricifolia*	ORCHIDACEAE	0.025
I	*Haplormosia monophylla*	FABACEAE	0.062
I	*Hibiscus tiliaceus*	MALVACEAE	0.011
I	*Hydrocotyle bonariensis*	APIACEAE	0.021
I	*Iodes africana*	ICACINACEAE	0.003
I	*Ipomoea imperati*	CONVOLVULACEAE	0.006
I	*Ipomoea pes-caprae*	CONVOLVULACEAE	0.008
I	*Isonema smeathmannii*	APOCYNACEAE	0.019
I	*Landolphia leptantha*	APOCYNACEAE	0.037
I	*Lycopodiella affinis*	LYCOPODIACEAE	0.003
I	*Macaranga beillei*	EUPHORBIACEAE	0.06
I	*Machaerium lunatum*	FABACEAE	0.056
I	*Mapania mangenotiana*	CYPERACEAE	0.046
I	*Megastachya mucronata*	POACEAE	0.003
I	*Mesanthemum radicans*	ERIOCAULACEAE	0.024
I	*Monanthotaxis laurentii*	ANNONACEAE	0.005
I	*Oncoba echinata*	FLACOURTIACEAE	0.059
I	*Ormocarpum verrucosum*	FABACEAE	0.029

I	*Pellegriniodendron diphyllum*	FABACEAE	0.027
I	*Pycreus polystachyos*	CYPERACEAE	0.013
I	*Rhizophora racemosa*	RHIZOPHORACEAE	0.032
I	*Rhynchospora holoshoenoides*	CYPERACEAE	0.008
I	*Saxicolella submersa*	PODOSTEMACEAE	0.086
I	*Schizachyrium pulchellum*	POACEAE	0.008
I	*Spilanthes costata*	ASTERACEAE	0.081
I	*Sporobolus virginicus*	POACEAE	0.005
I	*Stemonocoleus micranthus*	FABACEAE	0.005
I	*Stenotaphrum secundatum*	POACEAE	0.011
I	*Synsepalum tsounkpe*	SAPOTACEAE	0.052
I	*Tapinanthus belvisii*	LORANTHACEAE	0.06
I	*Tapinanthus praetexta*	LORANTHACEAE	0.057
I	*Terminalia catappa*	COMBRETACEAE	0.06
I	*Torulinium odoratum*	CYPERACEAE	0.013
I	*Typha domingensis*	TYPHACEAE	0.016
I	*Uapaca paludosa*	EUPHORBIACEAE	0.008
I	*Utricularia foliosa*	LENTIBULARIACEAE	0.049
I	*Utricularia tortilis*	LENTIBULARIACEAE	0.005
I	*Warneckea membranifolia*	MELASTOMATACEAE	0.106
I	*Xylopia rubescens*	ANNONACEAE	0.013
II	*Eugenia coronata*	MYRTACEAE	0.006
II	*Ischaemum indicum*	POACEAE	0.003
II	*Macropodiella taylorii*	PODOSTEMACEAE	0.003
II	*Rivina humilis*	PHYTOLACCACEAE	0.014
III	*Argostemma pumilum*	RUBIACEAE	0.004
III	*Asplenium formosum*	ASPLENIACEAE	0.001
III	*Brachycorythis macrantha*	ORCHIDACEAE	0.005
III	*Bulbophyllum bidenticulatum*	ORCHIDACEAE	0.012
III	*Bulbophyllum cochleatum*	ORCHIDACEAE	0.001
III	*Cyphostemma rubrosetosum*	VITACEAE	0.003
III	*Dicranolepis laciniata*	THYMELAEACEAE	0.009
III	*Dryopteris manniana*	DRYOPTERIDACEAE	0.001
III	*Gladiolus aequinoctialis*	IRIDACEAE	0.006
III	*Kotschya ochreata*	FABACEAE	0.021
III	*Maesa lanceolata*	MYRSINACEAE	0.004
III	*Panicum sadinii*	POACEAE	0.008
III	*Polystachya dalzielii*	ORCHIDACEAE	0.026
III	*Polystachya leonensis*	ORCHIDACEAE	0.014
III	*Preussiella kamerunensis*	MELASTOMATACEAE	0.019
III	*Rubus pinnatus*	ROSACEAE	0.001
III	*Sericostachys scandens*	AMARANTHACEAE	0.028
III	*Syzygium staudtii*	MYRTACEAE	0.01
III	*Trichilia djalonis*	MELIACEAE	0.01
III	*Vernonia myriantha*	ASTERACEAE	0.001
IV	*Andropogon ivorensis*	POACEAE	0.034
IV	*Indigofera barteri*	FABACEAE	0.004
V	*Adenodolichos paniculatus*	FABACEAE	0.003
V	*Aedesia baumannii*	ASTERACEAE	0.002
V	*Aeschynomene lateritia*	FABACEAE	0.001
V	*Aloe schweinfurthii*	ALOACEAE	0.002
V	*Becium obovatum*	LAMIACEAE	0.003

V	*Beckeropsis uniseta*	POACEAE	0.014
V	*Bewsia biflora*	POACEAE	0.006
V	*Borreria pusilla*	RUBIACEAE	0
V	*Borreria ruelliae*	RUBIACEAE	0.007
V	*Borreria scandens*	RUBIACEAE	0.001
V	*Brachiaria brachylopha*	POACEAE	0.003
V	*Brachiaria disticha*	POACEAE	0.001
V	*Byrsocarpus coccineus*	CONNARACEAE	0.008
V	*Cissus corniculata*	VITACEAE	0.001
V	*Clematis hirsuta*	RANUNCULACEAE	0.002
V	*Crassocephalum togoense*	ASTERACEAE	0.001
V	*Crotalaria deightonii*	FABACEAE	0.005
V	*Crotalaria graminicola*	FABACEAE	0.001
V	*Cussonia barteri*	ARALIACEAE	0.011
V	*Cyperus karlschumannii*	CYPERACEAE	0.025
V	*Dolichos scarabaeoides*	FABACEAE	0.033
V	*Dyschoriste heudelotiana*	ACANTHACEAE	0.011
V	*Eriosema afzelii*	FABACEAE	0.006
V	*Fadogia cienkowskii*	RUBIACEAE	0.043
V	*Ficus capensis*	MORACEAE	0.003
V	*Gnidia kraussiana*	THYMELAEACEAE	0.003
V	*Haumaniastrum buettneri*	LAMIACEAE	0.003
V	*Hippocratea pallens*	CELASTRACEAE	0.001
V	*Hyparrhenia barteri*	POACEAE	0.002
V	*Hypoestes verticillaris*	ACANTHACEAE	0.001
V	*Indigofera confusa*	FABACEAE	0.001
V	*Kohautia grandiflora*	RUBIACEAE	0.003
V	*Laggera gracilis*	ASTERACEAE	0.004
V	*Laggera pterodonta*	ASTERACEAE	0.054
V	*Lepidagathis filifolia*	ACANTHACEAE	0.001
V	*Micrargeria barteri*	SCROPHULARIACEAE	0.004
V	*Mitracarpus villosus*	RUBIACEAE	0.001
V	*Psorospermum senegalense*	HYPERICACEAE	0.005
V	*Rytigynia neglecta*	RUBIACEAE	0.001
V	*Saba florida*	APOCYNACEAE	0.001
V	*Sapium ellipticum*	EUPHORBIACEAE	0.001
V	*Scleria atrovierensis*	CYPERACEAE	0.001
V	*Steganotaenia araliacea*	APIACEAE	0.004
V	*Synaptolepis retusa*	THYMELAEACEAE	0.004
V	*Trochomeria atacorensis*	CUCURBITACEAE	0.002
V	*Vernonia glaberrima*	ASTERACEAE	0.003
V	*Vernonia nestor*	ASTERACEAE	0.004
V	*Vernonia plumbaginifolia*	ASTERACEAE	0.001
V	*Vernonia poskeana*	ASTERACEAE	0.009
V	*Vernonia pumila*	ASTERACEAE	0.008
V	*Vigna nigritia*	FABACEAE	0
VI	*Brachiara villosa*	POACEAE	0.003
VI	*Capparis corymbosa*	CAPPARACEAE	0.01
VI	*Cassia sengueana*	FABACEAE	0.001
VI	*Glyricidia sepium*	FABACEAE	0.002
VI	*Ipomea coscinosperma*	CONVOLVULACEAE	0.003
VI	*Maeuria angolensis*	CAPPARACEAE	0.003

VI	*Mukia maderaspatena*	CUCURBITACEAE	0.001
VI	*Munechma ciliatum*	ACANTHACEAE	0.002
VII	*Acacia laeta*	FABACEAE	0.048
VII	*Acacia raddiana*	FABACEAE	0.021
VII	*Aerva javanica*	AMARANTHACEAE	0.06
VII	*Aristida funiculata*	POACEAE	0.097
VII	*Aristida mutabilis*	POACEAE	0.032
VII	*Aristida sieberiana*	POACEAE	0.133
VII	*Bergia suffruticosa*	ELATINACEAE	0.046
VII	*Boerhavia coccinea*	NYCTAGINACEAE	0.043
VII	*Boerhavia repens*	NYCTAGINACEAE	0.069
VII	*Boscia senegalensis*	CAPPARACEAE	0.039
VII	*Caralluma retrospiciens*	APOCYNACEAE	0.031
VII	*Cenchrus prieurii*	POACEAE	0.06
VII	*Chloris prieurii*	POACEAE	0.038
VII	*Chrozophora brocchiana*	EUPHORBIACEAE	0.04
VII	*Citrullus vulgaris*	CUCURBITACEAE	0.049
VII	*Cleome scaposa*	CAPPARACEAE	0.099
VII	*Cleome violacea*	CAPPARACEAE	0.019
VII	*Crotalaria arenaria*	FABACEAE	0.057
VII	*Cucumis ficifolius*	CUCURBITACEAE	0.053
VII	*Cyperus conglomeratus*	CYPERACEAE	0.002
VII	*Dalbergia melanoxylon*	FABACEAE	0.096
VII	*Euphorbia aegyptiaca*	EUPHORBIACEAE	0.03
VII	*Gisekia pharnacioides*	GISEKIACEAE	0.039
VII	*Grangea maderaspatana*	ASTERACEAE	0.077
VII	*Grewia tenax*	TILIACEAE	0.04
VII	*Hybanthus thesiifolius*	VIOLACEAE	0.297
VII	*Indigofera diphylla*	FABACEAE	0.014
VII	*Ipomoea coptica*	CONVOLVULACEAE	0.007
VII	*Leptadenia pyrotechnica*	APOCYNACEAE	0.016
VII	*Limeum pterocarpum*	MOLLUGINACEAE	0.059
VII	*Limeum viscosum*	MOLLUGINACEAE	0.032
VII	*Maerua crassifolia*	CAPPARACEAE	0.171
VII	*Merremia pinnata*	CONVOLVULACEAE	0.029
VII	*Mollugo cerviana*	MOLLUGINACEAE	0.055
VII	*Momordica balsamina*	CUCURBITACEAE	0.051
VII	*Pennisetum fallax*	POACEAE	0.029
VII	*Pergularia tomentosa*	APOCYNACEAE	0.113
VII	*Phyla nodiflora*	VERBENACEAE	0.042
VII	*Rogeria adenophylla*	PEDALIACEAE	0.304
VII	*Sesamum alatum*	PEDALIACEAE	0.047
VII	*Tephrosia lupinifolia*	FABACEAE	0.013
VII	*Tephrosia uniflora*	FABACEAE	0.049
VII	*Tetrapogon cenchriformis*	POACEAE	0.118
VII	*Tragus berteronianus*	POACEAE	0.036
VII	*Trianthema pentandra*	AIZOACEAE	0.002