Modelling the impact of future climate and land use change on vegetation patterns, plant diversity and provisioning ecosystem services in West Africa

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Chapter 1

Introduction

Global climate change and land use change will not only alter entire ecosystems and biodiversity patterns, but also the supply of ecosystem services. Severe consequences are expected for the African continent during the 21st century (IPCC, 2007). In particular, the rural poor are considered as highly vulnerable (MA, 2005). However, the consequences of environmental change on ecosystems, biodiversity as well as on ecosystem services, are only partly understood, particularly in under-investigated regions, such as West Africa.

Large-scale vegetation patterns in West Africa: Historical changes and recent trends

Global and continental scale vegetation patterns are dominated by the climate (Hansen *et al.*, 2001). Regions with similar climatic conditions and vegetation form large entities, the biomes. The current climate in West Africa is characterised by ascending air masses near the equator due to high solar heating (convection) which descend in the subtropics. Resulting pressure differences are balanced by trade winds (Hadley atmospheric circulation system). This causes a strong north-south bioclimatic gradient, with a few millimetres of annual rainfall in the Sahara desert to 4000 mm in the humid evergreen tropics (Hijmans *et al.*, 2005). The broad range of climatic zones from arid to equatorial climates (Köppen-Geiger climate classification) shaped five biomes in West Africa: desert, grassland, savanna, deciduous forest and evergreen forest. Figure 1 shows the West African countries and the current distribution of the major biomes. The vegetation cover changes gradually, following the north-south gradient and strongly correlates with annual mean precipitation (Foley *et al.*, 2003).

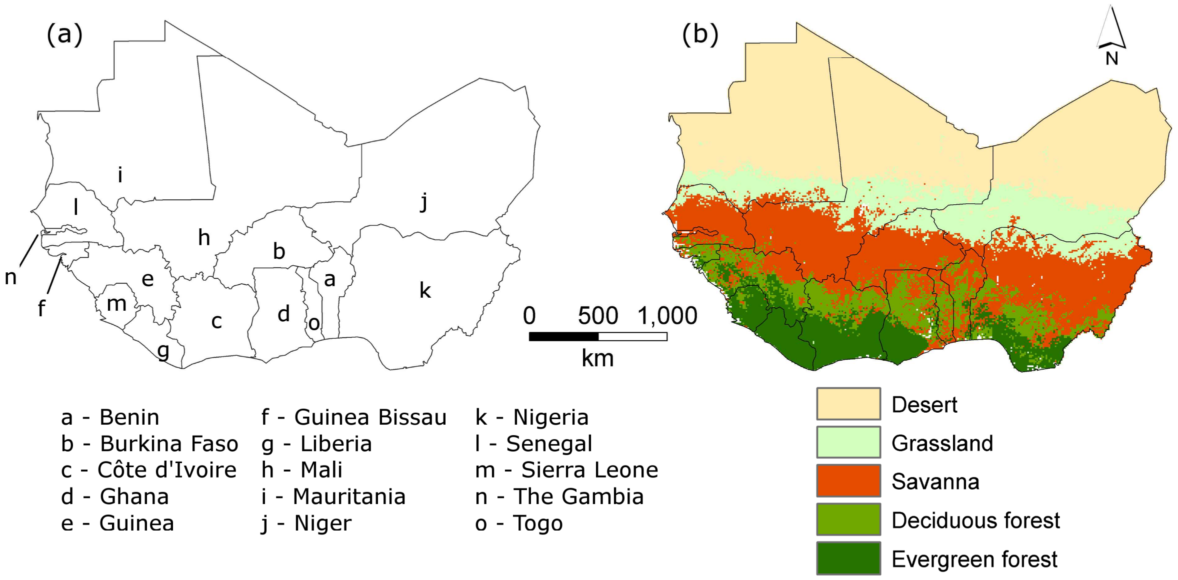

Figure 1 (a) West African countries and (b) the distribution of the major biomes in West Africa (based on the Global Land Cover dataset; Mayaux *et al.*, 2004, modified).

Natural atmospheric changes, which influence these vegetation patterns, have occurred in Africa ever since (Foley *et al.*, 2003). From the late Pleistocene until the middle Holocene, the Sahara and Sahel were much wetter than today which is known from fossil lakebeds and shorelines, pollen from flourishing vegetation and skeletal remains of grazing animals (Lezine *et al.*, 1990; Petit-Maire & Guo, 1996; Yu & Harrison, 1996). An abrupt change to drier conditions occurred approximately 5500 years ago (Foley *et al.*, 2003), which roughly shaped the vegetation patterns as observed today. This regime shift represented a tipping point (Lenton *et al.*, 2008), where two steady states were replaced. The green, vegetated Sahara was replaced by the 'desert Sahara' (Foley *et al.*, 2003). Fluctuating climate conditions in the late Holocene (Medieval Warm Period ~ 1100-800 cal yr BP and Little ice age 500-200 BP) also had a detectable impact on the African vegetation cover (Ngomanda *et al.*, 2007).

Furthermore, the African climate is characterised by inter-annual, inter-decadal and multi-decadal variations (Hulme *et al.*, 2001). While the 50s and 60s of the 20th century were relatively wet in West Africa (Hulme *et al.*, 2001), there was a more than two decades lasting extreme drought – the Sahel drought – which began in the 1970s (Nicholson *et al.*, 1998). The Sahel drought drew the attention of the public when a million people starved (Nicholson *et al.*, 1998) and widespread tree mortality was reported (Maranz, 2009). Whether or not this dramatic drought was part of the natural multi-decadal variations or a human-induced drought, was long under debate (Herrmann & Hutchinson, 2005). Charney (1975) attributed the drought to land degradation (internal feedback), where reduced vegetation cover increases the albedo, which prevents water to be recycled to the atmosphere through evapotranspiration (Eltahir, 1996). Others sought explanation in sea surface temperature (SST) anomalies [external forcing, Giannini *et al.*, (2003)]. Today, it is commonly assumed that a combination of both factors triggered the system to shift from ‘wet’ to ‘dry’ through strong non-linear vegetation–atmosphere feedbacks (Zeng *et al.*, 1999; Foley *et al.*, 2003; Herrmann & Hutchinson, 2005).

Currently, there is disagreement about West African vegetation dynamics. Local studies in West Africa have shown a ‘drying out’ which has caused plant species and vegetation zones to shift southwards (Gonzalez, 2001; Wezel & Lykke, 2006; Wittig *et al.*, 2007). In contrast, a southern spread of the Sahara was not observed for the 1980-1997 period, considering long-term satellite data (Tucker *et al.*, 1991; Tucker & Nicholson, 1999). Hickler *et al.* (2005) even found a greening trend (increasing NDVI index) in the Sahel owing to increasing precipitation, similar to local-scale findings (Rasmussen *et al.*, 2001). This contrast might be explained by the small-scale spatial heterogeneity of different trends (Hickler, 2011; pers. comm.). Thus, analysing satellite data from the entire Sahel, might obscure different tendencies. On the other hand, a remarkable tree planting takes place in many West African regions (e.g. Niger, see www.tree-nation.com/projects/1), which may increase the greening signal in satellite data.

This century, Africa is expected to face severe changes in climatic conditions (IPCC, 2007). The temperature in Africa is projected to increase between 3 and 4 °C, which is approximately 1.5 times as much as the global mean temperature response (IPCC, 2007). Precipitation projections from different climate models range from -9 to +13% in West Africa (2100, A1b). Definitely, these changes will strongly affect the vegetation patterns in West Africa. However, the few studies that investigated the potential impacts, show either strong (Delire *et al.*, 2008) or hardly any effects (Hély *et al.*, 2006) on vegetation. The results depend, and thus differ, on the GCMs and the climatic parameters that are considered. Thus, a better understanding of the future vegetation dynamics is strongly needed for West Africa. Furthermore, the climate impact research is hampered by the above mentioned high variability in precipitation projections over the African continent (IPCC, 2007). This was identified as a major source of uncertainty in predictive vegetation modelling (Scheiter & Higgins, 2009), as precipitation is the most limiting factor in this region (Scholes, 1997; FAO, 2001). However, there is a strong need to investigate the impact of climate change on large-scale vegetation patterns and biomes in West Africa, because lives and livelihoods of local people are intimately linked with these biomes as they provide food, fuel, fibre and a range of other ecosystem services (Norris *et al.*, 2010). Therefore, several climate models (general circulation models, GCMs) should be considered to increase the robustness of the results, while simultaneously assessing the uncertainty which is associated with these projections.

Besides climate, human pressure is an important influential factor that modifies vegetation patterns and causes tropical forest loss and degradation (Geist & Lambin, 2002). Indeed, savannas have been shaped by human land use for thousands of years (Ballouche & Neumann, 1995; Higgins *et al.*, 1999; Wittig *et al.*, 2003; Höhn, 2005) but there has been increasing human pressure with the beginning of the industrialisation. The human pressure which affects vegetation, includes agriculture, grazing, fire management and the harvesting of plants. Agricultural expansion and wood extraction have been identified as major drivers of forest loss and degradation in West Africa (Norris *et al.*, 2010). The West African countries exhibit a human population growth rate with up to 4% y^{-1} (FAO, 2010) and the African population is projected to double in the next 35 years (UNFPA, 2011). Consequently, this factor must be considered when assessing future vegetation change in West Africa.

Plant diversity and the impacts of climate and land use change

West Africa covers a broad gradient in plant diversity, which is mainly explained by the bioclimatic gradient. There is a rapid increase in plant diversity from the southern margin of the Sahara to the equator (Wieringa & Poorter, 2003; Schmidt *et al.*, 2005), with species richness more than doubling for every 10° of latitude (Linder, 2001). Rainfall is an excellent predictor and largely explains this gross pattern (Linder, 2001), not only in Africa. Gentry (1988) showed a linear increase in neotropical species richness with increased precipitation, reaching an asymptote at an annual precipitation of 4000 mm;

this amount is the maximum which is received in West Africa, at the monsoon-influenced coastal areas.

Climate change is expected to threaten this plant diversity (Mcclean *et al.* 2005, Sommer *et al.* 2010), and may also change the composition of species assemblages (Parmesan & Yohe 2003; Root *et al.* 2003). However, future projections of plant diversity in West African countries are extreme scarce (e.g. Da, 2010). And again, the increasing human pressure is an important factor to consider, which results from the expected high levels of economic and population growth in these regions (Jetz *et al.* 2007) and causes severe land use change. Future land use change is even assumed to be more important in threatening biodiversity than climate change (Sala *et al.* 2000). Thus, the scarcity of studies that incorporate land use change in assessing future biodiversity risk is surprising (Luoto *et al.* 2007; de Chazal & Rounsevell, 2009) and often results from a lack of reliable future land use simulations (Broennimann *et al.* 2006, Sommer *et al.* 2010).

The traditional land use in West Africa includes shifting cultivation (slash and burn), harvesting of non-timber forest products (NTFPs), hunting animals and also animal husbandry (cattle and small ruminants). Shifting cultivation is characterised by selective clearing and burning of forest or fallow land. This traditional management creates mosaic landscapes with fallows of different ages that retain a high biodiversity (Augusseau *et al.*, 2006). The land management also includes the deliberate retention of socio-economic important trees (e.g. shea tree), creating species rich agroforestry systems, also known as 'parklands' (Boffa, 1999; Augusseau *et al.*, 2006). However, the agricultural area increased by ca. 60% within the 1975–2000 period at the expense of natural vegetation in sub-Sahara Africa (Brink & Eva, 2009). Furthermore, the traditional management strategies are increasingly being replaced by a dynamic, market-oriented agriculture dominated by cash crops, e.g. cotton and cashew (Augusseau *et al.*, 2006). Negative impacts on plant diversity are expected by these changes. There is a strong need for integrated assessments which address the risk to plant diversity caused by climate and land use change. Calls have been made in the recent past, to specifically consider both factors and to investigate their interaction in threatening biodiversity, however, few attempts have been done so far (de Chazal & Rounsevell, 2009).

These assessments are often limited by the lack of species distribution data, particularly in tropical regions. However, Burkina Faso represents an exception with regard to plant species. The flora was comprehensively described by Guinko (1984). Additionally, research activities during the last decades (Wittig *et al.*, 2009) produced an outstanding vegetation database for Burkina Faso (Schmidt *et al.*, 2010b), as compared with other West African countries. Furthermore, the country covers a broad gradient in plant diversity, thus, the effects of climate and land change can be investigated in regions with different levels of plant diversity.

Provisioning ecosystem services: Non-timber forest products

Whether biological diversity itself is an ecosystem service or not, was controversially discussed in the Millenium Assessment Report (MA, 2005). However, several plant species provide important ecosystem services; these are generally defined as the benefits that people obtain from ecosystems and that make it worth living (Díaz *et al.*, 2006). Ecosystem services include supporting, provisioning, regulating, and cultural services; some of them directly affect people (MA, 2005). Obvious benefits that are obtained from nature are food, fibre, fuelwood which belong to the category of provisioning ecosystem services. According to the Millenium Ecosystem Assessment Report (MA, 2005), provisioning ecosystem services also include genetic resources, biochemicals, natural medicines and pharmaceuticals as well as fresh water.

In West Africa, important provisioning ecosystem services are represented by non-timber forest products (NTFPs), which make a major contribution to the livelihoods of the West African population (Burkill, 1985-2000). NTFPs include fruits, seeds, bark, leaves but also gums and latexes. More general, NTFPs include any products other than timber derived from woodlands or agroforestry systems (Choudhury & Jansen, 1998; Arnold & Pérez, 2001). Products from cultivated and non-native species should be separated from this category, even though a clear definition of the term NTFPs is still lacking (Heubach *et al.*, 2011).

The relevance of NTFPs for rural livelihoods in Africa results from both subsistence and cash income. Thus, NTFPs satisfy direct human needs and make a remarkable contribution to the annual total household income. This contribution was found to range from 15% in Malawi (Kamanga *et al.*, 2009) to roughly 40% in Mali (Faye *et al.*, 2010). Important NTFP-providing savanna species are for example *Vitellaria paradoxa* (subspecies *paradoxa*, Shea Tree or karité), *Parkia biglobosa* (African Locust Bean Tree or néré) and *Adansonia digitata* (African Baobab, Fig. 2). These species provide NTFPs, which traditionally serve as a dietary supplement, but are also increasingly demanded and traded on international markets (Besco *et al.*, 2007; INSAE, 2008). Cherished parts of these plants include the seeds (fatty acids), the fruit pulp (vitamin, proteins), and also the leaves as a condiment to sauces.

Figure 2 Important non-timber forest products from West African savanna species (from left to right): fruits, leaves and flower (not used) of *Adansonia digitata* (photo: J. Heubes), pods and seeds from *Parkia biglobosa* (photo: K. Schumann) and the seeds from *Vitellaria paradoxa* (photo: K. Hahn).

Global environmental change not only affects vegetation cover and diversity patterns, but will also alter the supply of these ecosystem services. Future projections of ecosystem services are scare and mostly limited to aspects of the carbon and water cycles (e.g. Schröter *et al.*, 2005). However, the environmental changes include potential threats to the benefits that are derived from NTFPs. With regard to the strong dependencies of the rural communities on NTFPs and the lacking income alternatives for the rural poor (Angelsen & Wunder, 2003; Shackleton & Shackleton, 2004; Shackleton *et al.*, 2007), the people may be considered as highly vulnerable towards the expected changes.

Thus, it is crucial to quantify and map the economic benefits that are derived from NFTPs to understand the socio-ecological system and the dependencies in West Africa. Future simulations of the monetary benefits then help to assess the risk that arises from environmental changes. Furthermore, such future simulations provide input for decision-makers to potentially modify current management strategies.

Model simulations for future predictions

Models generally represent simplified reflections of the reality. Predictive modelling has become a common tool to explore unknown states of the earth's system. Models also offer an opportunity to assess the impact of future climate change and the expected human pressure on large-scale vegetation patterns, species' range sizes, diversity patterns but also ecosystem services (Pereira *et al.*, 2010). Both correlative and process-based models are used (Shugart, 1998), and these mainly differ in their complexity. Large-scale future vegetation dynamics are commonly assessed by dynamic global vegetation models (DGVMs) (Sitch *et al.*, 2003; Woodward *et al.*, 2004). DGVMs incorporate key processes of the water, energy and carbon cycle where biomes are described as a fractional composition of plant functional types (PFTs). However, most DGVMs are unable to adequately represent certain tropical vegetation zones such as savannas (Hély *et al.*, 2006; Schaphoff *et al.*, 2006; Sato *et al.*, 2007). Thus, correlative models provide an alternative for predicting large-scale vegetation changes and potential biome shifts (see also Ferrier & Guisan, 2006). These correlative models, also known as 'bioclimatic envelope models', 'niche-based models', or 'species distribution models' (SDMs), rely on the niche concept (Guisan & Zimmermann, 2000) and have become central to both fundamental and applied research in biogeography (Araújo & Guisan, 2006). The empirical models quantify environmental niches and focus explicitly at the species level. Modelling numerous species with SDMs can, thus, be used to estimate patterns of current diversity and also future diversity in view of climate and land use change. The correlative models ignore the mechanisms driving species' demography and species' interactions. They rather relate field observations (e.g. species occurrence points) to environmental variables (predictors) by fitting response surfaces (Guisan & Zimmermann 2000) and assume that the fitted relationship is a good surrogate for the demographic processes (Austin, 2007).

The applications of SDMs include the modelling of single species distributions (e.g. Thiombiano *et al.*, 2006; Platts *et al.*, 2008), species assemblages and species richness (e.g. Ferrier *et al.*, 2002), assessing the impact of climate, land use and other environmental changes on species distributions (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Pompe *et al.*, 2008). SDMs were also used to assess species invasion risk (e.g. Peterson, 2003) and to support management and conservation planning (e.g. Araújo *et* *al.*, 2004). A promising new approach is using SDMs to investigate current and future provision of ecosystem services. This application is particularly suitable, when these services are derived from plant species, such as NTFPs.

This thesis

The overarching aim of this thesis is to investigate the impacts of future climate and land use change[1] on vegetation patterns and biome distributions, as well as on plant diversity and provisioning ecosystem services (NTFPs) in West Africa (Fig. 1).

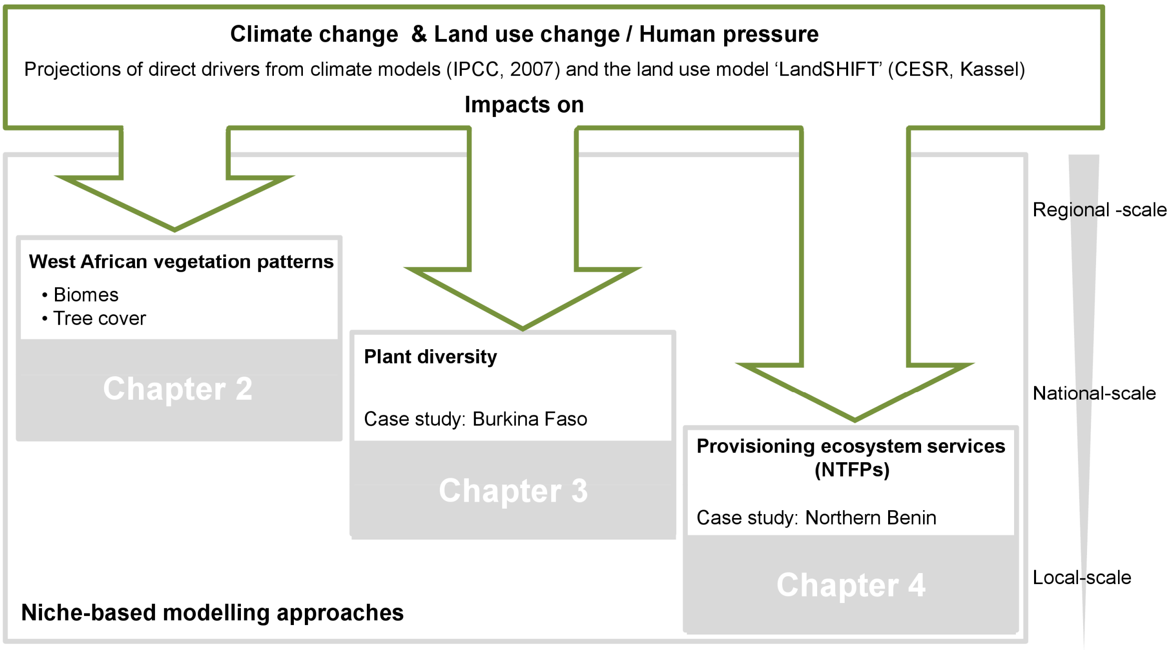

Figure 1 Schematic framework of this thesis.

There is very limited understanding of the potential impacts, and only few studies addressed these issues so far. In particular, the interactions between climate and land use change are poorly understood and its effects on plant diversity and provisioning ecosystem services have not been investigated in West Africa to date. This is even though this region must be considered as highly vulnerable, as people directly depend on these ecosystems and their services. This thesis fills an important gap of knowledge as it includes model simulations for the future (2050), assessing the impact of both climate

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[1] Land use differs from land cover, by describing the type of management within land cover typologies. Niche-based models make limited use of this information (e.g. different crop types), although provided by land use models. Thus, land cover change is actually investigated, however, the term 'land use' is used due to consistency throughout the thesis.

change and the human impact on entire ecosystems, plant diversity and provisioning ecosystem services. These issues were investigated at different scales ranging from regional to local scales. All studies have in common to include the human impact which is often ignored in climate impact studies.

Outline of the thesis

This thesis consists of three studies (Fig. 1). The first study deals with the impact of climate and land use change on regional-scale West African vegetation patterns (chapter 2). More specifically, I modelled trends and the extent of future biome shifts that may occur by 2050 using a variety of state-of-the-art correlative models and climate projections from 17 climate models. Furthermore, I modelled a trend in tree cover change by 2050, while accounting for the human impact. Finally, I explored and evaluated the future uncertainty, caused by different climate projections, to identify regions with high and low information value with regard to future trends. The potential biome shifts were analysed using six bioclimatic models while future tree cover change was analysed with generalized additive models (GAMs). Additionally, I considered fire intensity and human population density, as a proxy for the human impact, in the tree cover modelling procedure, because they represent important determinants. The study explores and helps to better understand the potential effects of climate change on regional-scale vegetation patterns in West Africa while accounting for the human impact.

The following study (chapter 3) focuses on potential changes in plant diversity related to climate and land use change. The West African country Burkina Faso was considered as a case study. The country covers a broad gradient in plant diversity, thus, the effects of climate and land change can be investigated in regions with different levels of species richness. Firstly, the available species distribution data (e.g. West African Vegetation database: Janßen *et al*. 2011; collection database of the Herbarium Senckenbergianum: http://sesam.senckenberg.de/) were improved by species inventories along a north-south transect, crossing Burkina Faso in the west (excursion in 2009 with Dr. Marco Schmidt). Secondly, as reliable land use simulations were lacking in West Africa, I established a cooperation with the Centre of Environmental System Research CESR (Kassel, Germany). Within this cooperation, I provided additional environmental data to set up a new base map in the LandSHIFT model. The following procedure required a collaborative input reiteratively on several model runs, which resulted in the final land use simulations. Then, one-class support vector machines, an algorithm from the machine learning methods, were used to investigate the impact and interplay of climate and land use change on the plant diversity. To my knowledge, this is the first study in West Africa where climate and land use change is considered in the modelling of future plant diversity.

In chapter 4, I introduce a novel approach to investigate the impact of climate and land use change on the economic benefits derived from NTFPs (provisioning ecosystem services). This study arose from an interdisciplinary cooperation with the socio-economist Katja Heubach from BiK-F. I used data on household economics that were provided from this colleague. These data comprise 60 household interviews from Northern Benin on annual quantities and revenues of collected NTFPs from the three most important savanna tree species in the studied area: *Adansonia digitata, Parkia biglobosa* and *Vitellaria paradoxa.* I assessed the current and future (2050) occurrence probabilities of the focal species, using niche-based models with climate and land use data. To assess future economic gains and losses, respectively, I linked modelled species' occurrence probabilities with the spatially assigned monetary values. This study improves our understanding of current and future benefits derived from savanna species, in order to help local policy-makers to design adaptive management strategies.

The results are brought together and contextualised in the synthesis chapter 5. This chapter also includes further research needs and an outlook. Finally, the results are summarised in chapter 6, followed by a German summary of the thesis.

Chapter 2

Modelling biome shifts and tree cover change for 2050 in West Africa

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ABSTRACT

Africa is expected to face severe changes in climatic conditions. Our objectives are to: 1) model trends and the extent of future biome shifts that may occur by 2050 in West Africa, 2) model a trend in tree cover change, while accounting for human impact, and 3) evaluate uncertainty in future climate projections. We modelled the potential future spatial distribution of desert, grassland, savanna, deciduous and evergreen forest in West Africa using six bioclimatic models. Future tree cover change was analysed with generalized additive models (GAMs). We used climate data from 17 general circulation models (GCMs) and included human population density and fire intensity to model tree cover. Consensus projections were derived via weighted averages to: 1) reduce inter-model variability, and 2) describe trends extracted from different GCM projections. Our results show that the strongest predicted effect of climate change was on desert and grasslands, where the bioclimatic envelope of grassland is projected to expand into the desert by an area of 2 million km^2. While savannas are predicted to contract in the south (by 54 ± 22 × 10^4 km^2), deciduous and evergreen forest biomes are expected to expand (64 ± 13 × 10^4 km^2 and 77 ± 26 × 10^4 km^2). However, uncertainty due to different GCMs was particularly high for the grassland and the evergreen biome shift. Increasing tree cover (1–10%) was projected for large parts of Benin, Burkina Faso, Côte d'Ivoire, Ghana and Togo, but a decrease was projected for coastal areas (1–20%). Furthermore, human impact negatively affected tree cover and partly changed the direction of the projected change from increase to decrease. We conclude that, considering climate change alone, the model results of potential vegetation (biomes) show a 'greening' trend by 2050. However, the modelled effects of human impact suggest future forest degradation. Thus, it is essential to consider both climate change and human impact in order to generate realistic future tree cover projections.

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[2] Modified Abstract

INTRODUCTION

Africa is expected to face severe changes in climatic conditions this century (IPCC, 2007) which will affect the spatial distribution of biomes and vegetation characteristics (e.g. tree cover). The continent is also characterised by a fast growing human population (up to 3% year^{-1}; FAO, 2007), which is imposing an increased pressure upon ecosystems ranging from tropical evergreen forest to deciduous forest, savanna and grassland. Yet the lives and livelihoods of local people are intimately linked with these biomes as they provide food, fuel, fibre and a range of other ecosystem services (Norris *et al.*, 2010). The Sahel drought, which began in the 1970s, drew the attention of the public when a million people starved (Nicholson *et al.*, 1998) and there were widespread reports of tree mortality (Maranz, 2009). Possible explanations for the drought are land degradation and sea surface temperature anomalies which triggered the system to shift from 'wet' to 'dry' through strong non-linear vegetation–atmosphere feedbacks (Zeng *et al.*, 1999; Foley *et al.*, 2003; Herrmann & Hutchinson, 2005). Currently, there is disagreement about West African vegetation dynamics. Local studies in West Africa have shown a 'drying out' which has caused plant species and vegetation zones to shift southward (Gonzalez, 2001; Wezel & Lykke, 2006; Wittig *et al.*, 2007). In contrast, long-term satellite data have not shown a southern spread of the Sahara in the 1980–1997 period (Tucker *et al.*, 1991; Tucker & Nicholson, 1999). Hickler *et al.* (2005) even found a greening trend [increasing normalized difference vegetation index (NDVI)] in the Sahel owing to increasing precipitation.

Besides climate, human pressure is an influential factor that causes tropical forest loss and degradation (Geist & Lambin, 2002), and so contributes to tropical biodiversity loss (Sala *et al.*, 2000; Gardner *et al.*, 2010). But other factors, such as fire and herbivory, can also strongly influence tree cover, particularly in savanna ecosystems (Jeltsch *et al.*, 2000; House *et al.*, 2003; Sankaran *et al.*, 2004). Even though it is assumed that both climate and human impact will substantially affect African ecosystems, there are only a few studies that have assessed future climate effects on vegetation in West Africa (but see Hély *et al.*, 2006; Delire *et al.*, 2008), and even fewer studies specifically considering future human impact [see Broennimann *et al.* (2006) for an example from South Africa].

Predictive modelling has become a frequently used tool for exploring future unknown states of the Earth's system. Both correlative and process-based models are used (Shugart, 1998), and these mainly differ in their complexity. Correlative models, also known as ‘bioclimatic envelope models’ or ‘species distribution models’, rely on the niche concept (Guisan & Zimmermann, 2000) and have become central to both fundamental and applied research in biogeography (Araújo & Guisan, 2006). They are simplistic compared to process-based models and they relate the spatial distribution of biotic objects (e.g. species, biomes) to environmental variables. Several techniques have been used which differ mathematically (e.g. see Breiman *et al.*, 1984; Yee & Mitchell, 1991; Thuiller, 2003; Elith *et al.*, 2006). In contrast, process-based models explicitly include a wide range of processes and their interactions. Large-scale future vegetation dynamics are commonly assessed by dynamic global vegetation models (DGVMs) (Sitch *et al.*, 2003; Woodward *et al.*, 2004). However, most DGVMs are unable to adequately represent certain tropical vegetation zones such as savannas (Hély *et al.*, 2006; Schaphoff *et al.*, 2006; Sato *et al.*, 2007). Furthermore, they are highly sensitive to demanding parameterizations (Clark *et al.*, 2001; Scheiter & Higgins, 2009) which might reduce tractability (Thuiller *et al.*, 2008). Thus, less complex correlative models provide an alternative for predicting potential biome shifts and tree cover change in West Africa.

The prediction of future vegetation change is based on climate projections which are generated by general circulation models (GCMs). However, there is extremely high variability in GCM projections over the African continent (IPCC, 2007). This was identified as a major source of uncertainty in predictive vegetation modelling (Scheiter & Higgins, 2009). Uncertainty is particularly high for precipitation, the most limiting factor in this region (Scholes, 1997; FAO, 2001). So far, most studies that have specifically assessed future vegetation dynamics in Africa have not considered more than one or two GCMs (Delire *et al.*, 2008; Scheiter & Higgins, 2009), while global studies with more GCMs are conducted at coarse resolutions (*c.* ≅ 1.5°, e.g. Scholze *et al*., 2006). Our objective in this study is to use a variety of state-of-the-art correlative models and climate projections to examine the effects of both climate and human impact on future vegetation patterns in West Africa. In particular we wanted to: (1) model trends and the extent of future biome shifts by 2050, (2) model trends in tree cover change, while accounting for human impact, and (3) evaluate uncertainty in future climate projections.

MATERIALS AND METHODS

Study area and environmental coverages

Five main biomes can be found in our study area of West Africa: evergreen forest, deciduous forest, savanna, grassland and desert. The spatial distribution of the vegetation zones is based on the GLC 2000 Global Land Cover dataset, which combines satellite information with local knowledge (Mayaux *et al.*, 2004). Cultivated or managed areas were assigned to the above mentioned biomes using the potential vegetation map of White (1983). The qualitative data were transformed to presence/absence data, i.e. each biome was modelled separately. We excluded 'desert' from the modelling procedure, assuming that a northern expansion of grassland would result in a southern contraction of desert (and vice versa).

Tree cover data (www.landcover.org), i.e. the proportion of each pixel covered by trees, were derived from all seven bands of the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor on board NASA's Terra satellite (Hansen *et al.*, 2003) with a resolution of 500 m. We used bilinear interpolation (ArcGIS 9.3, http://www.esri-germany.de/) to match the target resolution of 0.1° (*c.* ≅ 10 km × 10 km).

Predictive biome modelling was performed with climate data, as climate is the major driver for biome distributions at the continental scale. We used the WorldClim data base (Hijmans *et al.*, 2005; http://www.worldclim.org), which provides 19 climatic variables describing trends, seasonality and extremes. To account for multicollinearity we performed hierarchical variable clustering using complete linkage with squared Spearman's rank correlation coefficients as a similarity measure (Harrell, 2001). We defined clusters of correlated variables as those with a similarity level of ≥ 0.4. From each of the three resulting clusters, we selected the biologically most meaningful variable. As water availability is the most critical and limiting factor for ecosystem dynamics in Africa (Scholes, 1997; FAO, 2001), annual mean precipitation was selected from the first cluster and precipitation of the driest quarter from the second cluster. Minimum temperature of the coldest month was selected from the third cluster. This variable is assumed to describe the overall temperature increase, since flattening of the temperature profile is not expected in Africa (Hulme *et al.*, 2001). Two variables outside the defined clusters were excluded from the final variable set as single predictor generalized additive models suggested that they had a poor fit to the data.

Future climate projections (2050) were taken from 17 GCMs, scenario A2a, that participated at the 4th Assessment Report of the IPCC (2007) and downscaled to 0.1° (Ramirez & Jarvis, 2008). The IPCC SRES A2 storyline describes a heterogeneous world with continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other storylines. To describe the disturbance regime in modelling current and future tree cover, we included fire intensity and human population density alongside the extracted climate parameters. Human population density is a proxy for human activity while fire intensity is a crucial factor in reducing seedling establishment, particularly in the savanna biome (Higgins *et al.*, 2000). Current and future fire intensity were described by the average for the 1961–1990 and 2041–2060 periods, respectively, extracted from an adaptive DGVM (Scheiter & Higgins, 2009), with future projections being based on ECHAM5 (Roeckner *et al.*, 2003). Human population density (inhabitants/km^2) was taken from LandSHIFT (Schaldach & Koch, 2009) and log-transformed due to extreme outliers. LandSHIFT uses different driving forces describing the socioeconomic and agricultural development of a country, and was run with model drivers from the UNEP Global Environmental Outlook-4 (Rothman *et al.*, 2007). LandSHIFT simulations are provided at a spatial resolution of 5 arc minutes (*c.* ≅ 0.1°), the aDGVM output (1° grid cell size) was downscaled to the target resolution.

Biome modelling

Ensemble forecasting is a relatively new approach to ecology and biogeography, allowing the consensus among several projections to be calculated (REFS) (Araújo & New, 2007; Thuiller, 2007). Principal components analysis-consensus approaches have been shown to produce superior predictions, compared to individual model projections or averages of them (Araújo *et al.*, 2005). Here we used weighted averaging (WA, e.g. Marmion *et al.*, 2009) to build consensus models. Unless having real independent data to test transferability in time (Araújo *et al.*, 2005), however, there is no guarantee of getting superior predictions by WA. We calibrated six different algorithms for each biome (Fig. 1), implemented in the BIOMOD framework (Thuiller *et al.*, 2009): two regression methods (GAM – generalized additive models, GLM – generalized linear models), two classification methods (CTA – classification tree analysis, FDA – flexible discriminant analysis) and two machine learning methods (GBM – generalized boosting models, ANN – artificial neural networks). For this purpose the data were split into training and testing data. Threshold independent area under the receiver operating characteristic curve (AUC) values (Fielding & Bell, 1997) were calculated in a 3-fold cross-validation on 30% test data, while models were calibrated on the 70% training data. We then applied weights to the models according to their AUC values (models revealing high AUC values are given high weights and vice versa). Projected occurrence probabilities of biomes (continuous scale) are weighted averages of all six model simulations and were transformed into presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000). Final accuracy of the simulated biomes were assessed using ROC curves (e.g. Thuiller *et al.*, 2009).

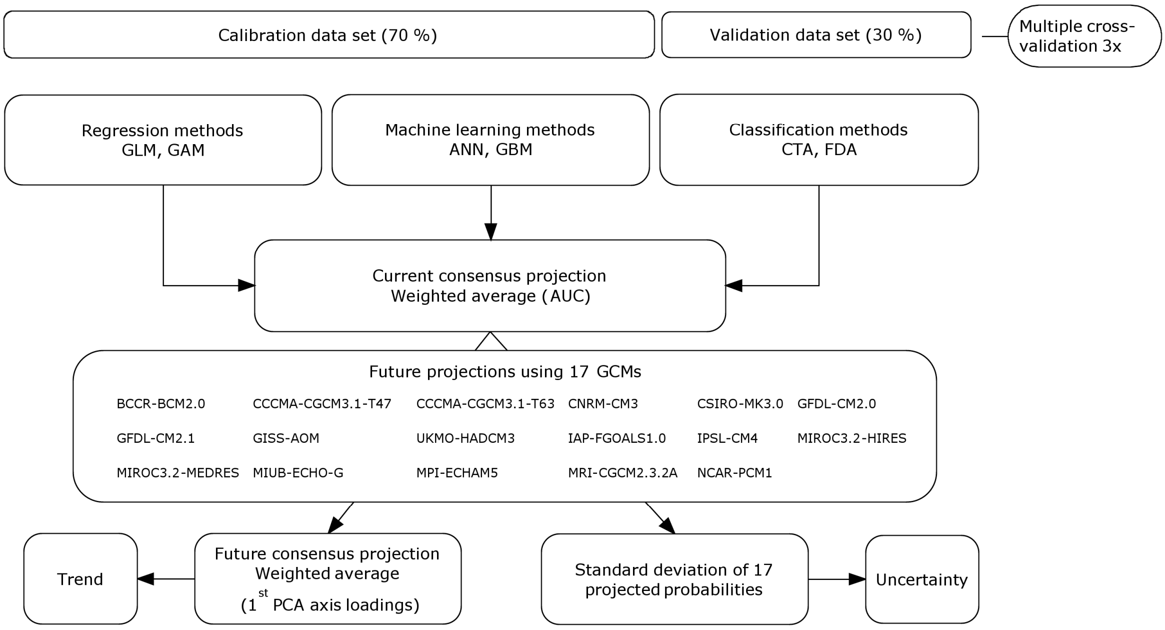


Figure 1 Analytical framework of the biome modelling. Six different models were used (from left to right): generalized linear models (GLMs), generalized additive Models (GAMs), artificial neural networks (ANNs), generalized boosting models (GBMs), classification tree analysis (CTA), flexible discriminant analysis (FDA). Models are weighted according to the values obtained from the area under the curve (AUC) of a receiver operating characteristic plot (sensitivity against 1 – specificity). General circulation models (GCMs) are weighted according to the first principal components analysis (PCA) axis loadings. Consensus projections are derived by weighted averaging.

Tree cover modelling

We used GAMs (Hastie & Tibshirani, 1986) to model tree cover, as this approach has been shown to perform best compared to other techniques (Moisen & Frescino, 2002). Dealing with proportional data, we fitted GAMs with a binomial error distribution and logit-link function. Residual deviance was smaller than the residual degrees of freedom, indicating no overdispersion. A generalized cross-validation procedure was used for smoothing parameter estimation (Wood, 2008), but it was restricted so as not to exceed 4 degrees of freedom to maintain generalization in predictive modelling. The analysis was performed using the R-package ‘mgcv’ (Wood, 2006).

Future consensus projections and uncertainty

Climate data from the 17 GCMs resulted in different projections of the future spatial distribution of biomes and tree cover by 2050. Principal components analysis (PCA) was used to derive consensus projections (Thuiller, 2004), resulting in a single future projection for the biomes and tree cover, thereby describing the future trend. However, the PCA-consensus approach can be used in several ways. Here, PCA was run with the 17 projected occurrence probabilities of biomes and tree cover in 2050, respectively. Weights were applied to the projections according to the first PCA axis loadings (Fig. 1). Thus, GCMs showing a common future climate trend are weighted up while the others are weighted down by maintaining all climate information. To obtain the ensemble mean, weighted averaging was applied across the projected future biome probabilities and tree cover values. Uncertainty was calculated as standard deviation (SD) from the same future projections for 2050. In summary, weighted averages were used twice, firstly to reduce inter-model variability (only biome approach) and secondly to extract trends derived from the GCMs (Fig. 1). All statistical analyses were calculated using the free software environment R, v. 2.10.1 (R Development Core Team, 2010).

RESULTS

AUC values were above 0.9 for the consensus projections (Fig. 2) and the single models (see Appendix S1 in Supporting Information), indicating a very good model performance. Our results show considerable biome shifts by 2050 (Fig. 2).

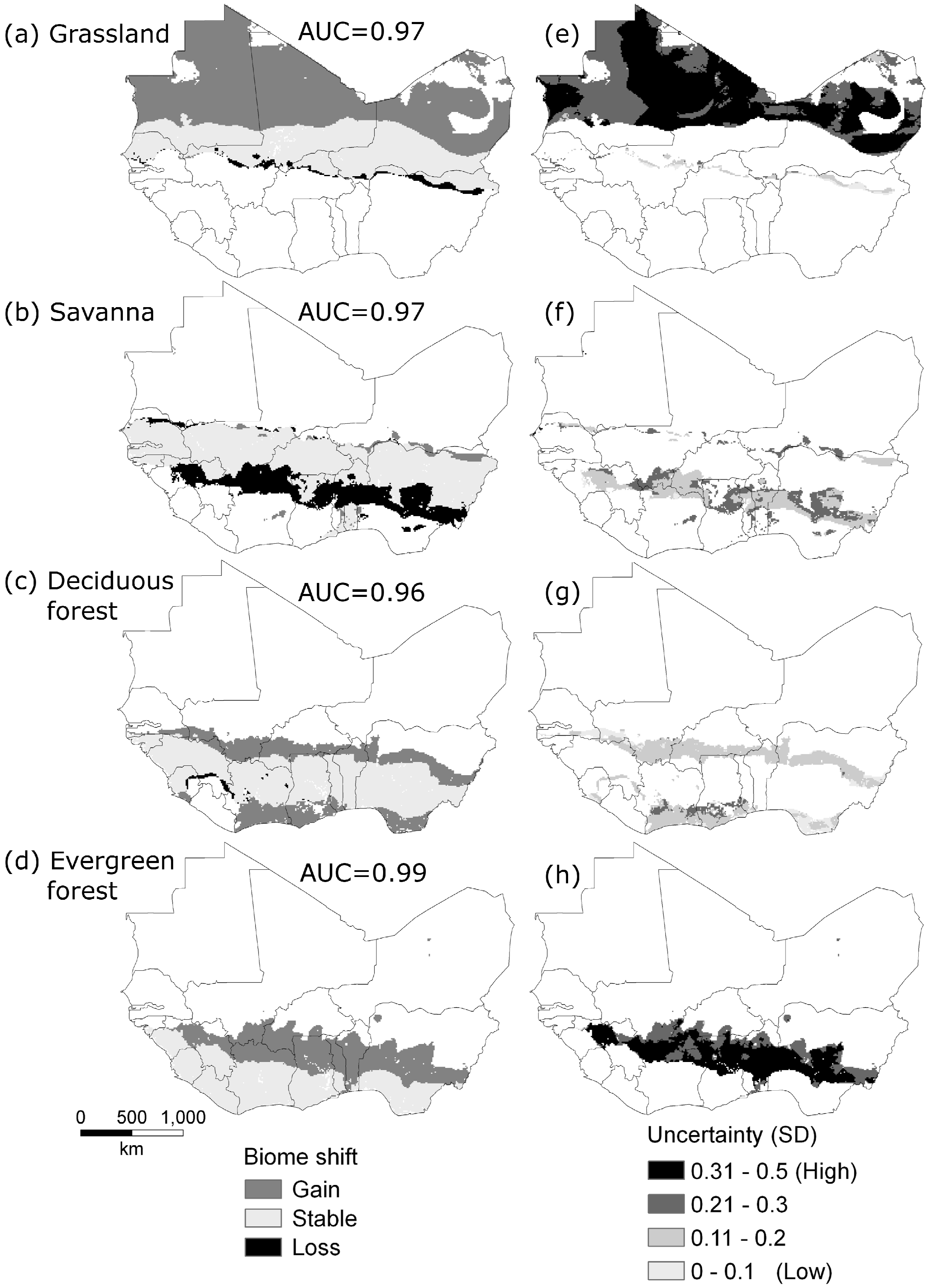


Figure 2 Projected biome shifts in West Africa for 2050: (a) grassland, (b) savanna, (c) deciduous forest, and (d) evergreen forest. Consensus projections (a–d) represent trends derived from 17 general circulation models (GCMs). The area under the receiver operating characteristic curve (AUC) value, indicates model performance and is given for the consensus projection for each biome. GCM based uncertainty (e-h) is shown for projected gain and loss of biome area. Uncertainty is expressed as standard deviation (SD) of future biome occurrence probability.

There is a northern expansion of grassland (203 ± 55 × 10^4 km^2) and evergreen forest (77 ± 26 × 10^4 km^2; Fig. 3). Deciduous forest is projected to expand northwards and southwards (overall gain: 64 ± 13 x 10^4 km^2) while savannas mainly lose area in the South (54 ± 22 × 10^4 km^2). Shifts in deciduous and evergreen forests show somewhat contradictory results due to current and future projected biome overlap (Fig. 2c, d). The more reliable trend (as indicated by higher AUC values) is given by the northern expansion of evergreen forest (Fig. 2 c, d, see Appendix S1). Note that the potential distribution of biomes was calculated, and observed shifts are merely caused by altered climate variables (i.e. ignoring CO_2 effects). According to our results, grassland and desert are the biomes most affected by climate change. However, the northern expansion of grassland is associated with high GCM-based uncertainty, similar to the northern spread of evergreen forest (Fig. 2e, h). Thus, discrepancies among underlying GCM projections are highest at both ends of the bioclimatic gradient, with standard deviations of the projected biome occurrence probabilities up to 0.5 (Fig. 2e, h). Considering uncertainty after the binary transformation of the probabilities, relatively high SD values are detected for the projected gain of savanna areas and loss of deciduous forest (Fig. 3). Significant changes in biome area were detected for all biomes (i.e. $P \leq 0.05$, two-sided *t*-test), except for savanna.

Tree cover projections (continuous scale) provide information about changes within the biomes. Opposing trends are observed within the evergreen biome, where tree cover decreases in coastal areas in the south but largely increases at the transition to deciduous forests in the north (Fig. 4b). Our findings of tree cover change give a more realistic picture of projected vegetation change since ‘real’ instead of potential vegetation was modelled. The trend derived from 17 GCMs highlights an increase of canopy cover of a magnitude of 1–10% for northern Côte d’Ivoire, Ghana, Togo, Benin, southern Burkina Faso and western Mauritania (Fig. 4b). In contrast, decreasing tree cover is projected for almost all coastal areas of West Africa (*c.* ≅ 1–20%; Fig. 4b). The results are concordant with decreasing occurrence probability of the evergreen biome in coastal areas (only binary values are shown in Fig. 2). However, human impact strongly modifies the climate-driven trend by negatively affecting tree cover (Fig. 4b vs. 4c, see Appendix S2).

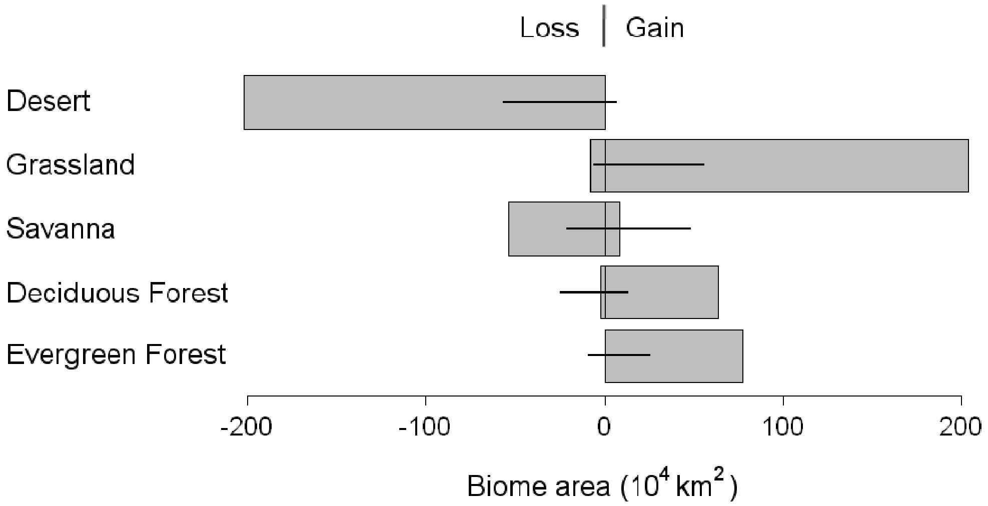
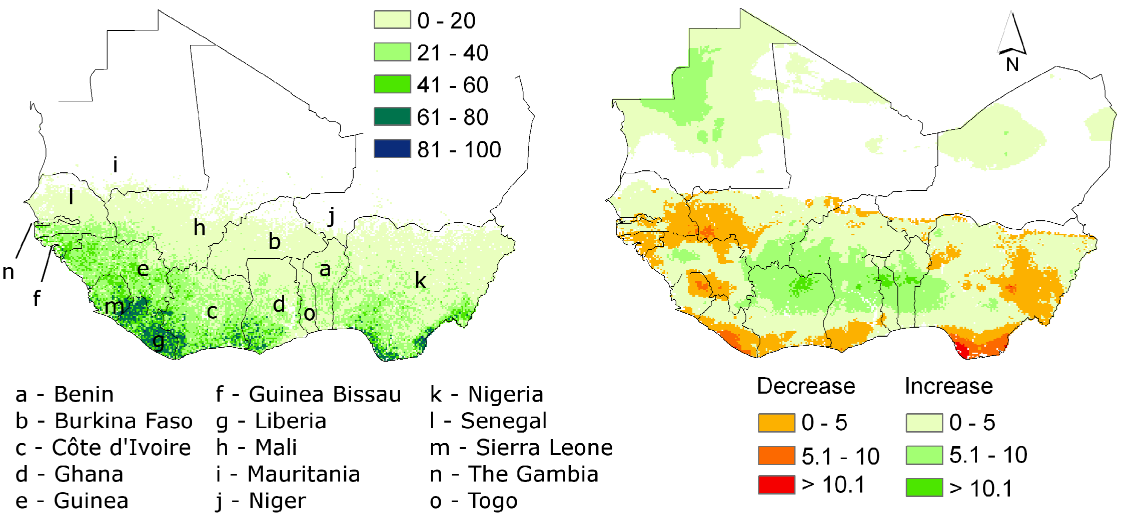


Figure 3 Projected future gain and loss of biome area in West Africa for 2050 compared to 2000 (grey bars). Calculations are based on consensus projections (trend) derived from 17 general circulation models (GCMs). Probability values of biome occurrence were transformed into presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted. Uncertainty (black line) is given by the standard deviation (SD) of gain and loss using different GCMs. SD values are drawn from zero-point since as they are calculated from the mean rather than the displayed weighted mean. Note that ‘desert’ was not explicitly modelled, but it was assumed that a northern expansion of grassland would result in southern contraction of desert.

Increasing coverage is attenuated while decreasing coverage is accelerated. The projected responsibility of humans in reducing canopy cover is in the magnitude of 1–6%. Incorporating human impact into the models even changed the direction of the projected tree cover change from increase to decrease (e.g. northern Nigeria and Liberia; Fig. 4b, c). Large parts of Nigeria are expected to lose 1–5% tree cover by 2050 (Fig. 4c). Low uncertainty (SD 0–10) is given for areas that show decreasing canopy cover (Fig. 4d). In contrast, there is spatial congruence of areas with high GCM based uncertainty (SD 5–20) and areas with projected increase of canopy cover (e.g. north-western Mauritania).

(a) Current tree cover (%)

(b) Climate-driven tree cover change (%)



(c) Climate and human driven tree cover change (%)

(d) Uncertainty

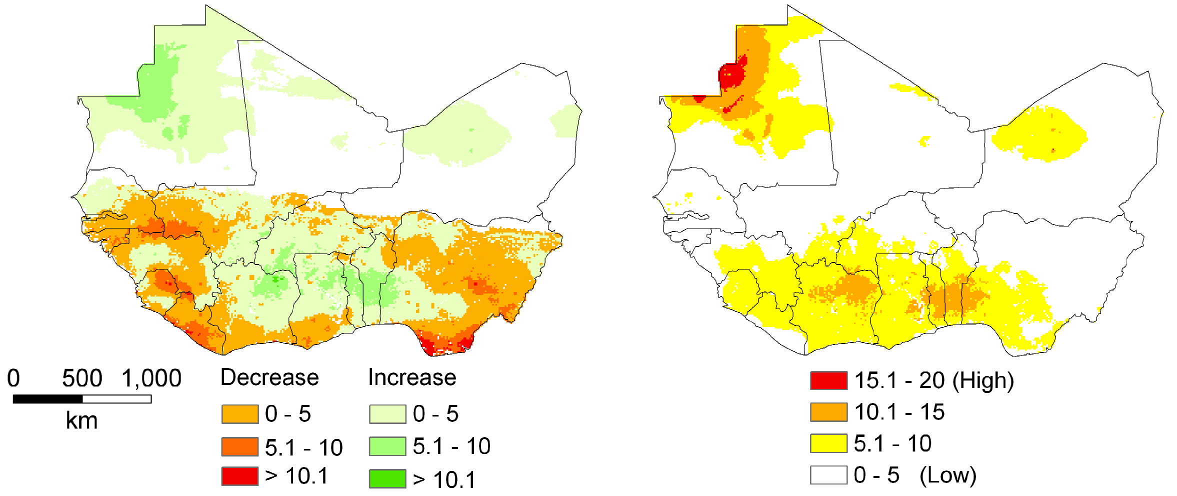


Figure 4 (a) West African percentage tree cover and projected tree cover change (%) for 2050 (b) ignoring human population growth and (c) incorporating human population growth. Consensus projections (b, c) represent trends derived from 17 general circulation models (GCMs). Uncertainty due to GCM-based variability is given as standard deviation (SD) of the projected tree cover in (d). Explained deviance of the full model is 90.1.

DISCUSSION

We used bioclimatic models to demonstrate potential future biome shifts while highlighting the interplay of climatic and human effects in modifying canopy cover. Furthermore, we presented a way of dealing with the high uncertainty in future climate projections for West Africa. While our results indicate a climate-driven greening trend, we also showed that human impact negatively affects tree cover in the simulations.

Biome shifts

With only three climatic variables the models yielded extremely good fits (AUC > 0.9), indicating excellent model performance (Swets, 1988). This suggests that, at the scale analysed, spatial distributions and transitions of biomes are governed by climate. The expected northward spread of grassland into the Sahara and the replacement of savannas by deciduous forest are concordant with results from Cramer *et al.* (2001), Scholze *et al.* (2006) and Scheiter & Higgins (2009), who attributed the greening to increased CO_2 levels (higher water-use efficiency, fertilization effect). Our models indicate that climatic change alone can yield this pattern. The expected ‘greening’ of the Sahara is primarily driven by increasing precipitation (see also Hickler *et al.*, 2005). While Scholze *et al.* (2006) found that monsoon-influenced tropical rain forest might regionally be transformed to non-forest area, we, however, were only able to find this effect when incorporating human influence into the model.

Our results showed spatial overlap of current evergreen and deciduous forest and ambiguous results concerning the future projected evergreen–deciduous forest transition. Despite very good model performance for both biomes, there might be difficulties in defining this transition zone using climate, as herbivory and fire are also influential factors. On the other hand, the biome transition is a mosaic of both forest types rather than a sharp border and so this results in overlapping projections. According to the model performances, northern expansion of the evergreen biome seems to be more certain than the southern expansion of deciduous forest. This is in contrast to simulations from Delire *et al.* (2008) who found evergreen forest types switching to deciduous forest types. However, comparing modelling results from different studies is hampered by the use of dissimilar predictor variables.

Hély *et al.* (2006) investigated the sensitivity of African biomes to changes in precipitation regimes (using LPJ-GUESS model) but could not identify biome shifts at their investigated sites, which were situated at similar latitudes but further east. The authors used simulated precipitation data, assuming an increase of 5 to 20%, based on IPCC (2001) statements. On the one hand, the authors may underestimate climate impact on biomes by ignoring temperature effects, which play a crucial role, particularly in Central and West Africa (Delire *et al.*, 2008). On the other hand, we might overestimate the rate of biome shift, because terrestrial vegetation response to altered climate conditions can be slow (Woodward *et al.*, 2004). However, since current vegetation patterns in Africa are highly correlated with precipitation (Foley *et al.*, 2003), we assume that the biomes and tree cover will follow shifting rainfall patterns caused by climate change.

The expected rainfall for the desert biome is far above the natural precipitation variability (see Appendix S3), supporting modelling results of desert greening. Increasing rainfall projections for the other biomes are within the natural variability, but long-term climate patterns, as used in our study (30 years mean), rather than short-term annual fluctuations in rainfall, influence vegetation types and canopy cover (Fuller & Ottke, 2002).

Limitations and climate uncertainty

We used bioclimatic models, which are particularly suitable in our study since we focused on the macro-scale where climate factors (e.g. precipitation) become dominant drivers (Pearson & Dawson, 2003). We focused on climate uncertainty and inter-model variability, without explicitly exploring the latter effect. However, bioclimatic models are not without limitations. Conceptual ambiguities as well as biotic and algorithmic uncertainties are associated with these models (Araújo & Guisan, 2006).

Modelling entire biomes corresponds to the Clementsian view of biomes as ‘organisms’ (Clements, 1936). However, biomes, similar to habitats or vegetation units (see Pompe *et al.*, 2010), are not expected to respond to climate change as intact units due to the individualistic nature of the response of plant species (e.g. Ferrier & Guisan, 2006). Midgley *et al.* (2002) showed that such a coarse biome approach underestimates the threats of both species loss and within-species genetic diversity loss considering the ‘Fynbos’ in South Africa. Among different community-level modelling approaches, our approach corresponds to the ‘assemble first, model later’ strategy (Ferrier & Guisan, 2006) and this might help to explain the biome overlap that we found for the evergreen and deciduous forest biome (Baselga & Araújo, 2010).

Bioclimatic models do not take into account increasing CO_2 levels (Midgley *et al.*, 2002, but see Rickebusch *et al.*, 2008) and the possible adaptation of vegetation to altered climate conditions [e.g. reduced leaf area index (LAI) values]. Both factors influence water availability for plants. Furthermore, we assume no dispersal limitation of the species our biomes consist of. This might be a crude assumption, except for winddispersed grassland species. However, species-specific knowledge about dispersal ability is lacking in West Africa. More critical remarks on bioclimatic models can be found e.g. in Dormann (2007). Despite these shortcomings, the top-down approach is powerful in regions like West Africa, firstly in regard to the sparse species distribution data, in practice more complete satellite-based information is available at the community level (Franklin, 1995; Austin, 1998; Ferrier & Guisan, 2006). Secondly, the correlative approach is useful, given the limited application of DGVMs in savanna regions (Hickler *et al.*, 2006; Sato *et al.*, 2007). However, considering the sources of uncertainty, we can only provide a coarse estimate of future vegetation change.

A specific problem for climate impact research in Africa is the exceptionally high uncertainty in future climate projections that may be related to GCM biases. GCMs project an annual mean temperature increase for West Africa, where the Sahara Desert will warm up more strongly (+ 2–4 °C) than the tropical regions (+ 1.5–3 °C) with one GCM projecting a 5 °C increase (NCAR-PCM1). More than 50% of the climate models show an increase of annual mean precipitation (see Appendix S3) for desert (–5 to +550 mm), grassland (–30 to +150 mm), savanna (–6 to +250 mm), deciduous forest (–90 to + 330 mm) and evergreen forest (–130 to +300 mm). The differences between GCM projections may be because of either an unclear relationship between Gulf of Guinea and Indian Ocean warming, or uncertainty about the relation between land use change and the West African monsoon (IPCC, 2007). There is a need to improve and harmonize climate models, e.g. by integrating strong non-linear climate-vegetation feedbacks. The next IPCC report with a focus on Africa is expected to shed light on this.

In this study we used statistically downscaled GCM projections (*c.* ≅ 10 km). Downscaling can be applied to make use of the coarse GCM projections (100–200 km) for regional climate impact research, however, there are limitations (Wilby & Wigley, 1997). This method is based on the assumption that firstly, changes in climates vary only over large distances (i.e. GCM cell size) and secondly, that relationships between variables in the baseline (‘current climates’) are maintained in the future. These assumptions might not hold true in mountainous areas where topography can cause strong variations in anomalies, but are considered as valid for homogeneous areas like the Sahara (Ramirez & Jarvis, 2010).

Tree cover change and human influence

We highlighted the importance of considering tree cover (modelled as a continuous response) rather than only presence/absence biome distributions (binary data) to describe future vegetation change. Again, the important environmental drivers were incorporated (explained 90% of the deviance), with annual mean precipitation being by far the most important variable. With the use of satellite images, reflecting the current vegetation state, we modelled ‘real’ rather than potential vegetation. We could clearly show effects of human activity negatively affecting tree cover (see Appendix S2), as also demonstrated by other case studies, e.g. in Senegal (Vincke *et al.*, 2010) and Mali (Ruelland *et al.*, 2010). Moreover, we highlighted the relevance of human activity in reducing tree cover in the future (2050). Thus, it is essential to consider both climate change and direct human impact to generate realistic future tree cover projections. The use of human population density as a proxy for human impact subsumes many human activities and consequently does not allow the identification of proximate causes of tree cover reduction. In West Africa, agricultural expansion, sometimes facilitated by other human activities such as wood extraction, have been identified as major drivers of forest loss and degradation (Norris *et al.*, 2010). In the Sahel, however, where trees are replaced by annual vegetation, it seems more difficult to assert that human pressure causes degradation (Seaquist *et al.*, 2009).

High uncertainty is associated with the simulations for increasing canopy cover (e.g. western Mauritania) due to differences in GCM projections. Thus, the tree cover increase remains speculative. In contrast, low uncertainty is indicated for the projected decrease of tree cover: this should be cause for concern, even assuming an unrealistic scenario of constant human population. The 5% decrease in tree cover until 2050 that is projected for large parts of West Africa, corresponds to a 0.13% decrease in tree cover annually. Given the current deforestation rate of 1.17% year^{-1} for West Africa (FAO, 2007) we are probably underestimating future forest degradation that might trigger desertification processes. Furthermore, one factor of human activity, tropical rain forest logging, causes drying of fuels and allows severe fires (Franklin & Forman, 1987), which again consume large parts of the biomass (Bond & Keeley, 2005; Higgins *et al.*, 2007). Our analysis does not incorporate such processes. The decreasing canopy cover may even result in positive feedbacks because of reduced monsoon rainfall due to higher albedo and decreased ability to recycle water back to the atmosphere through evapotranspiration (Eltahir, 1996). Increased atmospheric dust loading, caused by emerging bare soils, may further suppress rainfall due to a coalescence-suppressing effect (Rosenfeld *et al.*, 2001). Thus, such positive feedbacks might enforce forest degradation and desertification processes in West Africa.

CONCLUSIONS

Considering climate change alone, our model results of the potential vegetation (biomes) show a ‘greening’, even though the magnitude may be overestimated by our models. The consideration of tree cover was important to detect changes within the biomes. Furthermore, we highlighted the importance of the interplay between climate change and human activity. Incorporating human impact in our models showed that forest degradation, a trigger for desertification processes, might play a crucial role in the future. Thus, it is essential to consider both climate change and direct human impact to generate realistic future tree cover projections, and both should generally be considered in predictive vegetation modelling.

ACKNOWLEDGEMENTS

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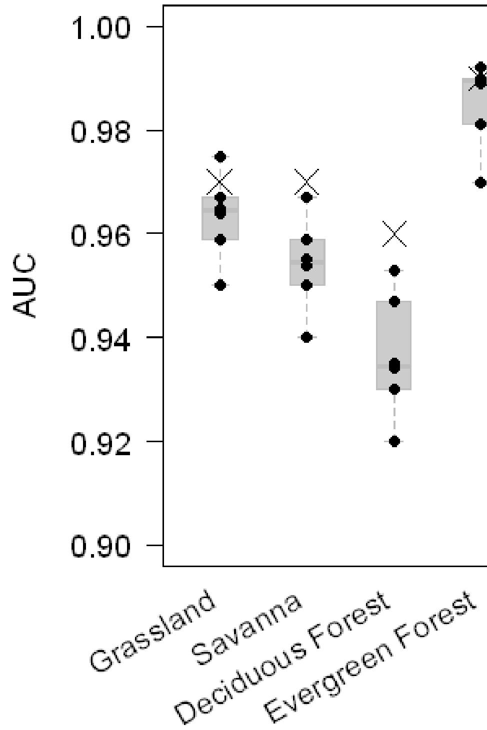
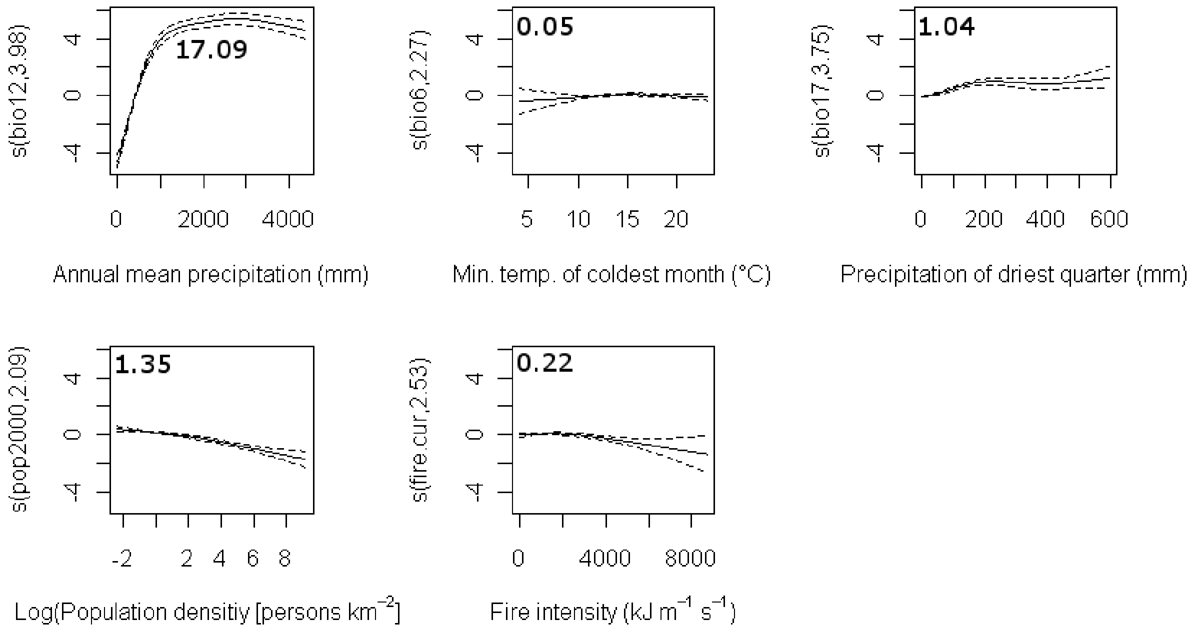
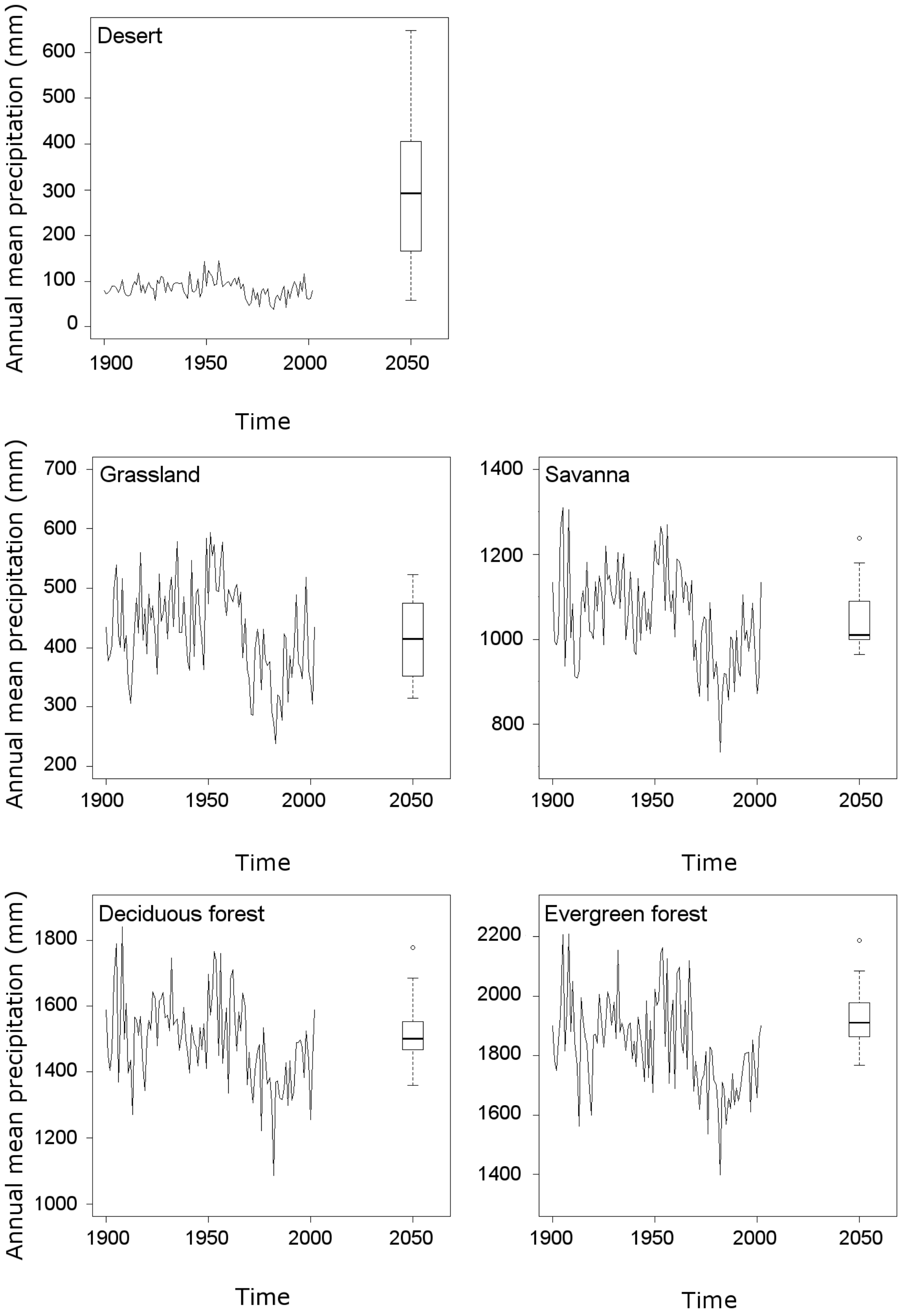
APPENDIX



Appendix S1 Model performance given as median, 25th and 75th percentiles of the area under the curve (AUC) of a receiver operating characteristic plot (sensitivity against 1 – specificity) from six different models: generalized linear models (GLM), generalized additive models (GAM), artificial neural networks (ANN), generalized boosting models (GBM), classification tree analysis (CTA) and flexible discriminant analysis (FDA). Black dots represent AUC mean values of a 3-fold cross validation splitting procedure (70:30) of the full data set. Evaluation was performed on the 30% test data. Whiskers represent minimum and maximum values, respectively. Predictive accuracy of the consensus projections (models weighted according to their AUC values) are given as black crosses.



Appendix S2 Generalized additive model (GAM) response curves including standard errors for predictors. The response curves relate West African tree cover to climate and disturbance variables. Degree of smoothing was estimated by generalized cross validation but restricted so as not to exceed 4 degrees of freedom to maintain generalization in predictive modelling. Population density was log-transformed due to extreme outliers. Left upper corner shows predictor contributions expressed as the percentage drop in explained deviance when excluded from the final model. Tree cover data (www.landcover.org) were derived from all seven bands of the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor on board NASA's Terra satellite (Hansen *et al.*, 2003).



Appendix S3 Precipitation records of the 20th century in West Africa and future projections (2050, SRES storyline A2a) from 17 different General Circulation Models (GCMs), that participated at the 4th assessment report of the (IPCC, 2007). The amount of projected annual rainfall from different GCMs are given as median, 25th and 75th percentiles. The precipitation data are shown for the different modelled biomes in West Africa: desert, grassland, savanna, deciduous forest and evergreen forest. Precipitation records of the 20th century were taken from the Climate Research Unit (http://www.cru.uea.ac.uk/cru/data/).

Chapter 3

The projected impact of climate and land use change on plant diversity: An example from West Africa

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Submitted manuscript

ABSTRACT

In West Africa, plant diversity is threatened by future climate and land use change, however, synergistic forecasts for this area are lacking to date. Species distribution models are valuable tools to explore the impact of both factors on biodiversity patterns. We investigated the impact and the interplay of future (2050) climate and land use change on plant diversity in Burkina Faso, which covers the major bioclimatic gradient in West Africa. This broad gradient in the country causes a similar gradient in plant diversity. Thus, the impact of climate and land use change can be investigated in regions with different levels of species richness. The LandSHIFT model was adapted for this study to derive novel regional spatially explicit future (2050) land use simulations for Burkina Faso. Additionally, the simulations include different socioeconomic assumptions. One-class support vector machines (SVMs) were performed with these land use simulations together with current and future (2050) climate projections at a 0.1° resolution (grid cell: ~ 10 × 10 km). Our modelling results showed that the flora of Burkina Faso will be primarily negatively impacted by future climate and land use changes. However, we found contrasting latitudinal patterns. Although climate change is predicted to cause species loss in the more humid regions in Southern Burkina Faso (~ 200 species per grid cell), we project an increase of species richness in the Sahel. However, land use change is expected to suppress this increase to the current species diversity level, depending on the socioeconomic assumptions. Climate change is more important than land use change under the assumption of technological stagnation. Our study highlights the impact and interplay of future climate and land use change on plant diversity along the broad bioclimatic gradient in West Africa. Our results suggest that, in general, the plant diversity in dry and humid regions of the tropics might respond differently to climate and land use change.

INTRODUCTION

Biodiversity is threatened by climate and land use change at the global level (Sala *et al.*, 2000; Parmesan, 2006). These changes affect species distributions and species richness and they also impact the composition of assemblages (Parmesan & Yohe, 2003; Root *et al.*, 2003). More substantive knowledge of these effects is particularly needed in under-investigated regions, such as West Africa, where contradictory trends have even been reported in the recent past concerning the tendency of 'greening' and 'drying out' (Gonzalez, 2001; Rasmussen *et al.*, 2001; Hickler *et al.*, 2005; Wezel & Lykke, 2006; Wittig *et al.*, 2007). Similarly, the role of land use change in affecting biodiversity and vegetation dynamics is not yet fully understood. Although land use change generally contributes to biodiversity loss in the evergreen tropics (Sala *et al.*, 2000; Norris *et al.*, 2010), it seems more difficult to assert that human activities influence vegetation dynamics in more arid regions, such as the Sahel (see Seaquist *et al.*, 2009). This observation demonstrates the need for better-integrated assessments, particularly because significant global species extinction risk is projected for the 21st century (Thomas *et al.*, 2004; Sommer *et al.*, 2010).

Future projections of plant diversity in West Africa are lacking so far, but continental and global scale studies indicate that large proportions of suitable habitats will be lost during this century due to climate change (Mcclean *et al.*, 2005; Sommer *et al.*, 2010). However, future land use change is another important factor and should be considered (Heubes *et al.*, 2011). The importance of this factor results from the expected high levels of economic and population growth in these regions (Sala *et al.*, 2000; Jetz *et al.*, 2007). Thus, the scarcity of studies that incorporate land use change in modelling studies is surprising (Luoto *et al.*, 2007) and often results from a lack of reliable land use simulations (Broennimann *et al.*, 2006; Sommer *et al.*, 2010). Studies that incorporate land cover have been aimed at the effects of model performance (Thuiller *et al.*, 2004; Luoto *et al.*, 2007) rather than at model outcomes (but see Randin *et al.*, 2009). In models of single-species distributions, land cover becomes particularly important at smaller scales (Pearson & Dawson, 2003), that is < 50 km resolution and the inclusion has been shown to improve model accuracy (Jetz *et al.*, 2007; Luoto *et al.*, 2007). The LandSHIFT model (Schaldach *et al.*, 2011) is a dynamic and spatially explicit land use and land cover model, which also accounts for climate and CO_2 induced land use changes; a specific strength of this model is given by the performance on the country level at high resolutions (~1 km resolution) and thus offers a novel tool for national scale studies.

Modelling numerous species to estimate the patterns of current and future species diversity is generally performed with species distribution models (SDMs) (Thomas *et al.*, 2004; Thuiller, 2004; Ferrier & Guisan, 2006). SDMs, also known as 'bioclimatic envelope models', rely on the niche concept (see Guisan & Zimmermann, 2000 for a review). Information on species absences are often not available (e.g. using data from atlases and herbarium records), which resulted in the development and application of various presence-only models (see Pearce & Boyce, 2006 for a review). One-class support vector machines (SVMs; Cortes & Vapnik, 1995), a type of machine learning algorithm, represent a promising new approach for predicting future species distributions in view of climate and land use change (Drake *et al.*, 2006).

However, climate impact research in Africa is hampered by the differences in the future climate projections produced by general circulation models (GCMs) (IPCC, 2007). The arbitrary selection of GCMs, the most frequent approach, might generate biased future predictions and, consequently, produce questionable recommendations. Extracting the information that describes a central tendency of different simulations provides an alternative to deal with this kind of variability (Thuiller, 2004; Araújo *et al.*, 2005; Araújo & New, 2007).

In this study, we focus on Burkina Faso, which covers the major bioclimatic gradient in West Africa. Research activities, particularly during the last decade (Wittig *et al.*, 2009), produced an outstanding vegetation database for Burkina Faso (Schmidt *et al.*, 2010b), as compared with other West African countries. Burkina Faso exhibits a high human population growth rate, which will probably cause severe land transformations. The country also covers a broad gradient in plant diversity. Thus, the effects of climate and land change can be investigated in regions with different levels of plant diversity.

Our overall objective was to explore the impact and interplay of climate and land use change on plant diversity in Burkina Faso. We expect severe land use change in this region, depending on the technological developments. We further expect that land use change is a more important threat to the plant diversity than climate change. To test our expectations we 1) developed novel land use simulations based on different socio-economic assumptions using the LandSHIFT model, 2) we investigated the impact and interaction of future climate and land use change using one-class SVMs and an extensive database on plant distributions in West Africa. To our knowledge, this is the first study in West Africa where both climate and land use change are considered in the modelling of future plant diversity.

METHODS

Study area

The West African country, Burkina Faso (10–15°N and 5.5°W–2.5°E), covers a broad bioclimatic gradient from a tropical savanna climate (~ 1,000 mm per year) to an arid climate (~ 300 mm per year; Köppen-Geiger climate classification). The country's climate produces a similarly broad gradient in the plant diversity and composition of taxonomic and functional groups. The plant diversity is high in the South and decreases continuously towards the North (Schmidt *et al.*, 2005; Schmidt *et al.*, 2011). The vegetation of Southern Burkina Faso is characterised by Sudanian dry forests and tall-grass savannas, whereas the North is covered by the arid *Acacia* savannas of the Sahel (Hahn-Hadjali, 1998; Thiombiano & Kampmann, 2011). A large increase in Burkina Faso's population is expected in view of the country's current annual human population growth rate of 2.3% per year (FAO 2007). Traditional management strategies of croplands (shifting cultivation with fallows) are still common among native farmers in Burkina Faso; these management strategies combined with the deliberate retention of trees (e.g. shea tree) create species rich agroforestry systems, also known as 'parklands' (Augusseau *et al.*, 2006).

Species records

Species occurrence points were taken from various databases that cover Burkina Faso and the adjacent countries. It is important to consider the environmental conditions of the species outside the study area because, even if a species does currently not occur in Burkina Faso, that species may find suitable conditions there in the future. We used data from the West African Vegetation database (Janßen *et al.*, 2011), which includes data from various Ph.D. and Master's theses (see the Acknowledgements). The majority of these studies had a focus on complete species inventories, which reduces the risk of a taxonomic bias in our species data. Furthermore, we used the SIG-IVOIRE database

(Chatelain *et al.*, 2011), herbarium records from the Herbarium Senckenbergianum (FR; http://sesam.senckenberg.de/), the Ouagadougou University Herbarium (OUA) and personal field surveys conducted in Burkina Faso (2009). By combining observation and collection data, we reduced the bias inherent in each data type (Schmidt *et al.*, 2010a). Most data originate from the 2001–2010 period, whereas a minority of herbarium specimens are from earlier periods. We considered only species with more than 20 occurrence points because lower values strongly decrease the accuracy of models (Stockwell & Peterson, 2002). The species occurrence points were aggregated within grid cells of a 0.1° resolution (~10×10 km). A total of 1390 species from 689 genera and 130 families were available for the final analysis. The nomenclature follows that of the African Plants Database (2011).

Climate data

We used the WorldClim database (Hijmans *et al.*, 2005; http://www.wordclim.org), which yields interpolated mean monthly variables that describe trends, seasonality and extremes. Three climatic variables (DI, drought index; T_{min}, minimum temperature of the coldest month; $Prec_{dry}$, precipitation in the driest quarter) were used as predictors in the SDMs. The DI is defined as the ratio of annual mean precipitation to potential evapotranspiration (PET). The latter variable was calculated following Thornthwaite (1948). Thus, the DI is a proxy for the water availability, which is the most important factor in this region (Scholes, 1997) and largely explains the species distribution patterns in West Africa. The $Prec_{dry}$ and T_{min} variables are limiting factors and have previously been shown to be important determinants in West African (Heubes *et al.*, 2011).

Extremely high variability in the GCM projections was identified as a major source of uncertainty in the predictive vegetation modelling (Scheiter & Higgins, 2009). Uncertainty is particularly high for the precipitation, which was used as a part of the drought index in this study. To find a GCM that describes the central tendency (consensus) of the future precipitation amounts, we ran a ‘principal component analysis’ (PCA) on the future (2050) annual mean precipitation projections (Ramirez & Jarvis, 2008) from 17 different GCMs (cf. Heubes *et al.*, 2011). The precipitation projections from $Miroc3.2_{medres}$ (Center for Climate System Research, Japan) were most strongly correlated with the first PCA axis and can, thus, be considered as a consensus projection (Thuiller, 2004; Araújo *et al.*, 2005). We chose the IPCC SRES A2 scenario, which assumes intermediate levels of CO_2 emissions and an intermediate increase in temperature which is in line with the current global trends (Canadell *et al.*, 2007). The future climate projections (2050, A2) from Miroc3.2$_{\text{medres}}$ were used for further analysis at our target resolution of 0.1°. We recognize that other climate models and storylines yield predictions that differ in their specifics in view of climate change (Appendix 1, Fig. S1), however, it is beyond the scope of the study to consider multiple scenarios of future climate

Land use data

The land use simulations were generated by LandSHIFT (Schaldach *et al.*, 2011), a dynamic and spatially explicit land use and land cover model. LandSHIFT uses biophysical and socio-economic drivers to simulate agricultural development on regional and continental scales and has been tested for the African continent in previous studies (e.g. Alcamo *et al.*, 2011). We specifically adopted LandSHIFT for West Africa in the present study: this version uses the GLC 2000 Global Land Cover dataset (Mayaux *et al.*, 2004) as a basemap and runs with a spatial resolution of ca. 0.01°. Appendix 2 gives a detailed description of the LandSHIFT model and the specifications. In Burkina Faso, four major land use categories can be found: grassland, cropland (> 50% cover), deciduous woodland and urban area. The term 'cropland' was retained for clarity, even though the term 'parkland' would better describe the agricultural system.

The climate data to generate the land use simulations were taken from Miroc3.2$_{\text{medres}}$ in accordance with the climate data used for the SDMs. LandSHIFT was run with the 'market first' scenario from the UNEP Global Environmental Outlook-4 (Rothman *et al.*, 2007), which roughly corresponds to the IPCC A2 storyline.

In general, socio-economic developments have greater effects on land use change than climatic drivers (Schröter *et al.*, 2005). Thus, we considered two different scenarios: technological change (e.g. mechanisation and fertilisation) and no technological change (hereafter termed 'technological stagnation'). The yields were dynamically modelled with LPJmL (Bondeau *et al.*, 2007), whereby the assumptions of technological change result in higher crop yields and, thus, in less demand for arable land. Additionally, we assumed that protected areas would be maintained until a lack of transformable land for crop cultivation is reached. Technically, this condition was achieved by reducing the potential agricultural suitability of protected areas, as defined by the IUCN and UNEP-WCMC (2010), to 30% of its original values. The potential agricultural suitabilities are based on the multicriterial analysis of the LandSHIFT model. The final current and future (2050) land use scenario maps were aggregated (nearest neighbour) to our target resolution (0.1°) and used as predictors in the SDMs (one categorical independent variable).

One-class Support Vector Machines

Support vector machines (SVMs) were developed by Cortes and Vapnik (1995) for binary classification and adopted by Schölkopf *et al.* (2001) to deal with the one-class problem (here, the species presence-only data). This approach avoids to estimate species absences, which might negatively affect the model's predictive accuracy by sampling the potential distribution area (Guo *et al.*, 2005). Thus, this type of machine learning algorithm is theoretically superior to the models that rely on the simulation of pseudo-absence data (Drake *et al.*, 2006) and represents an extension and refinement of other well-established presence-only models (Pearce & Boyce, 2006). One-class SVMs use species occurrence points and seek to find and optimise the smallest possible hyperspace that contains the data points and allows outliers (Pearce & Boyce, 2006). A full description of one-class SVMs can be found in Schölkopf *et al.* (2001) and Guo *et al.* (2005). Two parameters must be defined: v, an equivalent to the percentage of outliers in the training data set; and gamma, a kernel parameter within the radial basis function that is typically used in one-class SVMs (Tax & Duin, 1999; Schölkopf *et al.*, 2001). The radial basis function is introduced to increase the flexibility of the algorithm by allowing for non-spherically distributed data and non-linearity (Guo *et al.*, 2005). Due to the lack of true absence data, we were unable to estimate the true-negative rate (i.e. to use Kappa or TSS) (e.g.Thuiller *et al.*, 2009). However, we used the predicted area to support the evaluation of the model performances by plotting the true-positive rate and the predicted area as a function of v (cf. Guo *et al.*, 2005). Setting v to 0.04 appeared as an optimal parametrisation for a random set of species (n=300) to avoid overprediction and was, thus, used for subsequent analysis. A 10-fold cross-validation was applied to determine an optimal gamma parameter and the final accuracy (1 – false-negative rate). The final accuracy was estimated by averaging the accuracy of each test.

The analysis was carried out using the free software environment R (R Development Core Team, 2011, ver. 2.13.1). The tools for the support vector machines are available in the package 'e1071' (Dimitriadou *et al.*, 2011). To avoid unreliable future potential distributions, we constrained the migration of any species to a maximum of 1 km per year (Clark *et al.*, 1998). Functions for applying the dispersal filter on the binary SVM projections and calculating the turnover rates were taken from the BIOMOD package (Thuiller *et al.*, 2009). The turnover rate (T) reflects the changes in species composition by combining the species loss (L) and gain (G) and accounting for the overall species richness (SR) using the following equation:

$$T = 100 \cdot ([L+G] / [SR+G]). \qquad (1)$$

To disentangle the effects of future climate and land use change on plant diversity, we firstly calibrated the SVMs with both current climate and land use data. Secondly, SVMs were run with future climate data while assuming constant (i.e. current) land use. Thirdly, SVMs were run with future climate and future land use data (cf. Heubes *et al.*, 2011). Thus, the different components that influence plant diversity can be extracted. Simulations with current climate and future land use data do not add additional information. We did not focus on the effects of including land use information in SDMs itself (e.g. Thuiller *et al.*, 2004), because this was already shown to improve models performances at our scale, i.e. < 50 km resolution (Jetz *et al.*, 2007; Luoto *et al.*, 2007).

RESULTS

Our simulations show considerable future changes in land use (2050) and these changes are less severe if technological change is assumed (Fig. 1a, b). The demand for cropland is lower in the presence of technological change because of higher crop yields (e.g. efficient land management and fertilisation). Two major forms of land transformation are predicted to occur in Northern and Southern Burkina Faso by 2050. Grasslands of the Sahel are transformed into croplands (feasible due to increased precipitation and CO_2 concentrations) in the North, and deciduous woodlands are transformed into croplands in

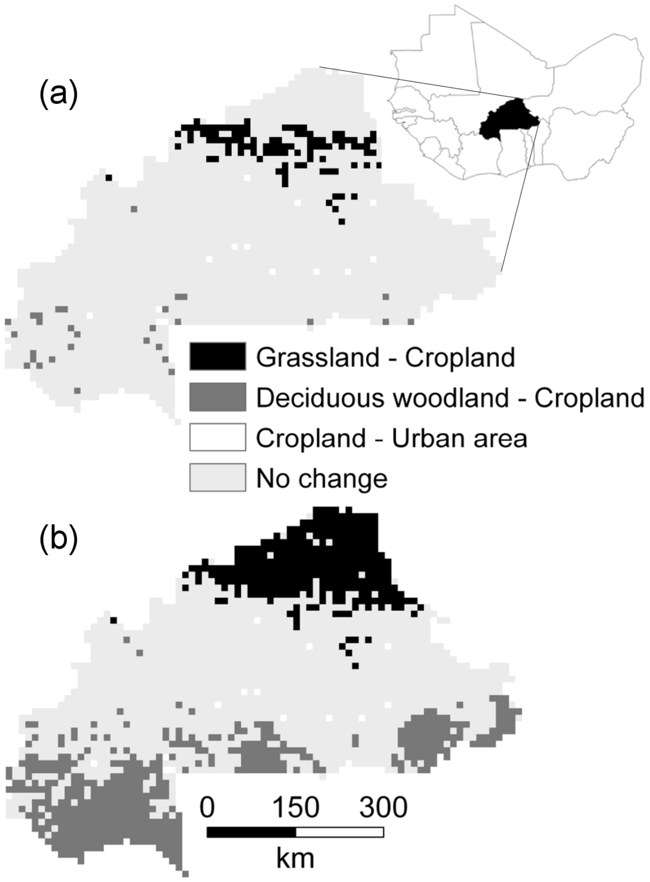

Figure 1 Projected land use change in Burkina Faso for 2050, assuming (a) technological change and (b) technological stagnation as simulated by LandSHIFT. The first land use unit represents the current use, whereas the latter refers to the projected future use.

the South. The predicted cropland expansion is caused by a 3-fold increase in the demand for agricultural products as assumed by the GEO-4 ‘market first’ scenario.

The calculated SVM model accuracies were very satisfactory, with an average of 0.87 ± 0.07. Currently, 1157 of the 1390 modelled species occur in Burkina Faso. The strong north-south gradient in the plant diversity, with the species richness gradually decreasing towards the north, is well represented by our models (Fig. 2a). The model’s projections show severe future changes, including species loss, gain and turnover, in Burkina Faso under climate and land use change, assuming a technological stagnation (Fig. 2b-d). A similar scenario, with only marginal differences, is given under assumptions of technological change: we expect a higher species loss (average across grid cells: 24 ± 12%) than species gain (11 ± 25%). However, the spatial distribution of changes generally showed considerable variation (Fig. 2b-d). Primarily, the northwestern and southern parts of Burkina Faso are affected by high rates of species loss and turnover (Fig. 2b, d), with exceptionally high losses of up to 50–60% (e.g. in the southeast).

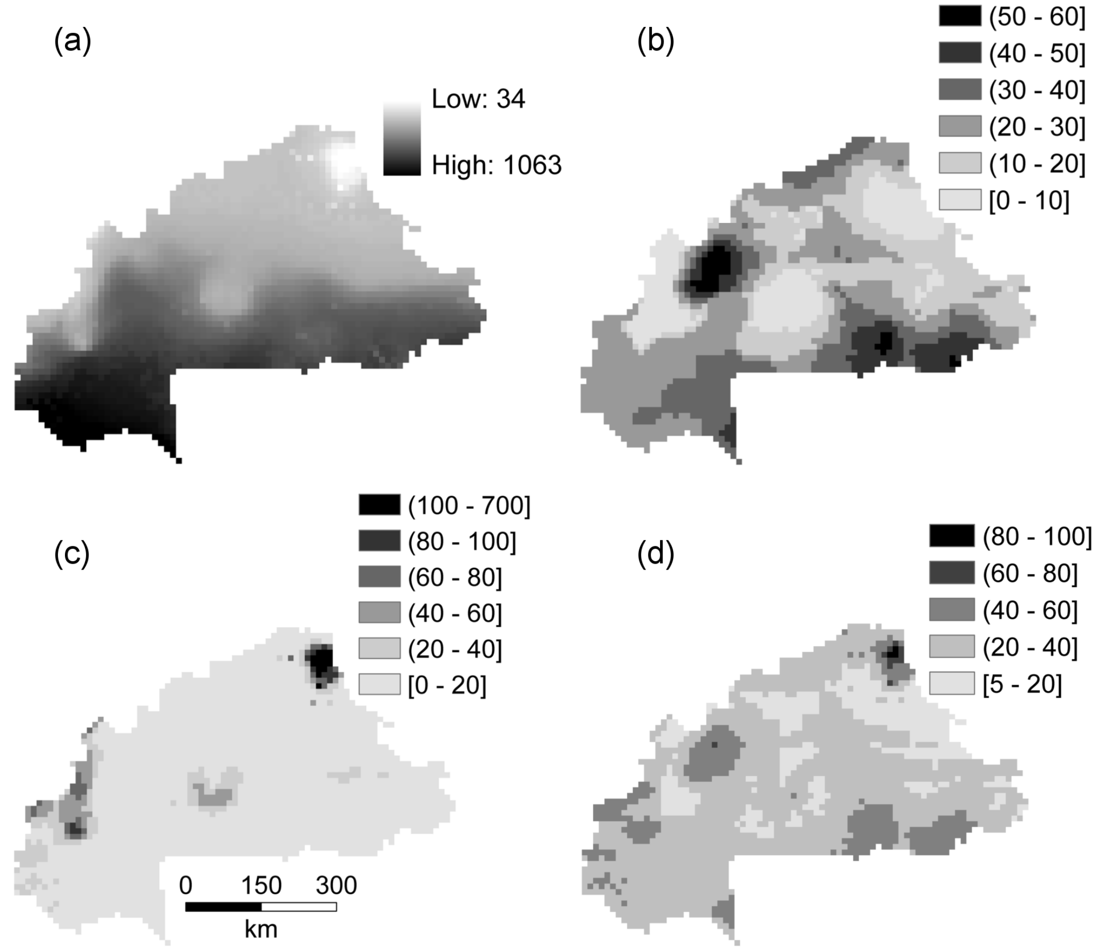

Figure 2 (a) Current modelled species richness in Burkina Faso and percentages of (b) species loss, (c) gain and (d) turnover projected for 2050, as calculated by one-class support vector machines. The simulations incorporate climate and land use change. The land use change projections are based on the assumption of technological stagnation.

High values of species gains are found in the Sahel (Fig. 2c). Note that these high values (i.e. > 100%) only occur because the current species richness of the Sahel is low (Fig. 2a).

Notwithstanding these strong changes, only 29 of the 1157 species currently present in Burkina Faso are predicted to be absent in the future, and a similar number of species (26) are predicted to be gained by migration from adjacent southern countries; these results are robust to different socio-economic assumptions.

Our modelling results suggest that future climate and land use change significantly reduce plant diversity ($P < 0.001$, paired Wilcoxon signed-rank test). The effect of climate change is more important than the effect of land use change (Fig. 3) under the assumption of technological stagnation. Southern Burkina Faso is most strongly and negatively affected by climate change, where species richness drops from ~ 1000 to 800 species per grid cell (Fig. 3). This loss results in a less pronounced north-south gradient of species richness by 2050. The transformation of deciduous woodland into cropland reinforces species loss (~ 10 species per grid cell), if we assume technological stagnation (Figs 1, 3). In contrast, climate change positively affects species richness in the Sahel (Fig. 3). However, this increase is suppressed by land use change. Accordingly, species richness remains at its current level, assuming technological stagnation (Fig. 3). Future projections of species richness based on climate and land use change with technological development differed only marginally from the 'climate-only' projections which are shown in Figure 3. Consequently, the loss of species richness is less severe under the assumption of a reduced expansion of croplands owing to technological development (Fig. 1).

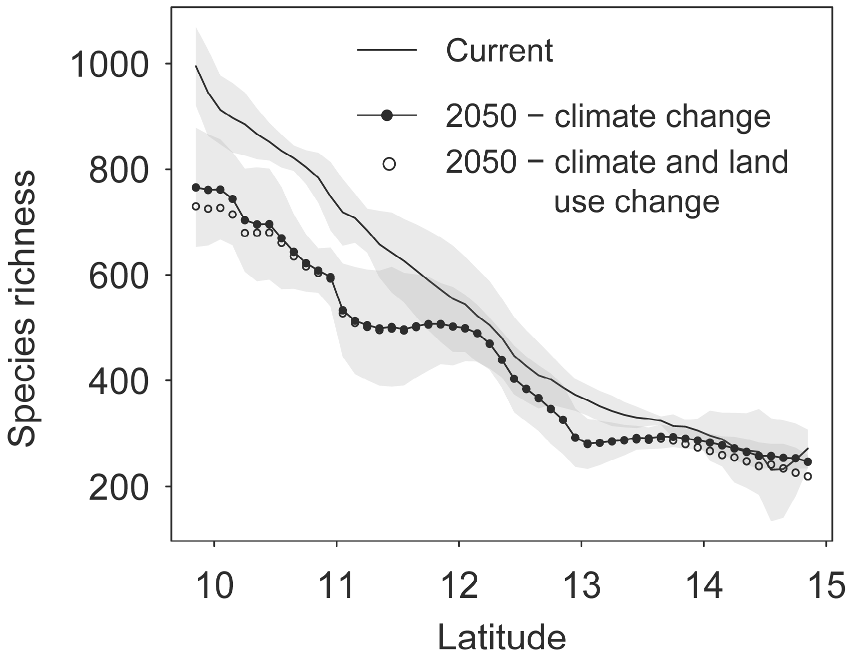

Figure 3 Projected latitudinal pattern of the current and future (2050) species richness in Burkina Faso. The lines represent the means; standard deviations are shown as gray areas. A dark gray shading indicates the overlap. The climate change projections (—●—) assume constant land use. The projections that include future land use change (○) are based on assumptions of technological stagnation in the agricultural sector.

DISCUSSION

Changes in plant diversity

Here, we present the first estimate of the effects of future climate and land use change on plant diversity in West Africa, specifically for Burkina Faso. The projected changes

suggest that large parts of Burkina Faso will be less species rich, however, the plant diversity of dry and humid regions responded differently to climate and land use change.
Our model simulations indicate northern shifts of the leading edges of species distributions. However, the northern shifts are more pronounced considering the trailing edges and, consequently, produce range contractions. This explains the projected species loss in Southern Burkina Faso and is caused primarily by a reduction in the water availability (i.e. a reduced drought index).

We use a dispersal filter of 1 km per year, a more realistic assumption (Clark *et al.*, 1998; Broennimann *et al.*, 2006) than the 'no or full dispersal' scenario (e.g. Mcclean *et al.*, 2005). A 'full dispersal' scenario in our study would have produced a much higher species gain in Southwestern Burkina Faso (20–40%) due to the migration of species from Côte d'Ivoire. However, dispersal rates might be higher than 1 km per year for specific plant groups, such as grasses, due to seed dispersal by wind and by pastoralism.

Our model results are consistent with the 'water-energy-richness hypothesis' (Hawkins *et al.*, 2003), which states that plant species richness is primarily controlled by ambient energy at high latitudes, whereas water availability becomes more important at low latitudes. In our study area (low latitudes), species richness gradually increases with higher water availability. Burkina Faso revealed a negative water balance and future projections also indicate a negative water balance. Thus, the expected increase in temperature will most likely cause species loss (Sommer *et al.*, 2010). In contrast, the projected increase of annual mean precipitation positively affects species richness, as indicated by the current positive correlation in Burkina Faso (Schmidt *et al.*, 2005). The northern and southern regions of Burkina Faso are projected to benefit from additional 100 mm per year (2050). Apparently, the positive effect of higher rainfall (see also Hickler *et al.*, 2005) is more distinct in the arid Sahel than in the more humid regions of Southern Burkina Faso and might counterbalance the negative effect of increasing temperatures. We found that these changes might even produce increased species richness in the Sahel, a pattern that has not been detected by global studies (Sommer *et al.*, 2010). The well-known north-south gradient of plant diversity (Linder, 2001) might be flattened in other African countries of the Northern Hemisphere if exposed to similar future climatic conditions. Moreover, our results suggest that the plant diversity in dry and humid regions might generally respond differently to climate and land use change.

The interplay of climate and land use

We included land use simulations, as land cover has been shown to furnish essential information to SDMs, in particular at smaller scales (<50 km) with a small geographic extent (Pearson & Dawson, 2003; Pearson *et al.*, 2004). Additionally, the incorporation of land cover has been shown to increase the predictive power and model accuracy at these scales (Luoto *et al.*, 2007). In contrast to Sala *et al.* (2000), our results suggest that climate change is a more important threat to plant diversity than land use change. This was found under the assumption of technological stagnation which includes the maintenance of the current traditional management strategies. This management is characterised by shifting cultivation and fallows of different ages which support high levels of biodiversity (Augusseau *et al.*, 2006). Our results indicate that land use per se must not necessarily cause severe species loss. However, technological developments in the agricultural sector must be taken into account, as the fate of biodiversity is linked to the ways in which people use land (Norris *et al.*, 2010). Increasingly, the traditional management strategies for croplands are being replaced by a dynamic, market-oriented agriculture dominated by cash crops (e.g. cotton and cashew), i.e. land use intensification. Indeed, we demonstrated that technological development might lessen the risk of species loss by reducing the demand for arable land due to higher crop yields per hectare. However, severe negative impacts on plant diversity are expected due to land use intensification (see discussion in the following section).

A advantage of incorporating land use simulations from LandSHIFT in SDMs is that this approach allows the indirect incorporation of CO_2 effects, which have rarely been included in previous SDMs (but see Rickebusch *et al.*, 2008). Using information on land use in addition to climatic parameters might add redundant information because current land cover is primarily determined by the climate (co-inertia). However, the climate is weakly correlated with the occurrence of some land use categories, notably the arable land (Thuiller *et al.*, 2004). We refrained from selecting specific land use categories as independent variables (e.g. Thuiller *et al.*, 2004) because the pre-processing of environmental predictors to avoid multicollinearity was shown to be unnecessary in SVM applications (Drake *et al.*, 2006).

Limitations and future research directions

The pros and cons of species distribution models are not discussed here, as several papers have already highlighted their limitations and methodological uncertainties (e.g. Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006; Dormann, 2007). We rather focus on specific limitations inherent to our approach and formulated future research directions. In our approach we considered species with more than 20 occurrence points only. This might underestimate the threat to narrow-ranged endemics, which are at highest risk in the tropics (Jetz *et al.*, 2007). Additionally, the occurrence data do not cover the entire distribution ranges of the species, i.e. we do not fully capture the climatic niche due to data gaps in large parts of West Africa. However, we considered species data in the north and south of Burkina Faso, covering the major bioclimatic gradient in West Africa from the evergreen tropics to the Sahara. This major north-south gradient is similar across the longitudes. Thus, we think that further species distribution data to the west and east of Burkina Faso would only marginally influence our projections of plant diversity.

Furthermore, there is uncertainty due to the variability of GCM projections for West Africa (IPCC 2007; Heubes *et al.*, 2011), namely, whether wetter or drier conditions are expected. Our results for Burkina Faso are based on increases of the precipitation (90 ± 26 mm per year), T_{min} (2.3 ± 0.16) and PET (392 ± 114 mm per year) as projected by Miroc3.2$_{medres}$. Although the common view from the climate modelling community is that no single climate model is superior (Fordham *et al.*, 2011), we used this GCM following the rational of consensus projections (Thuiller, 2004; Araújo *et al.*, 2005; Araújo & New, 2007). We think that this approach is better than arbitrarily selecting GCMs, however, there is no guarantee that Miroc3.2$_{medres}$ produces more robust future climate predictions. Improved and harmonized climate models are strongly needed to reduce divergence of the African climate forecasts; the next IPCC report is expected to focus on this issue.

Assessing the impact of land use change on plant diversity with the technological change scenario involves methodological limitations for our approach. Cropland will be used more intensively under the assumption of technological change, which might have severe negative impacts on the plant diversity. However, the SDMs only use the cropland/non-cropland information (e.g. the spatial extent of this land use type); thus, the land use intensification is not reflected in our approach. Consequently, we might underestimate species loss due to the changes in land use occurring under assumptions of technological change. More substantive knowledge is particularly needed to better understand effects of an intensified agriculture (e.g. cash crops) on biodiversity patterns. Therefore, SDM applications might be improved by gathering species presence/absence data and the incorporation of land cover typologies with different management intensities.

CONCLUSIONS

Both climate and land use change have primarily negative effects on species diversity in Burkina Faso, particularly in the more humid Southern regions. However, our study detected contrasting latitudinal patterns of impact. The species richness in the dry Sahel might increase due to climate change, but there is interference with the expected land use change. Our results suggest that plant diversity in dry and humid regions might generally respond differently to climate and land use change. Climate change was found to be more important than land use change in reducing species richness, when assuming technological stagnation. Technological development was shown to lessen the risk of species loss by reducing the demand for arable land. However, technological developments will also replace the traditional management strategies by a market oriented agriculture which includes land use intensification. The latter effect was not fully captured by our approach. Further integrated assessments are needed to adequately assess the effects of intensified agriculture on the patterns of biodiversity. Our results help to improve the understanding of the impact of climate and land use change on plant diversity.

ACKNOWLEDGEMENTS

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APPENDIX

Appendix 1

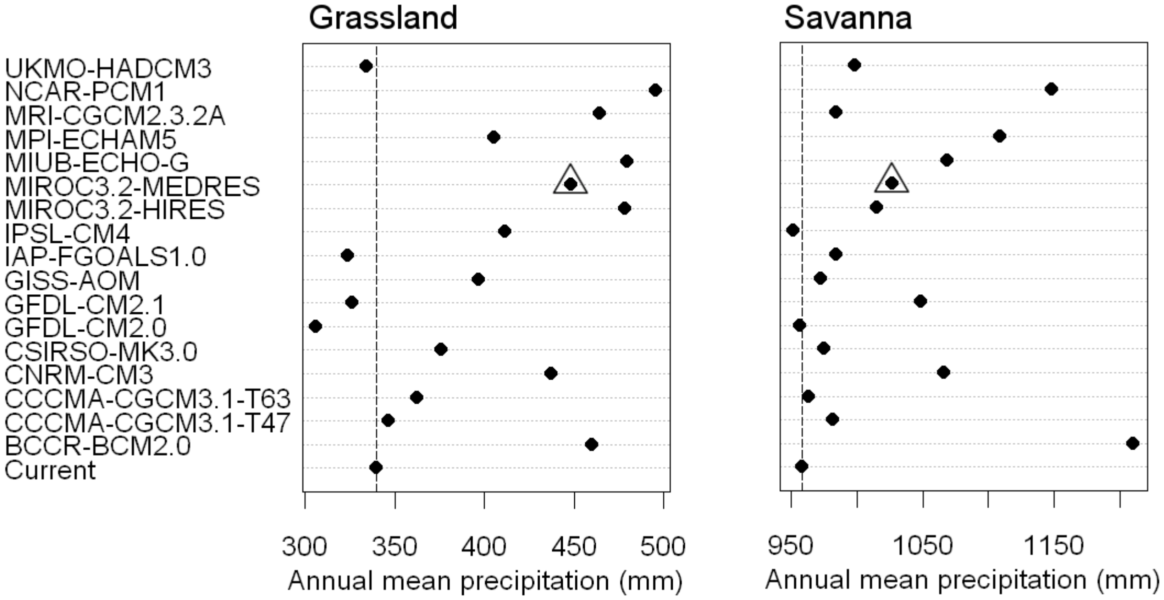

Figure S1 Current and future (2050) projected annual mean precipitation in the grassland biome and the savanna biome, which cover Burkina Faso. Names of the different GCMs are given on the y-axis. The vertical dashed line represents the current annual precipitation (WORDCLIM data base; (Hijmans *et al.*, 2005); http://www.worldclim.org), which was used as a part of the drought index in our study. Future projections (2050, SRES A2 storyline) were taken from 17 different General Circulation Models (GCMs), that participated at the 4th assessment report of the IPCC (2007). Future projected values were derived by adding climate anomalies (from GCMs) to the baseline of the WORDCLIM data set (Ramirez & Jarvis, 2008). In our study, we used future projections of annual mean precipitation from the GCM Miroc3.2$_{\text{medres}}$ (Δ).

Appendix 2

The LandSHIFT model is based on the concept of "land-use systems" (GLP 2005; Mather, 2006). It couples components that represent anthropogenic and environmental subsystems and explicitly simulates the spatial-temporal dynamics of different land-uses such as settlement and crop cultivation. A full description of the LandSHIFT model is given in Schaldach *et al.* (2011). The model input consists of a set of driving variables describing the socio-economic and agricultural development of a country (macro-level) and grid variables (micro-level) describing the local landscape characteristics and zoning regulations (e.g. the extent of nature conservation areas). Beside country statistics, the main model output comprises time-series of grid maps showing land-use type as well as population and livestock densities. The model operates on a raster resolution that can be adjusted in respect to study focus, here ~0.01°. It consists of three sub-modueles, (i)

METRO for settlement structures, (ii) AGRO for cropping activities and (iii) GRAZE for livestock grazing. Figure S2 schematically illustrates the model framework. In our study we excluded the GRAZE sub-module.

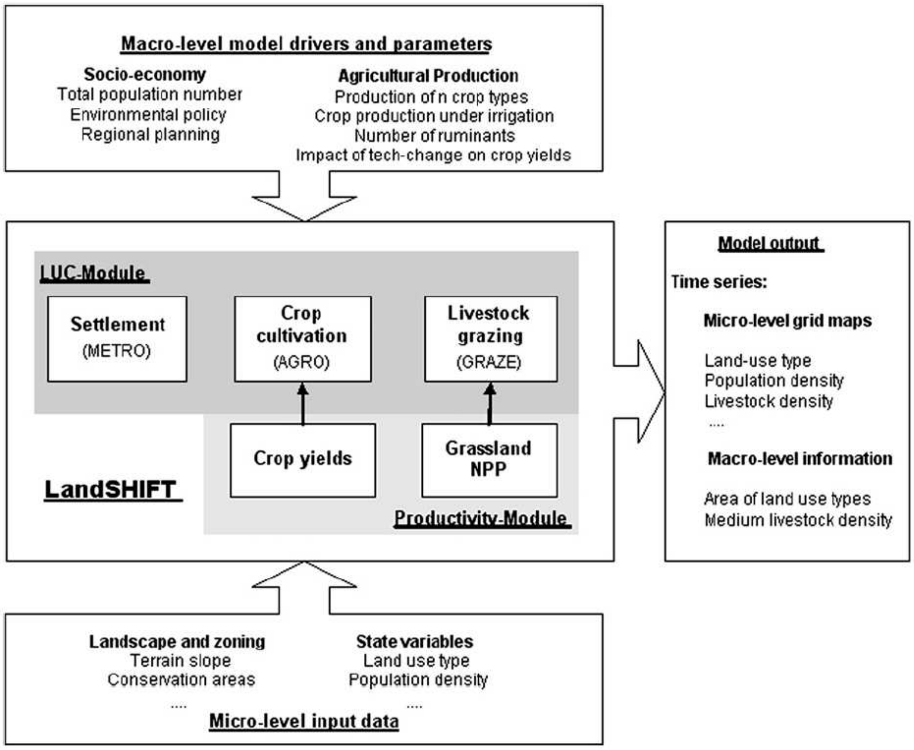

Figure S2 Schematic representation of LandSHIFT. The model version consists of three modules: a productivity model for cropland, a productivity module for landscape productivity and the LUC-module. The latter is the core element of LandSHIFT.

Core of the LandSHIFT model is a multi criteria analysis (MCA) that applies a common methodology for all land use types. It calculates potential suitability to support preference rankings over all country cells for all land use types. The preference value Ψ_k of grid cell *k* is calculated as follows:

$$\Psi_k = \underbrace{\sum_{i=1}^{n} w_i f_i\left(p_{i,k}\right)}_{\text{suitability}} \times \underbrace{\prod_{j=1}^{m} g_j\left(c_{j,k}\right)}_{\text{constraints}}, \text{ with } \sum_i w_i = 1, \quad \text{and } f_i\left(p_{i,k}\right), g_j\left(c_{j,k}\right) \in [0, 1] \tag{1}$$

The first term of the equation is the sum of weighted factors p_i that contribute to the cells' suitability for a particular land-use type. The weighting factors w_i determine the importance of each single factor p_i in the analysis. The second term defines constraints c_j to changing a cell's land-use type. For example, land use transitions from natural areas into agricultural land can be constrained by policies or potential protected area declarations. In our study, we applied a protected area constraint of 0.3 for those cells that are located within a protected area to reduce the calculated agricultural suitability's to 30% of the original MCA values. Suitability factors and constraints are derived from the state variables (at time-step t), landscape characteristics (LC), zoning regulations (ZR) and spatial neighborhood characteristics (White & Engelen, 1997). Both p_i and c_j are standardized by the value functions f and g which have a co-domain from 0 to 1 (Geneletti, 2004). Table S1 lists crucial suitability factors (p_i), constraining factors (c_j) and the data sources we applied in the West Africa study. However, the list is not static; it can be extended in respect to the research question to address.

Table S1 Suitability factors (p) and constraining factors (c) used in the different sub-models of LandSHIFT.

Sub-Model	**Factors (p) and constraints (c)**	**Model variable**	**Description**	**Reference**
Urban	p1	LC1	Terrain slope (500m resolution)	http://srtm.csi.cgiar.org/ [2010]
Urban	p2	LC2	Road infrastructure	http://www.naturalearthdata.com [2010]
Urban	c1	Trans	Trans Land-use transition	LandSHIFT algorithm
Urban	c2	ZR1	Conservation area	IUCN and UNEP-WCMC (2010)
Agriculture	p1	LC1	Terrain slope (500m resolution)	http://srtm.csi.cgiar.org/ [2010]
Agriculture	p2	LC3	Crop yields	LPJmL (Bondeau et al., 2007)
Agriculture	p3	LC2	Road infrastructure	http://www.naturalearthdata.com [2010]
Agriculture	p4	PDENS	Population density	Salvatore et al. (2005)
Agriculture	p5	NBR	Neighbourhood to cropland cells	LandSHIFT algorithm
Agriculture	p6	NBR	Distance to urban area/markets	LandSHIFT algorithm
Agriculture	c1	Trans	Land-use transition	LandSHIFT algorithm
Agriculture	c2	ZR1	Conservation area	IUCN and UNEP-WCMC (2010)

The model has been applied in different spatial raster resolutions and geographical regions (Koch *et al.*, 2008; Alcamo *et al.*, 2011). An evaluation of the LandSHIFT model for a continental African case study is provided by Alcamo *et al.* (2011). This evaluation includes procedures for model testing, sensitivity analysis and simulations of land-use scenarios up to the year 2050, based on model drivers from the UNEP Global Environmental Outlook-4 (Rothman *et al.*, 2007). The model is able to compute the spatial distribution of cropland distribution and continental average deforestation rates better than the spatial distribution of deforestation. The authors identified high model sensitivity to assumptions of potential future climate change due to the influence of climate on crop yields. It is therefore able to develop consistent scenarios of land use change for Africa by computing the effect of driving forces and competitions between land use sectors in a single spatially explicit model framework (Alcamo *et al.*, 2011).

Chapter 4

Impact of climate and land use change on non-timber forest product provision in Benin, West Africa: Linking niche-based modelling with ecosystem service values

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ABSTRACT

Non-timber forest products (NTFPs) make a major contribution to the livelihoods of the West African population. However, these ecosystem services are threatened by climate and land use change. Thus, our study aims at 1) the quantification and monetary mapping of important NTFPs and 2) developing a novel approach to assess the impacts of climate and land use change on the economic benefits derived from these NTFPs. We performed 60 structured interviews on a household basis in Northern Benin to gather data on annual quantities of collected NTFPs from the three most important savanna species: *Adansonia digitata*, *Parkia biglobosa* and *Vitellaria paradoxa*. Respective current market prices were derived from local markets to map the monetary values. We assessed the species' current and future (2050) occurrence probabilities by calibrating niche-based models with climate and land use data at a 0.1° resolution (cell: ~ 10 × 10 km). Future climate projections (2050) were taken from the general circulation model Miroc3.2$_{\text{medres}}$. The land use model LandSHIFT provided novel current and future land use simulations. To assess future economic gains and losses, respectively, we linked modelled species' occurrence probabilities with the spatially assigned monetary values. Our results show that the highest annual current benefits are obtained from *V. paradoxa* (54,111 ± 28,126 US$/cell), followed by *P. biglobosa* (32,246 ± 16,526 US$/cell) and *A. digitata* (9,514 ± 6,243 US$/cell). However, in the prediction large areas are projected to lose up to 50% of their current economic value by 2050. Our findings provide a first benchmark for local policy-makers to economically compare different land use options and adjust existing management strategies.

INTRODUCTION

For millennia, the livelihoods of rural West African communities have been based on goods and services provided by plants and animals of surrounding ecosystems. In particular, products of native plant species (e.g. fruits, leaves, bulbs) have played a central role in satisfying household subsistence needs including nutrition needs, medical treatment, energy supply, as well as construction material and firewood. Furthermore, non-timber forest products (NTFPs) contribute to the household economy by generating cash income helping to diversify livelihood strategies, and coevally they hold an important insurance function in times of financial crisis (Cavendish, 2002; Angelsen & Wunder, 2003). The extraction of NTFPs particularly attracts the African rural poor because no professional skills or equipment are required (low-threshold activity), extraction sites are characterised by open or semi-open access, and labour markets are generally thin, i.e. income alternatives are scarce (Angelsen & Wunder, 2003; Shackleton & Shackleton, 2004; Shackleton *et al.*, 2007).

The economic relevance of NTFPs for rural livelihoods in Africa, both in terms of subsistence and cash income, has been increasingly reported. Their contribution to the annual total household income was found to range from 15% in Malawi (Kamanga *et al*., 2009) to roughly 40% in Mali (Faye *et al*., 2010). In Northern Benin, NTFPs make up 39% of the yearly income (Heubach *et al*., 2011); major contributors to this NTFP income are three native woody species: *Vitellaria paradoxa* (subspecies *paradoxa*, Shea Tree or karité), *Parkia biglobosa* (African Locust Bean Tree or néré) and *Adansonia digitata* (African Baobab) (Vodouhê *et al.*, 2009). All three species occur throughout the Sudanian zone from Senegal to Sudan within the isohyets of 600 and 1400 mm; the baobab tree also occurs throughout the savanna regions of eastern and southern Africa (Arbonnier, 2004). NTFPs of these three species traditionally serve as a dietary supplement. In particular, two products are increasingly demanded and traded on international markets: shea butter due to its qualities as surrogate for cocoa butter (INSAE, 2008) and baobab fruit powder because of its health benefits (Besco *et al*., 2007).

However, Africa is expected to face severe changes in climatic conditions and land use this century (Sala *et al.*, 2000; IPCC, 2007). How will these environmental changes affect ecosystem functions and, therewith, the provision of ecosystem services such as NTFPs? Given that rural communities often heavily depend on a constant provision of

NTFPs (Heubach *et al.*, 2011) and, thus, can be considered as highly vulnerable to the expected changes, what are the immediate consequences for their well-being and livelihoods? Additionally, there might be low adaptive capacity in this regard due to a comparatively weak ability of the regional government to regulate environmental impacts (Uneca, 2005).

Subsequently, it is crucial to map the economic value of ecosystem services such as NTFPs reflecting their current use, and simulate future monetary benefits, in order to potentially adapt management practices in view of environmental changes (Costanza *et al.*, 1997; Chen *et al.*, 2009). In the past years, a remarkable number of methods, at different scale, have been developed to evaluate ecosystem services (Eade & Moran, 1996; Hein *et al.*, 2006; Troy & Wilson, 2007; Egoh *et al.*, 2008). However, little attention has been given to their spatial visualisation and regional mapping of direct use monetary values of ecosystem services (Chen *et al.*, 2009). Large scale mapping of ecosystem services often only represents crude estimates (cf. Naidoo *et al*., 2008), due to the lack of primary data (Eigenbrod *et al*., 2010). Moreover, projections of ecosystem services, contingent on scenarios, are scare and mostly limited to aspects of the carbon and water cycles (e.g. Schröter *et al.*, 2005). There is a strong need for more detailed on-site knowledge as derived from local field data. However, relating primary data (e.g., on household economics) to specific areas is challenging.

As NTFPs are derived from plants, the NTFP supply is related to the species' occurrence probabilities. To calculate changes in these occurrence probabilities and therewith NTFP availability, niche-based models (NBMs) can be used. NBMs, also known as 'bioclimatic envelope models', rely on the niche concept (Guisan & Zimmermann, 2000). These models fit a relationship between the presence/absence of species and the environmental conditions (e.g., climate and land use). Linking the monetary values of NTFPs with the occurrence probabilities of the NTFP-providing species represents a promising new approach to assess the impact of climate and land use change on provisioning ecosystem services. To our knowledge, this novel approach has not been applied so far.

With regard to both the local importance and the growing international relevance of several NTFPs, the objective of the study is to increase the understanding of current and future benefits derived from savanna species, in order to help local policy-makers to design adaptive management strategies.

The article is organized as follows: Section 2 describes the socio-economic environment of the study area, the investigated savanna species, the data collection, the monetary mapping and the niche-based modelling approach. In section 3 we present and discuss our results and the approach. Section 4 closes with some concluding remarks and sheds light on possible implications for future management of the investigated NTFP-providing species.

METHODS

Biophysical and socio-economic environment of the study area

The research was conducted in the surroundings of three villages in Northern Benin, West Africa. The villages were selected to cover the different phytogeographical districts (Adomou, 2005) of Northern Benin (Fig. 1): These phytogeographical districts are characterised by their species composition (major plant formations and exclusive species). From north to south the study villages are: Sampéto (district 'Mékrou-Pendjari': tree and shrub savannas, dry and riparian forest on ferruginous soils; precipitation: 950–1000 mm/yr), Niangou (district 'Chaîne de l'Atacora': riparian and dry forest, woodland on poorly evolved soils and mineral soils; precipitation: 1000–1200 mm/yr) and Papatia (district 'Borgou-Nord': dry forest, woodland, and riparian forest on ferruginous soils on crystalline rocks; precipitation: 1000–1200 mm/yr). All three study areas are characterised by one rainy season.

Rural livelihoods in the studied villages are preponderantly based on rain-fed crop production in traditional shifting cultivation systems. After few years of tillage the cleared fields lie fallow between 6 and 15 years which, by reason of habitual small-scale land use, leads to a typical mosaic pattern of cultivated area and fallow. Crops grown for the local diet encompass sorghum, millet, maize, legumes, yams and manioc, amongst others.

While clearing an area for cultivation, particular socio-economically important trees are spared from felling (Boffa, 1999). This type of agroforestry system, also known as parkland, includes cultivation and conserving of NTFP-providing tree species, thereby forming an inherent aspect of the savanna landscape. Animal husbandry is only a minor income activity.

NTFP providing tree species

We investigated the three socio-economically most important NTFP-providing woody species in Northern Benin: *V. paradoxa*, *P. biglobosa,* and *A. digitata*. The finding is based on previous research in this region (Heubach *et al*., unpublished data), which included household surveys and participatory field work with rural dwellers and traditional healers. The shea tree is the multi-purpose useful tree species most commonly conserved in the agroforestry parklands of West Africa (Breman & Kessler, 1995; Boffa, 1999). Typically, 25–60 *V. paradoxa* trees are found per hectare (Schreckenberg, 1996). The shea seeds contain 20–50% fatty acids (Teklehaimanot, 2004) contributing to the local diet as principal cooking oil (*beurre de karité*, shea butter), whereas the fruit pulp is an excellent source of protein, calcium and sugar (Maranz *et al.*, 2004). The average annual consumption of shea butter in Sub-Saharan countries is estimated with 7–10 kg per person (Boffa, 1999; Dah-Dovonon & Gnangle, 2006). The international market demands for shea butter as a surrogate for coconut oil and cocoa butter in the chocolate industry as well as excipient of cosmetic and pharmaceutical products (INSAE, 2000).

Parkia biglobosa often accompanies the shea tree in parklands due to similar habitat requirements (Boffa, 1999), but is far less abundant: In central Benin, its density is 2–5 trees per hectare (Agbahungba & Depommier, 1989; Schreckenberg, 1996). One of the major uses of néré is as '*moutarde*', a local protein-rich condiment of its fermented seeds which is used to supplement sauces. In contrast to the shea tree, *P. biglobosa* has no relevance for the international market.

The fruits of *A. digitata* offer a vitamin C-rich fruit pulp (Gebauer *et al*., 2002) which is added to the local drink *l'eau blanche* and the local porridge *bouille*; the roasted seeds are greatly appreciated in sauces (Sidibé & Williams, 2002). The leaves of *A. digitata* are an important source of protein, minerals and vitamins, prepared as *sauce gluante de la brousse* (Yazzie *et al*., 1994). Beyond, the baobab is a key species in the indigenous spirituality and belief systems being tightly connected to healing procedures. While *A. digitata* is hardly found on fields and fallows, its density within the settlement area is given with 1–14 trees per hectare (Schumann *et al.*, 2010; Heubach *et al.*, unpublished data). Recently, the international market has become interested in baobab products – notably, since a recently published study noted that the baobab fruit pulp reveals a four time higher antioxidant activity compared to kiwi and apple pulps (Besco *et al*., 2007).

Furthermore, the European Union decided to allow dried fruit pulp for trade in Europe under the Novel Food Regulation in 2008 (Vassiliou, 2008).

NTFP data collection and monetary mapping

Traditional collectors of NTFPs are women. Consequently, firstly, we randomly selected 20 women from individual households in each of the three studied villages to gather data on extracted annual quantities of the harvested products from *V. paradoxa*, *A. digitata* and *P. biglobosa*. Secondly, the individually harvested trees were recorded by a GPS (Garmin 60CSx). The quantities were reported in locally used measuring units (e.g., *bassine, sac de 100 kilograms*). Thirdly, we observed current market prices of the respective products' quantities on each village's local market. Thus, we could calculate the annual monetary benefits that are derived from NTFPs for each woman. Current market prices were reported in CFA-Franc and converted to US Dollar (exchange rate August 2011). The structured interviews as well as the market surveys took place in June 2009 (Papatia), September 2010 (Sampéto) and February 2011 (Niangou), in collaboration with local assistants. Since opportunity costs of NTFP extraction are low (no labour alternatives, no high-capital equipment required), labour was not deducted from gross benefits. That is, net income (per woman) from these products equals their gross benefits. Prices are not inflation-adjusted since prices for locally sold NTFPs occur to be very conservative.

We chose a 0.1° resolution for mapping the economic values, in accordance with the resolution of the spatial probability projections from the NBMs. To describe the direct use values (Torras, 2000) of the grid cells that cover the surroundings of the studied villages, we calculated mean monetary values (n=20) over the respective women. The averaging over 20 women is a conservative estimate, as women with no income in the questioned year (due to pregnancy or diseases) were included, following the random sampling design. These values were then assigned to all grid cells sharing the same phytogeographic districts (benefit transfer) using ArcGIS 10 (http://www.esri-germany.de/). Used phytogeographic districts (i.e., plant species composition) represent an optimal generalisation basis, because many interacting factors such as climate, geology, type of soil, land form and historical factors are included (Adomou, 2005). Finally, this average monetary estimate was multiplied with the number of women that live within a grid cell. Detailed data on population density (gender aspect, different age classes) were derived from the INSAE (2008). As the human population data were based on commune-level, they were transferred to a grid at our target resolution of 0.1°. Unmarried and old women do not actively collect NTFPs (Heubach *et al*., unpublished data). Therefore, we considered only women aged between 15 and 79 years in our analysis. Furthermore, we excluded four grid cells from the analysis which contained the biggest cities in Northern Benin, to avoid unrealistic high economic values from NTFPs in urbanised areas.

Additionally we calculated economic values on a per-hectare basis and per woman (mean, n=60) to better contextualise our results. Therefore, we related the reported monetary values from each woman to the respective areas where the women actively collected NTFPs. The areas were derived by calculating convex hulls (De Berg *et al.*, 2008) from the coordinates of the harvested trees. The analysis was performed using the R-package 'spatstat' (Baddeley & Turner, 2005).

Niche-based modelling

Species records

Species occurrence points of *A. digitata*, *P. biglobosa* and *V. paradoxa* were taken from various databases that cover Benin, Burkina Faso and Côte d'Ivoire. It is also important to consider species occurrence points outside of the study area, where the environmental conditions differ, to fully capture the environmental niche of the species. We used data from the West African Vegetation database (Janßen *et al*., 2011), the SIG-IVOIRE database (Chatelain *et al*., 2011), herbarium records from the Herbarium Senckenbergianum (FR; http://sesam.senckenberg.de/), the Ouagadougou University Herbarium (OUA) and personal field surveys conducted in Benin and Burkina Faso (2009). The species occurrence points were aggregated within grid cells of a 0.1° resolution, resulting in 122 (*A. digitata*), 127 (*P. biglobosa*) and 192 (*V. paradoxa*) grid cells with species presences.

Environmental coverages

We focused on two climatic parameters and one land use predictor. The drought index (DI) is a proxy for the water availability, which is the most important climatic factor in this region (Scholes, 1997) and largely explains the spatial distribution patterns of the focal species. The DI is defined as the ratio of annual mean precipitation to potential evapotranspiration (PET). While the first parameter was taken from the WorldClim database (Hijmans *et al*., 2005; http://www.wordclim.org), the latter one was calculated following Thornthwaite (1948). The minimum temperature of the coldest month (T_{min}) was included as 15.5° C (T_{min}) is an important lower threshold for the survival of tropical trees (Sitch *et al*., 2003).

Extremely high variability is given for future precipitation projections based on different GCMs, causing a remarkable uncertainty (Scheiter & Higgins, 2009; Heubes *et al.*, 2011). Extracting the information that describes a central tendency of different simulations provides an alternative to deal with this kind of variability (Thuiller, 2004; Araújo *et al.*, 2005; Araújo & New, 2007). Therefore, we ran a 'principal component analysis' (PCA) on the future (2050, SRES A2 scenario) annual mean precipitation projections, which is used as part of the drought index, from 17 different GCMs (cf. Heubes *et al.*, 2011). The precipitation projections from Miroc3.2$_{medres}$ (Center for Climate System Research, Japan) were most strongly correlated with the first PCA axis and can, thus, be considered as a consensus projection (Thuiller, 2004; Araújo *et al.*, 2005). Consequently, we used the future climate projections (2050) from Miroc3.2$_{medres}$ (Ramirez & Jarvis, 2008) for further analysis at our target resolution of 0.1°. We chose the IPCC SRES A2 scenario, which assumes intermediate levels of CO_2 emissions and an intermediate increase in temperature. We recognize that other climate models and storylines yield predictions that differ in their specifics in view of climate change, however, it is beyond the scope of the study to consider multiple scenarios of future climate.

The land use simulations were generated by LandSHIFT (Schaldach *et al*., 2011), a dynamic and spatially explicit land use and land cover model. LandSHIFT was specifically adopted for West Africa and runs with a spatial resolution of ~0.01°. The study area is primarily covered by the land use categories 'cropland (> 50% cover)' and 'deciduous woodland'. In this study, 'cropland (> 50% cover)' was renamed as 'parkland' to better describe the agricultural system, which is characterised by the deliberate retention of trees on fields. The climate data to generate the land use simulations were taken from Miroc3.2$_{medres}$ in accordance with the climate data used for the NBMs. LandSHIFT was run with the 'market first' scenario from the UNEP Global Environmental Outlook-4 (Rothman *et al.*, 2007), which roughly corresponds to the IPCC A2 storyline. We assumed no technological change, as crop yields have been stagnant during the past few decades (Norris *et al.* 2010). The spatial projections of parkland were aggregated to the target resolution ('nearest neighbour') and used as a predictor in the NBMs, as the three key species are tightly linked to this land use unit.

Algorithm

Three familiar modelling techniques from regression methods, machine learning methods and classification methods, which are implemented in the BIOMOD package (Thuiller *et al.*, 2009), were used to model species distributions: 1) generalized additive models (GAM) with cubic-smooth splines (polynomial of degree 3), 2) generalized boosting models (GBMs) with a maximum of 3000 trees fitted, and 3) flexible discriminant analysis (FDA). Pseudo-absences were randomly selected (n=1000) in Côte d'Ivoire, Burkina Faso and Benin. To evaluate the model performances, the data were split into training (30%) and testing data (70%). Models were calibrated on the training data, while threshold independent area under the receiver operating characteristic curve (AUC) values (Fielding & Bell, 1997) were calculated on the test data. We applied a 3-fold cross-validation to increase the robustness. Final accuracy of the consensus projections were assessed using receiver operating characteristic (ROC) curves (e.g. Thuiller *et al.*, 2009). To maintain a maximum of information, we considered the probability values of the models rather than transforming these into presence and absence information. The average probabilities across the three model simulations were used for subsequent analysis. All statistical analysis and modelling was carried out using the free software environment R, v. 2.13.1 (R Development Core Team, 2011).

Calculating future monetary gain and loss

To calculate future monetary values per grid cell, we linked the monetary values derived from current NFTP collection with the current standardised occurrence probabilities of the three target species (Fig. 1). The latter were generated by the NBMs. We then used this relation, together with the future NBM generated occurrence probabilities of the plant species, to derive the future monetary values (Fig. 1). Thus, we assume that higher occurrence probabilities would result in higher NTFP quantities, and therewith in higher monetary values (and vice versa). The change in monetary value due to predicted climate and land use change then equals the change in marginal value.

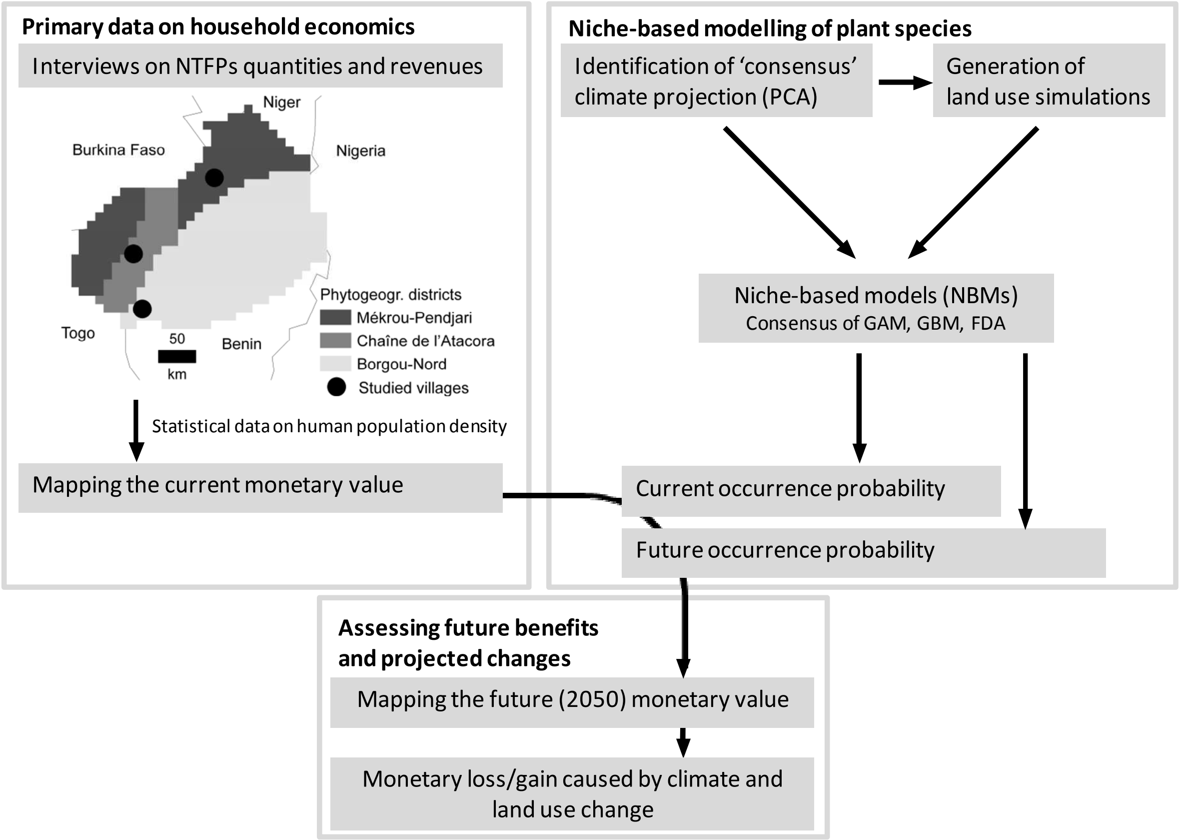

Figure 1 Schematic of generating monetary ecosystem service values from NTFPs (left), the niche-based modelling procedure (right) and the linkage of both parts, in order to generate future (2050) monetary gain/loss (bottom).

RESULTS AND DISCUSSION

The current economic relevance of the three species

The majority of interviewed women collected fruits of *V. paradoxa* and *P. biglobosa* as well as leaves of *A. digitata*. Only few respondents in Papatia stated to gather baobab fruits. Our results show that the monetary value flows differ between the three savanna species (Fig. 2). Annual monetary benefits increased from *A. digitata* (9,514 ± 6,243 US$/ cell) over *P. biglobosa* (32,246 ± 16,526 US$/ cell) to *V. paradoxa* (54,111 ± 28,126 US$/ cell, Fig. 2). The differences correspond to the per-hectare values, extracted per year and woman: *A. digitata* is the least important species with 0.3 US$/ha. Higher annual benefits are obtained from *P. biglobosa* (~2 US$/ha), while the highest value is found for *V. paradoxa* (6 US$/ha). We report median values, as there was considerable variability among the women. Note that the per-grid values include all collecting women, while the per-hectare values refer to a single woman (median); the latter values were not derived by downscaling the grid values. Our findings can be also compared to the relative economic contributions of the three species to the total annual income of a rural household in Northern Benin as identified by Heubach *et al*. (unpublished data): In Papatia, the average income share of *A. digitata* was 2%, while *P. biglobosa* contributes with 10% and *V. paradoxa* even with 13% to the total income. The total NTFP-income accounted for 39% of the annual household income, which represented the second largest income share next to crop production (Heubach *et al*., 2011). It was also found, that the majority of collected NTFPs is sold on local markets: On average, 89% of collected shea nuts, 88% of néré seeds and 73% of baobab fruit powder are sold to other rural dwellers or middlemen on local markets (Heubach *et al*., unpublished data)

Summed up for all three species, the per-hectare values (ca. US$ 8/ha) range at the bottom level compared with studies from Central and Latin America. Here, actual per-hectare returns from extracted forest / woodland products ranged between US$ 9–17 (Gram, 2001), US$ 18–24 (Godoy *et al.*, 2000) and US$ 7–35 (Shone & Caviglia-Harris, 2006), respectively. However, our figures only comprise three selected NTFP-providing species. Yet, as adequate studies for African tree species are largely missing, our data fill an important knowledge gap concerning NTFP-benefits.

As stated in the introduction, the seeds of *V. paradoxa* are not only exceedingly important at the local level, but are of constantly rising international interest. In 2006, the shea nut (botanically a berry) was the third most important export product of Benin after cotton and cashew nuts (Dah-Dovonon & Gnangle, 2006). Importing nations are predominantly European states (INSAE, 2000; Teklehaimanot, 2004). In Benin, export peaks were reached in the years 1993-1994 (15,000 tons), 2003-2004 (34,000 tons) and again in 2008-2009 (35,000 tons) (Dah-Dovonon & Gnangle, 2006; ProCGNR, 2011). In 2010, a ton of shea seeds was sold at US$ 300 (Businesstimes, 2010). Interestingly, we found similar prices at the investigated local markets. A ton of collected shea seeds was sold at 343 US$ on average. However, there are strong regional differences: In Sampéto a ton shea seeds was 160 US$/ton, in Niangou 395 US$/ton and 474 US$/ton in Papatia, which might be explained by the seasonal availability of the NTFPs as well as international and local market dynamics.

Comparing our results with the international market prices it becomes evident that these savanna products are not only important for the rural poor as major income source, but represent high value export goods.

Besides species-specific differences there is variation in the spatial distribution of monetary flows for each species (Fig. 2a-c). While the patterns in Figure 2a, c are largely explained by the number of NTFP-collecting women they also rise by the abiotic environment (Fig. 2b). The vertical structured area with low annual economic returns (1,300–10,000 US$/cell; Fig. 2b), represents the 'Chaîne de l'Atacora'. This mountain range exhibits poorly evolved soils, which resulted in low provision of NTFP quantities and respective monetary benefits. Regional differences become more evident, considering the average benefits per woman from the different studied sites: The lowest revenues are derived at the 'Chaîne de l'Atacora' from *P. biglobosa* and *V. paradoxa* (36 US$/yr and 54 US$/yr). Highest average benefits for all species are found in the 'Mékrou-Pendjari' district with 26 US$/yr (*A. digitata*), 70 US$/yr (*P. biglobosa*) and 121 US$/yr (*V. paradoxa*).

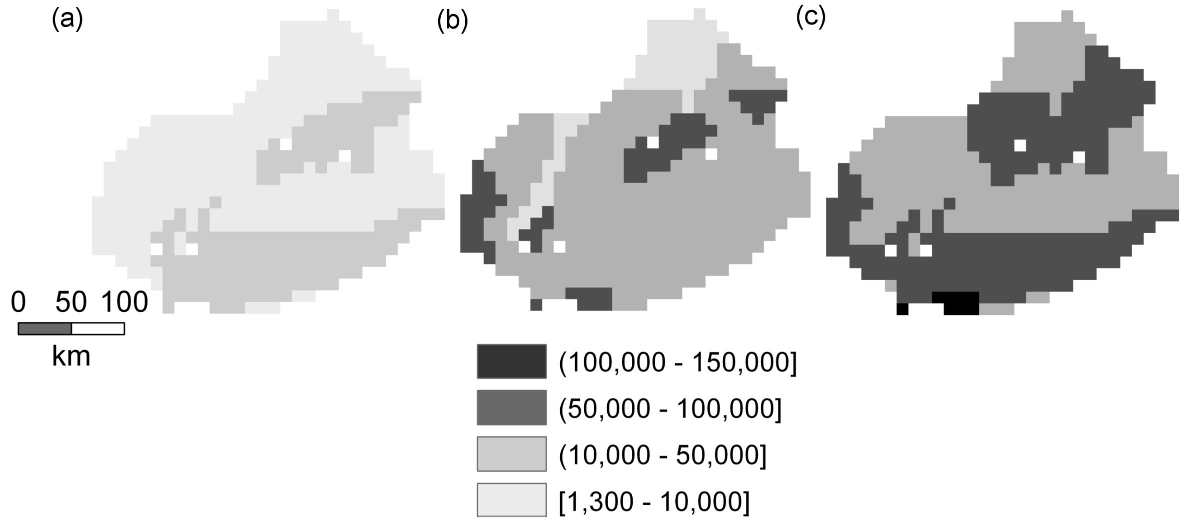

Figure 2 Economic value map (US$/yr) of three savanna species in Northern Benin at a 0.1° resolution (~10×10 km): (a) *Adansonia digitata*, (b) *Parkia biglobosa*, (c) *Vitellaria paradoxa.*

Predicted future changes

The model performances of the three species were good (cf. Swets, 1988) with AUC values of 0.88 (*A. digitata)*, 0.84 (*P. biglobosa)* and 0.86 (*V. paradoxa)* for the consensus projections. Projected climate and land use change (2050) have primarily negative effects on the value flows (Fig. 3). Our models project losses of 1–50% (Fig. 3a-c), however, the three species are affected differently. The highest loss is projected for *V. paradoxa* and this should particularly be cause for concern, because it is also the economically most important species (Fig. 2c). However, models projected spatially varying impacts with also positive effects (monetary gain) in the south-eastern parts for all species, and in the western regions for *A. digitata.* While the tree species, predominantly *A. digitata,* profit from decreasing moisture (reduced drought index), there is negative interference with the increasing temperature. The highest monetary gain is projected for *A. digitata* (1–20% monetary gain), whereas gains are less pronounced for *P. biglobosa* and *V. paradoxa*. The expected absolute values of changes range between -3,302–2,635 US$/cell (*A. digitata*), -28,530–9,727 US$/cell (*P. biglobosa*) and -52,980–19,320 US$/cell (*V. paradoxa*). However, the projected absolute values of change for 2050 should be considered with caution and rather be seen as a tendency, as we assumed constant human population development for this prediction. We refrained from calculating these changes on the basis of future (2050) population density as the knowledge of the tipping points after depletion and overexploitation of these agroforestry systems is very limited. Furthermore, the benefits from NTFPs can also decrease, as traditional crops are increasingly replaced by cash crops, such as cotton. Note that cotton cultivation requires a complete clearance of the parklands (Schreckenberg, 2004) and recently has been progressively promoted by the government. Even if farmers are encouraged to replant the focal species along the field boundaries, they would likely refuse to do so since exotic species like mango or cashew trees are economically more rewarding. Such aspects (intensification of land management) are not reflected in our approach, as NBMs can only use the information on the spatial extent of different land use types.

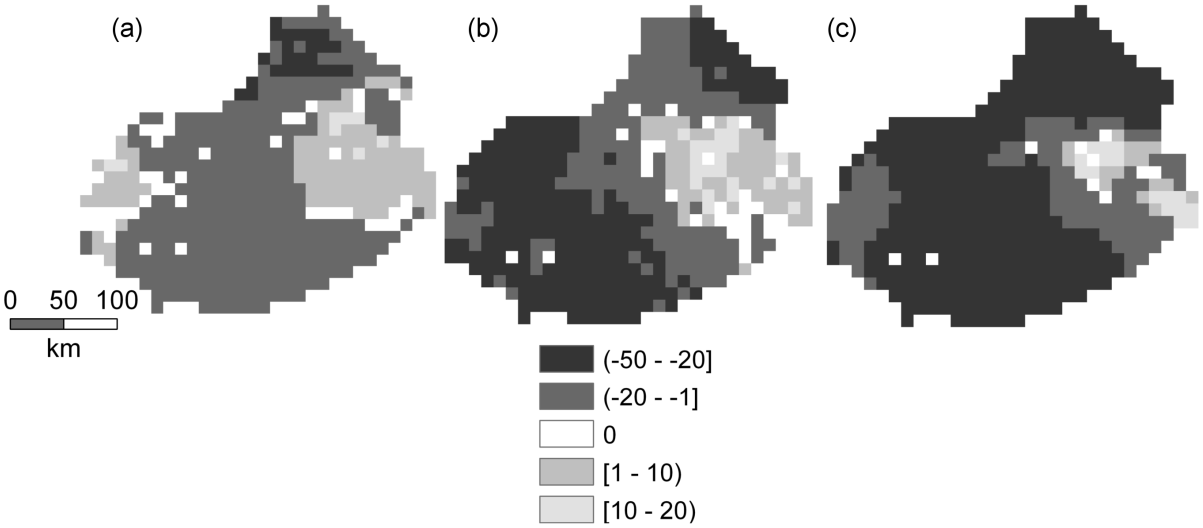

Figure 3 Projected future monetary gain and loss (%) for 2050 in Northern Benin, considering three savanna species: (a) *Adansonia digitata*, (b) *Parkia biglobosa*, and (c) *Vitellaria paradoxa.* Calculations are based on consensus projections of three different niche-based models (GAM, GBM, FDM). The projections include climate and land use change scenarios (2050), whereby the latter assumes technological stagnation.

Yet, as the predicted monetary changes (in percentage) correspond to the altered occurrence probabilities of the species, severe negative impacts on the livelihoods of the local poor are expected by 2050. The projected income loss from the NTFP-providing species will likely increase the pressure on remaining income opportunities, for instance, it could foster non-sustainable cotton production or reduce expenditures on household needs; the latter would inevitably reduce human well-being.

Local elasticity for NTFP-providing species

Since income alternatives, in particular for women, are practically absent in the study region, investigated communities face only little economic elasticity concerning the provision of NTFPs. Asked for possibilities to substitute currently as dietary supplement used NTFPs, women from Papatia (n = 200, Heubach, unpublished data) reported, that shea butter could be replaced by palm oil which is derived from the native palm tree *Elaeis guineensis*. However, women noted that palm oil is far too expensive to be used on a daily basis, *E. guineensis* is less abundant than *V. paradoxa* and, in addition, is exclusively managed by men, i.e. women have to pay men for seed extraction. A second surrogate for shea butter could be peanut oil, that seems to be a slightly better alternative, especially because peanuts can be independently cultivated by women and oil processing is less labour and time intensive. Beyond that, peanuts are highly marketable. The seeds of *P. biglobosa* could be replaced by 12 other products as ingredient in sauces whereof the five most important surrogates were fish, Maggie (a manufactured condiment) or the field crops peanut, chillies, and onion. But all products are more expensive. Favoured to replace *'moutarde'* are also the seeds of *Ceiba pentandra*. In case of baobab fruits (7 substitutes), major surrogates are sesame and peanut, but also the seeds of the local species *Blighia sapida* were highly treasured. The baobab leaves (6 substitutes) are mainly replaced by lady's fingers or sesame, but also by the leaves of the native woody species *Vitex doniana*. However, before promoting these substitute-providing species, further research is needed to investigate their future performance in view of climate and land use change and in terms of sustainability.

Methodological limitations and uncertainty

Even though gathering primary data by interviews for the monetary mapping, we could not avoid 'benefit transfer' as our approach assumes equal value flows of the grid cells which share the same phytogeographic district. Thus, our approach might include a generalization error due to extrapolation (Costanza *et al.*, 2006; Plummer, 2009) leading to some areas being overestimated and others being understated. However, we used plant species composition (phytogeographic districts), which is an optimal generalisation basis as it includes many interacting factors such as climate, geology, type of soil, land form and historical factors (Adomou, 2005).

The pros and cons of niche-based modelling methods are not discussed here, as several studies have already highlighted their limitations and methodological uncertainties (e.g. Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006; Dormann, 2007). We rather focus on specific aspects that are related to this study. Our approach assumes that an increased species occurrence probability would result in higher monetary value flows (and vice versa). The assumption follows a rational logic: Higher habitat suitability (which is in fact modelled) increases the performance and vitality of species and, consequently, increases the fruit production (e.g., Glèlè Kakaï *et al.*, 2011) and benefits. However, the latter also depends on future market dynamics (see discussion below). Furthermore, our results are based on climate projections from the GCM Miroc3.2$_{\text{medres.}}$ Although the common view from the climate modelling community is that no single climate model is superior, we used this GCM following the rational of consensus projections (Thuiller, 2004; Araújo *et al.*, 2005; Araújo & New, 2007). We think that this approach is better than arbitrarily selecting GCMs, however, the climate uncertainty remains a major source of uncertainty in predictive modelling for this region (Heubes *et al.*, 2011).

There are also ecological and economical limitations inherent to our approach. That is, the fruit productivity of trees might differ inside the same district due to small-scale varying environmental conditions and, additionally, may alter between years (Gram, 2001). Moreover, the NTFP-providing trees may be inhomogeneously distributed within the parklands and abiotic factors such as lateritic soils may locally prevent the species to grow.

Even though the reported per-hectare yields are a result of a conservative calculation, including women who did not collect at all, there might be an overestimation of value flows, as we assume all women aged between 15–79 years to equally take part in NTFP extraction activities. Considering the economical factors we cannot fully exclude a recall bias (i.e. the respondents having problems to precisely remember the collected amounts of NTFPs), as annual per-hectare values are calculated on the basis of respondents' self-reported quantities. However, given the demonstrated socio-economic importance of NTFPs in rural household economics, we assume the data to be reliable.

More generally, we would like to address several issues of marginal values and discounting. That is, the change in monetary value due to predicted climate and land use change should equal the change in marginal value. In economic analysis marginal values are in general associated with unit changes of assets. The precondition is that each unit is homogenous and yields the same return which, in fact, does not hold true for our resources in question: as mentioned above, NTFP-providing trees are not equally distributed over the studied area and might not show the same productivity. Thus, the per-hectare values calculated in our study do not strictly reflect the range of real marginal values of each single hectare but an average value across all units (Costanza *et al.*, 2006). One possible attempt to elaborate on this issue is to gain more species-specific ecological data (abundance, productivity).

Whether to discount or not to discount long-term monetary values derived from ecosystem services is a matter of ongoing scientific and political debate and has not yet been concludingly answered yet (Newell & Pizer, 2003; Costanza *et al.*, 2006; Dasgupta, 2008; Sukhdev, 2008; Goklany, 2009). Assuming that future generations are better off than the present one, i.e. in a world of unbowed economic growth, discounting aims at determining the current value of a future cash flow from a particular commodity or asset or ecosystem service. Coherently, standard economic discounting hypothesizes that present gains are more valuable than those obtained in the future, if the net present value is equal or higher than the future value under the chosen discount rate. However, in terms of ecosystem service flows this assumption may be biased since the ongoing depletion of non-substitutable natural resources (i.e. natural capital) and biophysical infrastructure (i.e. ecosystem functions) is likely to increase ecosystem services' scarcity and, accordingly, their economic value. Furthermore, applying a positive discount rate might fortify decision-making that disproportionally prefers short-term benefits from ecosystem services while coevally postponing involved costs (e.g. restoration costs for damaged ecosystems. i.e. externalities) into the future. Certainly, in view of intergenerational equity this should be out of the question. Thus, the consideration to apply even a negative discount rate on ecosystem service flows has emerged in the debate recently (Stern, 2006). With regard to this controversial discussion, we decided to apply a zero discount rate in this study.

CONCLUSIONS

In this study we present a novel approach of assessing the impact of climate and land use change on provisioning ecosystem services. Therefore, we related primary data on household economics with niche-based models. We demonstrated the transfer of the economic data to specific areas, to map the monetary value flows of three woody species in Northern Benin. Thus, we shed light on their remarkable socio-economic importance for the local poor. Based on current monetary maps of these NTFP-providing species we calculated future flows of ecosystem service values in order to estimate possible economic gains and losses, respectively.

We showed that the projected changes will preponderantly negatively impact the economic returns of the three socio-economically important woody species in Northern Benin, *V. paradoxa*, *P. biglobosa,* and *A. digitata* by 2050. Our results further indicate that in particular the benefits obtained from *V. paradoxa* are threatened and should raise major concern with respect to current management policies. Possible pathways to cope with the reduced species occurrence probabilities are, on the one hand, to foster plantations of shea tree, néré and baobab in appropriate regions (e.g. in the eastern part of the ‘Borgou-Nord’ district) in order to safe-guard local livelihoods and maintain export activities. On the other hand, substitute-providing species could be promoted after proper previous analysis of their performances under projected climate and land use change as well as the consideration of sustainability criteria. Finally, more effort is needed to create alternative income opportunities, particularly for women.

To further increase our understanding of this complex socio-ecological system, higher sample sizes of interviewed women together with long-term observation of monetary values are needed as well as gathering data on the ecological performance of the investigated species (productivity, abundance). On the other hand there is a strong need to improve and harmonize climate models to reduce the inter-model variability.

In this study, we present a valuable first benchmark for local decision-makers to economically compare different land-use options today and adjust existing management strategies.

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Chapter 5

Synthesis

The thesis integrates different model simulations to investigate the impacts of future environmental changes on large-scale vegetation patterns, aspects of biodiversity and ecosystem services in West Africa. All studies have in common to include proxies describing the human impact which is often ignored in climate impact studies. Thus, the thesis took heed of the call for investigating the effects of both drivers, climate change and the human impact (de Chazal & Rounsevell, 2009). While climate change had spatially varying impacts (positive and negative effects) on the vegetation dynamics and plant diversity, I predominantly found negative effects resulting from human pressure, described by increasing population density and land transformation (chapter 2 and 3, respectively). Regional contrasting impacts of environmental change were also found considering the provisioning ecosystem services in Northern Benin (chapter 4). However, only the synergistic effects of climate and land use were investigated in the latter study. Niche-based models were used for all the simulations (chapter 2-4), which commonly focus on the species level only (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). In this thesis I demonstrated the suitability and application of these models, ranging from regional scales to local scales, addressing different issues concerning the West African biome distributions and tree cover (chapter 2), plant diversity in Burkina Faso (chapter 3) and provisioning ecosystem services in Northern Benin (chapter 4).

Considering the current vegetation dynamics in West Africa, different results have been reported (Gonzalez, 2001; Rasmussen *et al.*, 2001; Hickler *et al.*, 2005; Wezel & Lykke, 2006; Wittig *et al.*, 2007, Maranz, 2009). At the same time the public debate is dominated by desertification (Foley *et al.,* 2003). In the context of future climatic changes, the results of this thesis point to a ‘greening’ trend in West Africa, whereby a plethora of climate models were taken into account (chapter 2). The biomes in West Africa were shown to shift to the north, for example replacing parts of the Sahara desert by grasslands. However, the simulation of West African tree cover provided interesting insights, e.g. divergent trends within the evergreen biome. Furthermore, the study demonstrated that an increased human population density causes forest degradation, which might trigger desertification processes. Consequently, it is essential to incorporate human impact in order to generate realistic future predictions on vegetation cover. This thesis shows that high climate uncertainty hampers concrete statements on vegetation change in some interior parts of West Africa. More certainty is given for the declining forest cover and therewith timber availability at the coastal areas of West Africa. This should be cause for concern, as timber is a major natural resource for the local human population. The results fill an important gap of knowledge in terms of understanding the potential impacts of future climate change and the impact of human activities on vegetation. However, further enhanced simulations with process-based DGVMs are necessary to get a realistic estimate of the delayed response of the vegetation to altered climate conditions. The response might be slower than suggested by the models used in this thesis (see also Woodward *et al.*, 2004) and might explain the only marginal future vegetation change, found by Hély *et al.* (2006). However, the authors neglected temperature effects, which have major impacts on vegetation in this region (Delire *et al.*, 2008). Furthermore, data on grazing intensity would strongly improve the model simulations which could be integrated as predictor variables. The difficulty in this regard is to get reliable data on flock sizes and to model future population dynamics, respectively. Generally, future model simulations might also include scenarios of decision making and management practices.

An important aspect that hampers climate impact research in Africa is the high future climate uncertainty, caused by a remarkable inter-model variability of the general circulation models (GCMs). The reasons for the discrepancies among underlying GCM projections still remain unclear, but the next IPCC report with a focus on Africa is expected to shed light on this. Currently, uncertainty is particularly high for the future precipitation amounts. This thesis suggests a framework on how to deal with this kind of uncertainty, while maintaining all available climate information (chapter 2). Additionally, the climate uncertainty was explored to identify regions with high and low informative value with regard to the future trend. Plant diversity and provisioning ecosystem services (chapter 3 & 4) were investigated, using a climate model from the Center for Climate System Research in Japan (Miroc3.2$_{medres}$) which also describes the central precipitation tendency and, thus, can be considered as a consensus projection. To further increase the understanding of possible future climate impacts and to show the entire range of changes, the simulations of chapter 3 and 4 might be extended in terms of using all available climate models and socio-economic scenarios. Chapter 3 focused on potential future changes in plant diversity with a specific focus on the generation and integration of land use simulations to improve the predictions. Therefore, not only novel land use simulations were generated with the LandSHIFT model in cooperation with the CESR (Kassel, Germany), but also the species distribution data were improved. Additional species inventories were conducted in the western parts of Burkina Faso during this thesis to fill species distribution data gaps, thereby more comprehensively capturing the environmental niche of the species. The results from this study showed that the flora of Burkina Faso will be primarily negatively impacted by future climate and land use changes. However, contrasting latitudinal patterns of impacts arose, which have not been detected by global and continental-scale studies so far (Mcclean *et al.*, 2005; Sommer *et al.*, 2010). While climate change will cause severe species loss in the more humid regions in Southern Burkina Faso, an increase of species richness was projected in the Sahel. However, there is negative interference with future land use change, which might suppress the increase to the current diversity level. The modelling approach of this study resulted in an improved representation of the current diversity gradient in Burkina Faso (Schmidt *et al.*, 2005; Da, 2010). Similarly, Da (2010) suggests that future climate change will cause severe loss of suitable habitats for many plant species, however, his results differed with respect to the considered GCM. Overall, this study highlights the impact and interplay of future climate and land use change on plant diversity along a broad bioclimatic gradient in West Africa. The results suggest that plant diversity in dry and humid regions of the tropics might generally respond differently to climate and land use changes. This needs to be proven, e.g. in other African regions. Another major and unexpected result of this thesis, which contradicts to other studies (e.g. Sala *et al.*, 2000), is that climate change is a more important threat to the plant diversity than land use change in Burkina Faso. This is under the assumption of technological stagnation in the agricultural sector (chapter 3). The finding is underpinned by results from Schumann (2011) who showed that land use per se does not lead to species loss but rather depends on the maintenance of traditional management strategies. Increasingly, these strategies for croplands are being replaced by a dynamic, market-oriented agriculture dominated by cash crops (e.g. cotton and cashew) resulting in agricultural intensification (Brink & Eva, 2009). The approach in chapter 3 and 4 cannot account for these effects. For a better understanding of an intensified agriculture impacting on biodiversity patterns, further studies are needed. Emphasis should be given to the improvement of species distribution data, particularly in other West African countries, including information on species absences which are currently not available. Land use simulations must be further developed by including land cover typologies with different management intensities not only crop types; these typologies should be separately represented in land use models (this thesis used 'cropland' only) and subsequently incorporated into the SDMs. To further explore the species performances in relation to environmental conditions (response curves), additional models might provide valuable insights. Indeed, the algorithm that was used in chapter 2 (one-class support vector machines) represents an up-to-date algorithm for presence-only data, which is highly suitable to investigate the impacts of climate and land use change on plant diversity (Drake *et al.*, 2006). However, the black-box character of this method does not allow for the investigation of response curves. Algorithms (e.g. maximum entropy) could add further details on the ecological behaviour of the plant species. More generally, species distribution models would benefit from including more process-based components. This thesis implicitly included an important process, which has rarely been done so far (but see Rickebusch *et al.*, 2008): the response of plants to elevated atmospheric CO_2 concentrations. This is, due to the incorporation of land use simulations from LandSHIFT, which account for CO_2 effects. However, more demographic processes might be included, a step towards hybrid-models (e.g. Cabral & Schurr, 2010). Therefore, more effort is needed to investigate the species' biology (e.g. describing seed dispersal, reproduction, mortality and local extinction).

Whether biological diversity itself, which was investigated in chapter 3, is an ecosystem service or not, was controversially discussed in the Millenium Assessment Report (MA, 2005). However, without doubt there are many plant species in West Africa, which are of major direct importance for the local people. Many savanna species like the shea tree, the locust bean and the baobab provide non-timber forest products (NTFPs), which are important provisioning ecosystem services as they provide for example fruits and seeds. This thesis explores the economic benefits that are derived from these savanna species and investigates the potential impacts of future climate and land use change on these benefits in Northern Benin. Therefore a novel approach was developed to relate primary data on household economics to specific areas and to link these data to simulations that were generated with niche-based models. The results point to the remarkable economic benefits, that the local communities derive from the three savanna species and highlight the strong dependencies on NTFPs. Furthermore, the growing importance of the species' products on the international markets is emphasized in this study. Even on the local scale, the future simulations showed spatially varying impacts of environmental change. In particular the baobab showed higher economic benefits in some regions. However, the most valuable species, *V. paradoxa* and *P. biglobosa* will be mainly negatively impacted, resulting in a loss of the economic returns. Thus, it is suggested to promote alternative species which might substitute important NFTPs. However, this includes a previous investigation of the future performances of the substitute providing species, with regard to climate and land use change and their sustainable use. Overall, this study makes the economic benefits from savanna species visible and increases our understanding of the impacts of climate and land use change on these benefits. This novel approach might be considered as a pilot study and gives a first estimate only, however, it helps local policy-makers to design adaptive management strategies. These strategies must focus on creating alternative income opportunities, in particular for women, who are responsible for collecting the NTFPs. To increase the robustness of the results and to consolidate the suggested management strategies, more interviews in different regions of Northern Benin are needed. Furthermore, the niche-based models might be improved and run with additional climate scenarios, as mentioned above. Another interesting point that needs to be examined is the direct relation of the species' occurrence probabilities and the economic returns from the species' NTFPs, which is assumed in our approach. A higher vitality of species might produce an increasing fruit production and therewith economic benefits, however, there is little empirical evidence on this phenomenon in West Africa (but see Glèlè Kakaï *et al.*, 2011). Further research is needed, to explore this relation. Finally, this approach might be geographically extended to Benin and other West African countries and extended by other socio-economic important plant species to comprehensively study the effects of climate and land use change on well-being of the rural communities.

Overall, this thesis improves our understanding of the impacts of climate and land use change on West African vegetation patterns, biome distributions, plant diversity and provisioning ecosystem services. It is the first time that the last two aspects are investigated in West Africa in view of climate and land use change. Further research must particularly focus on improving the primary data (e.g. species distribution data in undersampled regions, see also García Márquez, 2010), reducing the GCM-based climate uncertainty and investigating the effects of an intensified agriculture on biodiversity and ecosystem services.

Chapter 6

Summary

Global climate change and land use change will not only alter entire ecosystems and biodiversity patterns, but also the supply of ecosystem services. A better understanding of the consequences is particularly needed in under-investigated regions, such as West Africa. The projected environmental changes suggest negative impacts on nature, thus representing a threat to the human well-being. However, many effects caused by climate and land use change are poorly understood so far.

Thus, the main objective of this thesis was to investigate the impact of climate and land use change on vegetation patterns, plant diversity and important provisioning ecosystem services in West Africa. The three different aspects are separately explored and build the chapters of this thesis. The findings help to improve our understanding of the effects of environmental change on ecosystems and human well-being.

In the first study, the main objectives were to model trends and the extent of future biome shifts in West Africa that may occur by 2050. Also, I modelled a trend in West African tree cover change, while accounting for human impact. Additionally, uncertainty in future climate projections was evaluated to identify regions with reliable trends and regions where the impacts remain uncertain. The potential future spatial distributions of desert, grassland, savanna, deciduous and evergreen forest were modelled in West Africa, using six bioclimatic models. Future tree cover change was analysed with generalized additive models (GAMs). I used climate data from 17 general circulation models (GCMs) and included human population density and fire intensity to model tree cover. Consensus projections were derived via weighted averages to: 1) reduce inter-model variability, and 2) describe trends extracted from different GCM projections. The strongest predicted effect of climate change was on desert and grasslands, where the bioclimatic envelope of grassland is projected to expand into the Sahara desert by an area of 2 million km^2. While savannas are predicted to contract in the south (by $54 \pm 22 \times 10^4$ km^2), deciduous and evergreen forest biomes are expected to expand ($64 \pm 13 \times 10^4$ km^2 and $77 \pm 26 \times 10^4$ km^2). However, uncertainty due to different GCMs was particularly high for the grassland and the evergreen forest biome shift. Increasing tree cover (1–10%) was projected for large parts of Benin, Burkina Faso, Côte

d'Ivoire, Ghana and Togo, but a decrease was projected for coastal areas (1–20%). Furthermore, human impact negatively affected tree cover and partly changed the direction of the projected climate-driven tendency from increase to decrease. Considering climate change alone, the model results of potential vegetation (biomes) showed a 'greening' trend by 2050. However, the modelled effects of human impact suggest future forest degradation. Thus, it is essential to consider both climate change and human impact in order to generate realistic future projections on woody cover.

The second study focused on the impact and the interplay of future (2050) climate and land use change on the plant diversity of the West African country Burkina Faso. Synergistic forecasts for this country are lacking to date. Burkina Faso covers a broad bioclimatic gradient which causes a similar gradient in plant diversity. Thus, the impact of climate and land use change can be investigated in regions with different levels of species richness. The LandSHIFT model from the Centre of Environmental System research CESR (Kassel, Germany) was adapted for this study to derive novel regional, spatially explicit future (2050) land use simulations for Burkina Faso. Additionally, the simulations include different assumptions on the technological developments in the agricultural sector. One-class support vector machines (SVMs), a machine learning method, were performed with these land use simulations together with current and future (2050) climate projections at a 0.1° resolution (cell: ~ 10 × 10 km). The modelling results showed that the flora of Burkina Faso will be primarily negatively impacted by future climate and land use changes. The species richness will be significantly reduced by 2050 ($P < 0.001$, paired Wilcoxon signed-rank test). However, contrasting latitudinal patterns were found. Although climate change is predicted to cause species loss in the more humid regions in Southern Burkina Faso (~ 200 species per cell), the model projects an increase of species richness in the Sahel. However, land use change is expected to suppress this increase to the current species diversity level, depending on the technological developments. Climate change is a more important threat to the plant diversity than land use change under the assumption of technological stagnation in the agricultural sector.

Overall, the study highlights the impact and interplay of future climate and land use change on plant diversity along a broad bioclimatic gradient in West Africa. Furthermore, the results suggest that plant diversity in dry and humid regions of the tropics might generally respond differently to climate and land use change. This pattern has not been detected by global studies so far.

Several of the plant species in West Africa significantly contribute to the livelihoods of the population. The plants provide so-called non-timber forest products (NTFPs), which are important provisioning ecosystem services. However, these services are also threatened by environmental change. Thus, the third study aimed at developing a novel approach to assess the impacts of climate and land use change on the economic benefits derived from NTFPs. This project was carried out in cooperation with Katja Heubach (BiK-F) who provided data on household economics. These data include 60 interviews that were conducted in Northern Benin on annual quantities and revenues of collected NTFPs from the three most important savanna tree species: *Adansonia digitata*, *Parkia biglobosa* and *Vitellaria paradoxa*. The current market prices of the NTFPs were derived from respective local markets. To assess current and future (2050) occurrence probabilities of the three species, I calibrated niche-based models with climate data (from Miroc3.2$_{\text{medres}}$) and land use data (LandSHIFT) at a 0.1° resolution (cell: ~ 10 × 10 km). Land use simulations were taken from the previous study on plant diversity. Three different niche-based models were used: 1) generalized additive models (regression method), 2) generalized boosting models (machine learning method), and 3) flexible discriminant analysis (classification method). The three model simulations were averaged (ensemble forecasting) to increase the robustness of the predictions. To assess future economic gains and losses, respectively, the modelled species' occurrence probabilities were linked with the spatially assigned monetary values. Highest current annual benefits are obtained from *V. paradoxa* (54,111 ± 28,126 US$/cell), followed by *P. biglobosa* (32,246 ± 16,526 US$/cell) and *A. digitata* (9,514 ± 6,243 US$/cell). However, in the prediction large areas will lose up to 50% of their current economic value by 2050. *Vitellaria paradoxa* and *Parkia biglobosa,* which currently reveal the highest economic benefits, are heavily affected. *Adansonia digitata* is negatively affected less strongly by environmental change and might regionally even supply increasing economic benefits, in particular in the west and east of the investigation area. We conclude that adaptive strategies are needed to create alternative income opportunities, in particular for women that are responsible for collecting the NTFPs. The findings provide a benchmark for local policy-makers to economically compare different land use options and adjust existing management strategies for the near future.

Overall, this thesis improves our understanding of the impacts of climate and land use changes on West African vegetation patterns, plant diversity and provisioning ecosystem services. Climate change had spatially varying impacts (positive and negative effects) on the vegetation cover and plant diversity, while predominantly negative effects resulted from human pressure. Regional contrasting impacts of environmental change were also found considering the provisioning ecosystem services.

Zusammenfassung

Die globalen Klima- und Landnutzungsveränderungen im 21. Jahrhundert werden die Ökosysteme der Erde und die damit zusammenhängenden Biodiversitätsmuster, Ökosystemdienstleistungen und somit auch das menschliche Wohlergehen grundlegend beeinflussen.

Aus der Vergangenheit sind Massenaussterbeereignisse bekannt, die durch globale Klimaveränderungen hervorgerufen wurden. Temperatur- und Niederschlagsveränderungen im Quartär haben nachweislich zu enormen Nord-Süd-Verschiebungen gesamter Biome geführt.

Seit Beginn der Industrialisierung hat der anthropogen verursachte Klimawandel bereits nachweisbare Effekte auf Biome, Biodiversität und Ökosystemdienstleistungen gezeigt. Vielfach verschieben sich gesamte Vegetationseinheiten und damit auch Habitate für Pflanzen und Tiere entlang von Breitengraden und Höhengradienten. Dabei wirken sich die klimatischen Veränderungen besonders stark auf die gemäßigten Breiten und die polaren bzw. alpinen Regionen aus. Im Gegensatz zu den Tropen scheint in diesen Regionen der Landnutzungswandel eine weniger wichtige Rolle zu spielen. Die tropischen Regionen zeichnen sich durch eine enorme Artenvielfalt aus, aber großenteils auch durch Armut in der Bevölkerung. Das hohe Bevölkerungswachstum und die teilweise rasante ökonomische Entwicklung tropischer Länder führt zu einer tiefgreifenden Umwandlung der natürlichen Ökosysteme und damit zu einer Bedrohung der Biodiversität und Ökosystemdienstleistungen.

Die Zusammenhänge und Auswirkungen sind allerdings oft unzureichend verstanden, vor allem die tropischen Regionen betreffend. Die Mehrzahl der Studien über die Auswirkungen des Klimawandels beziehen sich auf die Industrienationen und dominieren gegenüber Studien bezüglich der Auswirkungen von Landnutzungswandel. Des Weiteren werden die Konsequenzen von Klima- und Landnutzungswandel oft nur singulär untersucht und nicht in ihrem Zusammenwirken. Dabei ist bekannt, dass es durch die Kombination der beiden Faktoren zu unerwarteten, synergistischen Effekten kommen kann. Ein besseres Verständnis der Auswirkungen von Klima- und Landnutzungswandel ist deshalb vor allem in unzureichend untersuchten Gebieten wie Westafrika notwendig.

Das Hauptziel dieser Arbeit ist daher, den Einfluss von Klima- und Landnutzungsveränderungen auf großskalige Vegetationsmuster, Pflanzenvielfalt und wichtige Ökosystemdienstleistungen in Westafrika zu untersuchen. Die drei verschiedenen Aspekte wurden in separaten Studien behandelt und bilden eigenständige Kapitel in dieser Arbeit. Die Erkenntnisse verbessern das Verständnis bezüglich der Auswirkungen von Umweltveränderungen auf Ökosysteme und schließlich auf das menschliche Wohlergehen.

In der ersten Studie wurden - unter Verwendung statistischer Modelle - Prognosen, über die zukünftige Verbreitung westafrikanischer Biome im Jahr 2050 erstellt. Des Weiteren wurden Trends über potentielle Veränderungen der Baumbedeckung in Westafrika unter Berücksichtigung des menschlichen Einflusses ermittelt. Zusätzlich wurden die Unsicherheiten analysiert, die mit den Klimaprojektionen in Verbindung stehen, um Aussagen über verlässliche Trends treffen zu können. Um potentielle, zukünftige Biomveränderungen quantifizieren zu können, kamen sechs verschiedene Nischenmodelle zur Anwendung. Veränderungen in der Baumbedeckung wurden unter Verwendung der Regressionsmethode ‘generalized additive models’ (GAMs) untersucht. Die Studie berücksichtigt 17 verschiedene Klimamodelle. Um die Veränderungen in der Baumbedeckung besser abbilden zu können, wurden die menschliche Bevölkerungsdichte und die Feuerintensität in die Modelle integriert. Konsensusprojektionen dienten einer Reduzierung der interspezifischen Modellvariabilität, aber auch der Beschreibung von Trends, die sich aus den verschiedenen Klimamodellen ergaben. Die Konsensusprojektionen wurden über gewichtete Mittelwerte gebildet. Deren Anwendung ist neu im Bereich der Ökologie und Biogeographie. Bisherige Untersuchungen zeigten, dass mit Konsensusprojektionen robustere Vorhersagen getroffen werden können. Bei den Ergebnissen wird deutlich, dass die Wüsten- und Graslandbiome am stärksten vom prognostizierten Klimawandel betroffen sind. Die bioklimatische Nische des Graslandes wird sich demnach um 2 Millionen km^2 nach Norden in das Wüstenbiom ausdehnen. Die Savannen werden im Süden an Fläche verlieren ($54 \pm 22 \times 10^4$ km^2), während sich laubwerfende Wälder und immergrüne, tropische Regenwälder ausdehnen ($64 \pm 13 \times 10^4$ km^2 bzw. $77 \pm 26 \times 10^4$ km^2). Die Variabilität der Klimaprojektionen führt allerdings zu großen Unsicherheiten, gerade in Bezug auf die Ausdehnung des Graslandes und der immergrünen Regenwälder.

Eine höhere Baumbedeckung im Jahr 2050 (1–10%) wurde für große Teile von Benin, Burkina Faso, Côte d'Ivoire, Ghana und Togo prognostiziert; für die Küstenregionen wurde eine Abnahme der Baumbedeckung projiziert (1–20%). Der Trend über die Abnahme der Baumbedeckung ist hierbei robuster als der Trend über die Zunahme. Außerdem konnte gezeigt werden, dass sich der menschliche Einfluss negativ auf die Baumbedeckung auswirkt. Dies beruht auf dem empirischen Zusammenhang, dass sich die menschliche Bevölkerungsdichte indirekt proportional zur Baumbedeckung verhält. Teilweise wurde durch den menschlichen Einfluss eine Umkehr des projizierten zukünftigen Trends in der Baumbedeckung beobachtet, von einer Zunahme (klimatischer Einfluss) zu einer Abnahme (klimatischer und menschlicher Einfluss). Besonders auffällig war dieser Effekt in großen Teilen Nigerias. Lässt man den direkten menschlichen Einfluss außer Acht und betrachtet lediglich den Effekt von Klimawandel auf die potentielle Vegetation (Biome), zeigt sich ein Trend zur Ergrünung bis zum Jahr 2050. Allerdings deuten die modellierten Effekte des menschlichen Einflusses auf eine Degradierung der Wälder hin. Dies ist häufig ein Auslöser für Erosion und beginnende Desertifikationsprozesse. Die Studie macht daher die Notwendigkeit deutlich, sowohl den Klimawandel als auch den menschlichen Einfluss und vor allem deren Zusammenwirken zu betrachten, um realistische Zukunftsprojektionen über künftige Baumbedeckung zu generieren.

Baumbedeckung korreliert allerdings nicht zwangsläufig mit Diversität. Deshalb wurde in der zweiten Studie untersucht, welche Einflüsse der künftige Klima- und Landnutzungswandel (2050) und das Zusammenwirken der beiden Faktoren auf die Pflanzenvielfalt haben. Dies wurde in dem westafrikanischen Land Burkina Faso untersucht, das sich besonders als Modellregion eignet, da es einen Großteil des westafrikanischen, bioklimatischen Gradienten aufweist. Außerdem besteht in diesem Land eine außerordentlich gute Datengrundlage bezüglich der Pflanzenverbreitung aufgrund langjähriger Kooperationen. Der bioklimatische Gradient spiegelt sich ebenfalls in der Pflanzenvielfalt wider, weshalb die Effekte von Klima- und Landnutzungswandel in Regionen mit unterschiedlicher Pflanzenvielfalt untersucht werden können. Derartige synergetische Effekte von Klima- und Landnutzungswandel wurden in diesem Land bisher noch nicht untersucht. Dies mag unter anderem am Mangel zukünftiger Landnutzungsszenarien liegen. Aus diesem Grund wurde das bestehende globale und kontinentale Landnutzungsmodell *LandSHIFT* vom *Centre of Environmental System*

Research (Kassel, Deutschland) speziell für diese Studie angepasst, um neue, räumlich explizite Landnutzungssimulationen in Burkina Faso und den Anrainerstaaten für die Gegenwart und die Zukunft (2050) zu generieren. Die Simulationen beinhalten zusätzlich zwei verschiedene Annahmen über die technische Entwicklung im landwirtschaftlichen Bereich: technologische Stagnation und eine Entwicklung gemäß des „markets-first“ Szenarios (GEO-4). Diese Landnutzungssimulationen dienten zusammen mit Klimadaten aus Gegenwart und Zukunft (2050) als Prädiktoren in *one-class support vector machines* (SVMs). Dies ist ein Algorithmus aus dem Bereich der *machine-learning methods*, der eine überdurchschnittliche Modellgüte aufweist. Die Simulationen wurden in einer Auflösung von 0.1° generiert. Die Ergebnisse zeigen, dass sich die Klima- und Landnutzungsveränderungen hauptsächlich negativ auf die Pflanzenvielfalt in Burkina Faso auswirken. Allerdings wurden, in Abhängigkeit des Breitengrades, divergierende Muster gefunden. Demnach wird der Klimawandel im humideren Süden des Landes zu einem großen Artenverlust führen (~200 Arten pro Gridzelle). Im Sahel dagegen wurde eine Erhöhung der Pflanzenvielfalt projiziert. Der Landnutzungswandel wirkt - in Abhängigkeit der sozio-ökonomischen Annahmen - diesem Trend allerdings entgegen, womit die Pflanzenvielfalt im Sahel auf dem heutigen Niveau verbleibt. Unter der Annahme einer technologischen Stagnation im landwirtschaftlichen Sektor zeigt der Klimawandel einen gravierenderen Effekt auf die Pflanzenvielfalt als der Landnutzungswandel. Ferner konnte in der Studie gezeigt werden, dass technologische Entwicklungen im landwirtschaftlichen Sektor zu einem geringeren Flächenverbrauch führen, da mehr Erträge pro Hektar erwirtschaftet werden können. Der geringere Flächenbedarf landwirtschaftlich genutzter Flächen wirkt sich positiv auf die Pflanzenvielfalt in Burkina Faso aus. Allerdings gehen mit dem technologischen Wandel auch Nutzungsveränderungen einher, wie z.B. erhöhter Mechanisierungsgrad, Einsatz von Bioziden, verkürzte Brachzeiten. Derartige Effekte konnten nicht berücksichtigt werden. Insgesamt wurde in dieser Studie, entlang eines starken bioklimatischen Gradienten in Westafrika, aufgezeigt wie sich Klima- und Landnutzungswandel einzeln und in Kombination auf die Pflanzenvielfalt auswirken. Die Ergebnisse deuten daraufhin, dass die Pflanzendiversität in trockenen und feuchten Gebieten der Tropen generell unterschiedlich auf Klima- und Landnutzungsveränderungen reagiert. Derartige Muster konnten auf dem afrikanischen Kontinent mit global-skaligen Studien bisher nicht identifiziert werden.

Viele der Pflanzen in Westafrika tragen wesentlich zum Lebensunterhalt der Bevölkerung bei. Sie liefern wichtige Ökosystemdienstleistungen in Form der sogenannten *non-timber forest products* (NTFPs). Allerdings sind auch diese von Umweltveränderungen bedroht. Ziel der dritten Studie war daher, einen neuen Ansatz zu entwickeln, mit dem sich der Einfluss von Klima- und Landnutzungsveränderungen auf den ökonomischen Nutzen von NTFPs abschätzen lässt. Dieses Projekt ist durch eine Kooperation mit meiner Kollegin Katja Heubach am BiK-F entstanden, die insgesamt 60 Interviews in Nordbenin durchgeführt hat um jährliche Sammelmengen und entsprechende Erlöse von NTFPs zu ermitteln. Die Befragungen konzentrierten sich auf die drei wichtigsten Savannenbaumarten in Nordbenin: *Adansonia digitata*, *Parkia biglobosa* und *Vitellaria paradoxa*. Vor allem die Früchte und Samen dieser Arten dienen als wichtige Nahrungsergänzung wegen der darin enthaltenen Proteine und Vitamine. Die jeweiligen Marktpreise wurden auf lokalen Märkten erfragt, in deren Umgebung die Umfragen stattfanden. Zudem wurden mittels GPS die Koordinaten aller Bäume erfasst, die von den Befragten besammelt wurden. Mit diesen räumlichen Daten konnte ein Flächenbezug der ökonomischen Haushaltsdaten hergestellt werden. Für die Erstellung der Karten über die monetäre Bedeutung der NTFPs wurden zusätzliche Bevölkerungsstatistiken in Nordbenin berücksichtigt. Um die heutigen und zukünftigen (2050) Auftrittswahrscheinlichkeiten der drei Savannenarten zu bestimmen, wurden Nischenmodelle mit Klimadaten (von Miroc3.2$_{\text{medres,}}$ Center for Climate System Research, Japan) und Landnutzungsdaten kalibriert. Das Landnutzungsmodell LandSHIFT lieferte Landnutzungsdaten unter der Annahme technologischer Stagnation. Die Simulationen basieren auf einer 0.1° Auflösung. Drei verschiedene Nischenmodelle kamen zur Anwendung: 1) *generalized additive models* (Regressionsmethode), 2) *generalized boosting models* (*machine learning*-Methode) und 3) *flexible discriminant analysis* (Klassifikationsmethode). Die drei Modellsimulationen wurden gemittelt (*ensemble forecasting*) um die Robustheit der Projektionen zu erhöhen. Um die zukünftigen potentiellen Gewinne bzw. Verluste zu bestimmen, wurden die generierten Auftrittswahrscheinlichkeiten der Arten mit den räumlich zugewiesenen monetären Werten verknüpft. Die derzeitig höchsten Erlöse pro Jahr erzielte die Art *Vitellaria* *paradoxa* (54.111 ± 28.126 US$/Gridzelle), gefolgt von *Parkia biglobosa* (32.246 ± 16.526 US$/Gridzelle) und *Adansonia digitata* (9.514 ± 6.243 US$/Gridzelle). Allerdings zeigen die Zukunftsprojektionen für das Jahr 2050, dass große Flächen in Nordbenin bis zu 50% dieses ökonomischen Wertes verlieren könnten. Am stärksten betroffen sind dabei die Arten *Vitellaria paradoxa* und *Parkia biglobosa*, die derzeit den höchsten Nutzwert haben. *Adansonia digitata* wird weniger stark aber ebenfalls negativ beeinflusst werden in weiten Teilen von Nordbenin. Hier zeigen sich jedoch regional ausgeprägte Unterschiede. Vor allem im Westen und im Osten des Untersuchungsgebietes können die Umweltveränderungen zu erhöhten Auftrittswahrscheinlichkeiten und damit höheren Erlösen im Jahr 2050 führen. Insgesamt zeigen die Ergebnisse, dass Adaptationsmaßnahmen erforderlich sind um alternative Einkommensquellen zu erschließen. Dies gilt insbesondere für Frauen, die für das Sammeln der NTFPs verantwortlich sind. Die Ergebnisse liefern Politikern eine Orientierungsmöglichkeit um verschiedene Landnutzungsoptionen ökonomisch zu vergleichen und etwaige Anpassungen von rezenten Nutzungsstrategien vorzunehmen.

Die Arbeit trägt in ihrer Gesamtheit dazu bei, Wissenslücken in einer bisher unzureichend untersuchten Region zu schließen. Mit Hilfe von Modellsimulationen wurden die Effekte von Klima- und Landnutzungsveränderungen auf großskalige Vegetationsmuster, Pflanzenvielfalt und Ökosystemdienstleistungen in Westafrika untersucht. Während sich der Klimawandel regional sehr unterschiedlich auf die Vegetationsmuster und die Pflanzenvielfalt auswirken wird, zeigte der menschliche Einfluss überwiegend negative Effekte. In Folge der Umweltveränderungen wird sich zusätzlich der ökonomische Nutzen von NTFPs verändern, was ebenfalls regional unterschiedlich ausfallen kann.

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Erklärung über Eigenanteil

Die dritte Studie dieser Arbeit “Impact of future climate and land use change on Non-Timber Forest Product provision in Benin, West Africa: Linking niche-based modelling with ecosystem service values” (Chapter 4) ist in Zusammenarbeit mit meiner Kollegin Katja Heubach (BiK-F) entstanden. Die Eigenanteile sind klar ersichtlich und voneinander abgrenzbar: Katja Heubach übernahm die haushaltsökonomischen Umfragen in Nord-Benin und war für die GPS-Kartierung der Gehölzarten verantwortlich. Diese Daten wurden mir zur Verfügung gestellt. Sämtliche anschließenden Analysen, d.h. die Modellierung der Gehölzarten sowie die Verknüpfung dieser Modellsimulationen mit den haushaltsökonomischen Daten, die Zukunftsprojektionen, sowie das Erstellen der Abbildungen und das Verfassen der entsprechenden Textpassagen habe ich eigenständig durchgeführt.