



ORIGINAL
ARTICLE



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

Jonathan Heubes^{1*}, Ingolf Kühn², Konstantin König^{1,3}, Rüdiger Wittig^{1,4}, Georg Zizka^{1,4,5} and Karen Hahn^{1,4}

¹Biodiversity and Climate Research Centre (LOEWE BiK-F), Senckenberganlage 25, D-60325 Frankfurt/Main, Germany, ²UFZ, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, D-06120 Halle, Germany, ³World Agroforestry Center – ICRAF, Amazon Initiative Consortium, EMBRAPA Amazônia Oriental, Travessa Enéas Pinheiro, 66095-100 Belém, Pará, Brazil, ⁴Institute of Ecology, Evolution and Diversity, J.W. Goethe-University, Siesmayerstraße 70, D-60323 Frankfurt/Main, Germany, ⁵Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, D-60325 Frankfurt/Main, Germany

ABSTRACT

Aim Africa is expected to face severe changes in climatic conditions. Our objectives are: (1) to model trends and the extent of future biome shifts that may occur by 2050, (2) to model a trend in tree cover change, while accounting for human impact, and (3) to evaluate uncertainty in future climate projections.

Location West Africa.

Methods 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.

Results 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 km². While savannas are predicted to contract in the south (by $54 \pm 22 \times 10^4$ km²), deciduous and evergreen forest biomes are expected to expand ($64 \pm 13 \times 10^4$ km² and $77 \pm 26 \times 10^4$ km²). 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.

Main conclusions 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.

Keywords

Africa, bioclimatic envelope models, climate change, desertification, forest degradation, generalized additive model, human impact, species distribution modelling.

*Correspondence: Jonathan Heubes, Biodiversity and Climate Research Centre (LOEWE BiK-F), Senckenberganlage 25, D-60325 Frankfurt/Main, Germany. E-mail: jonathan.heubes@senckenberg.de

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 characterized 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 southwards (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 with 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 (<http://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 database (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

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 was assessed using receiver operating characteristic (ROC) curves (e.g. Thuiller *et al.*, 2009).

Tree cover modelling

We used GAMs (Hastie & Tibshirani, 1986) to model tree cover, as this approach has been shown to perform best compared with 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). There is a northern expansion of grassland ($203 \pm 55 \times 10^4 \text{ km}^2$) and evergreen forest ($77 \pm 26 \times 10^4 \text{ km}^2$; Fig. 3). Deciduous forest is projected to expand northwards and southwards (overall gain: $64 \pm 13 \times 10^4 \text{ km}^2$) while savannas mainly lose area in the south ($54 \pm 22 \times 10^4 \text{ km}^2$). 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. 2c,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 CO₂ 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 because ‘real’ instead of potential vegetation was modelled. The trend derived from 17 GCMs highlights an increase in 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). Increasing coverage is attenuated while decreasing coverage is accelerated. The projected responsibility of humans in reducing canopy cover is in the

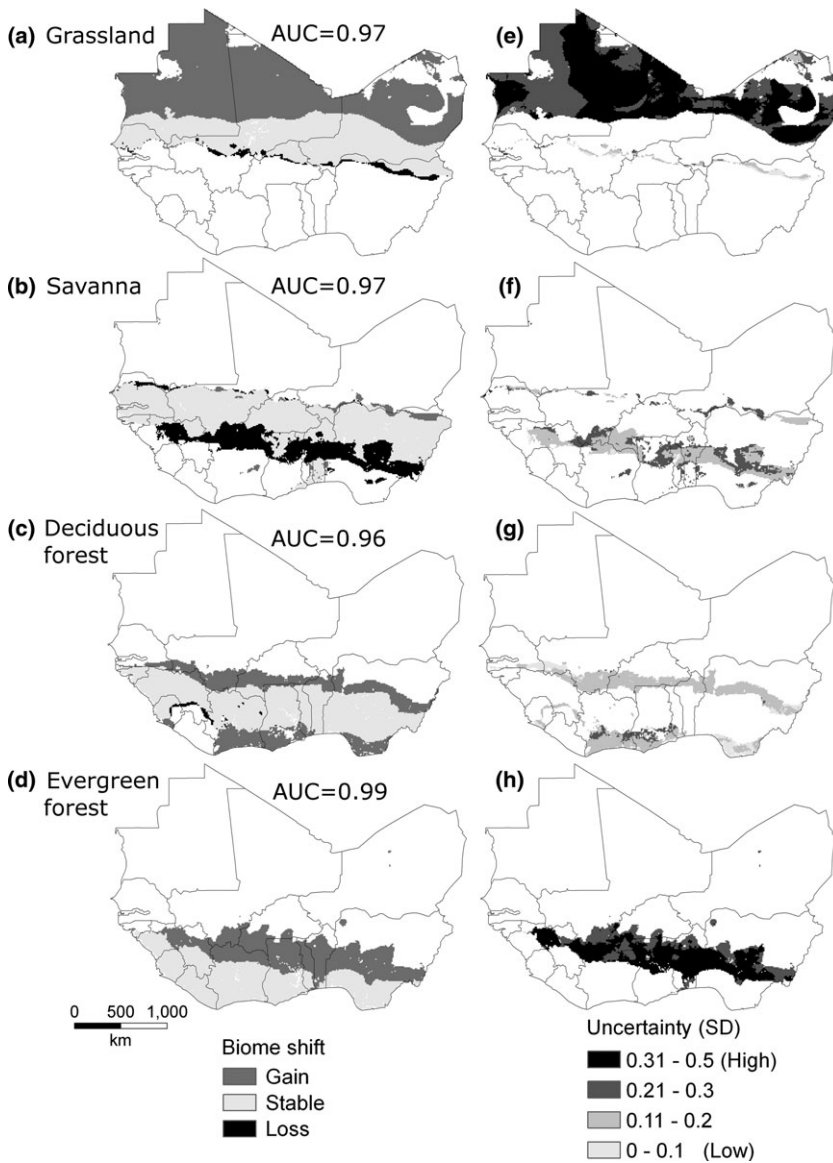


Figure 2 Projected biome shifts in West Africa for 2050: (a) grassland, (b) savanna, (c) deciduous forest, and (d) evergreen forest. Consensus projections (a–d) represent trends derived from 17 general circulation models (GCMs). The area under the receiver operating characteristic curve (AUC) value, 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.

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).

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 CO₂ 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

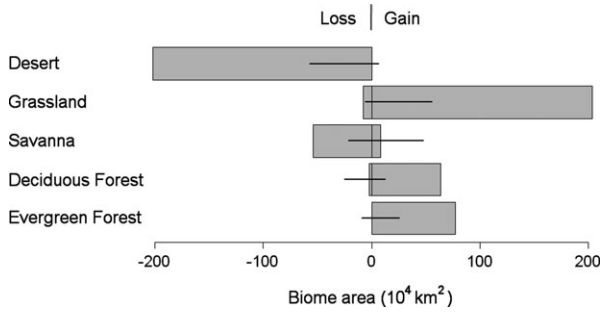


Figure 3 Projected future gain and loss of biome area in West Africa for 2050 compared to 2000 (grey bars). Calculations are based on consensus projections (trend) derived from 17 general circulation models (GCMs). Probability values of biome occurrence were transformed into presence/absence using a 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 because 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 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 the 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

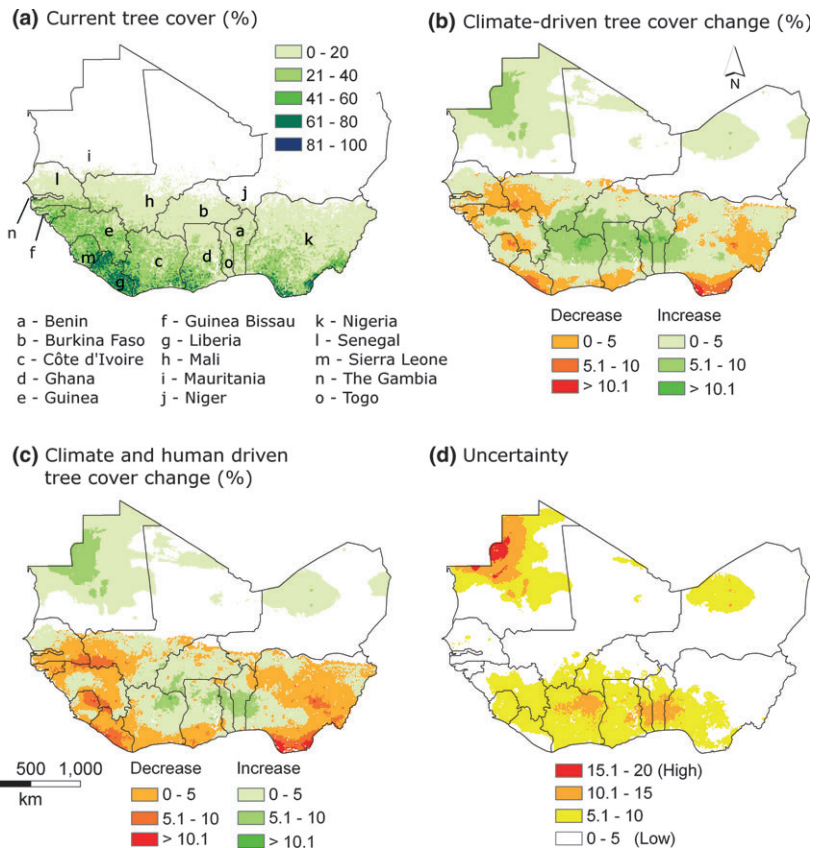


Figure 4 (a) West African percentage tree cover and projected tree cover change (%) for 2050 (b) ignoring human population growth and (c) incorporating human population growth. Consensus projections (b, c) represent trends derived from 17 general circulation models (GCMs). Uncertainty due to GCM-based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

overestimate the rate of biome shift, because terrestrial vegetation response to altered climate conditions can be slow (Woodward *et al.*, 2004). However, because 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 because 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 CO₂ 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 wind-dispersed grassland species. However, species-specific knowledge about dispersal ability is lacking in West Africa. More critical remarks on bioclimatic models can be found, for example in Dormann (2007). Despite these shortcomings, the top-down approach is powerful in regions like West Africa, firstly with 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 relationship 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 assumptions that firstly, changes in climates vary only over large distances (i.e. GCM cell size) and secondly, 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, has 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

The present study was funded by the research funding programme 'LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz' of Hesse's Ministry of Higher Education, Research, and the Arts. We thank Jaime R.G. Márquez for critical reading of the manuscript and R.B. O'Hara for improving the writing style.

REFERENCES

- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.
- Araújo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.
- Austin, M.P. (1998) An ecological perspective on biodiversity investigations: examples from Australian eucalypt forests. *Annals of the Missouri Botanical Garden*, **85**, 2–17.
- Baselga, A. & Araújo, M.B. (2010) Do community-level models describe community variation effectively? *Journal of Biogeography*, **37**, 1842–1850.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387–394.
- Breiman, L., Friedman, F., Olshen, F. & Stone, C. (1984) *Classification and regression trees*. Wadsworth, Pacific Grove, CA.
- Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology*, **12**, 1079–1093.
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O., Schlesinger, W.H., Wall, D.H. & Wear, D. (2001) Ecological forecasts: an emerging imperative. *Science*, **293**, 657–660.
- Clements, F.E. (1936) Nature and structure of the climax. *Journal of Ecology*, **24**, 252–284.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Delire, C., Ngomanda, A. & Jolly, D. (2008) Possible impacts of 21st century climate on vegetation in Central and West Africa. *Global and Planetary Change*, **64**, 3–15.
- Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, **8**, 387–397.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Eltahir, E.A.B. (1996) Role of vegetation in sustaining large-scale atmospheric circulations in the tropics. *Journal of Geophysical Research – Atmospheres*, **101**, 4255–4268.
- FAO (2001) *Global forest resources assessment 2000: main report*. Committee on Forestry, Food and Agriculture Organization, Rome.

- FAO (2007) *State of the world's forest*. Food and Agriculture Organization, Rome.
- Ferrier, S. & Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393–404.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Foley, J.A., Coe, M.T., Scheffer, M. & Wang, G.L. (2003) Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in northern Africa. *Ecosystems*, **6**, 524–539.
- Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.
- Franklin, J.F. & Forman, R.T.T. (1987) Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology*, **1**, 5–18.
- Fuller, D.O. & Ottke, C. (2002) Land cover, rainfall and land-surface albedo in West Africa. *Climatic Change*, **54**, 181–204.
- Gardner, T.A., Barlow, J., Sodhi, N.S. & Peres, C.A. (2010) A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation*, **143**, 2293–2300.
- Geist, H.J. & Lambin, E.F. (2002) Proximate causes and underlying driving forces of tropical deforestation. *BioScience*, **52**, 143–150.
- Gonzalez, P. (2001) Desertification and a shift of forest species in the West African Sahel. *Climate Research*, **17**, 217–228.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hansen, M., DeFries, R., Townshend, J.R., Carroll, M., Dimiceli, C. & Sohlberg, R. (2003) *Vegetation continuous fields MOD44B, 2001 percent tree cover, collection 3*. University of Maryland, College Park, MD.
- Harrell, F.E.J. (2001) *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis*. Springer, New York.
- Hastie, T. & Tibshirani, R.J. (1986) Generalized additive models. *Statistical Science*, **1**, 297–318.
- Hély, C., Bremond, L., Alleaume, S., Smith, B., Sykes, M.T. & Guiot, J. (2006) Sensitivity of African biomes to changes in the precipitation regime. *Global Ecology and Biogeography*, **15**, 258–270.
- Herrmann, S.M. & Hutchinson, C.F. (2005) The changing contexts of the desertification debate. *Journal of Arid Environments*, **63**, 538–555.
- Hickler, T., Eklundh, L., Seaquist, J.W., Smith, B., Ardo, J., Olsson, L., Sykes, M.T. & Sjöstrom, M. (2005) Precipitation controls Sahel greening trend. *Geophysical Research Letters*, **32**, 1–4.
- Hickler, T., Prentice, I.C., Smith, B., Sykes, M.T. & Zaehle, S. (2006) Implementing plant hydraulic architecture within the LPJ Dynamic Global Vegetation Model. *Global Ecology and Biogeography*, **15**, 567–577.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, **88**, 213–229.
- Higgins, S.I., Bond, W.J., February, E.C., Bronn, A., Euston-Brown, D.I.W., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A.L.F., Scheiter, S., Sowry, R., Trollope, L. & Trollope, W.S.W. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, **88**, 1119–1125.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- House, J.I., Archer, S., Breshears, D.D. & Scholes, R.J. (2003) Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography*, **30**, 1763–1777.
- Hulme, M., Doherty, R., Ngara, T., New, M. & Lister, D. (2001) African climate change: 1900–2100. *Climate Research*, **17**, 145–168.
- IPCC (2001) *Climate change 2001: the scientific basis*, Vol. 1. Cambridge University Press, Cambridge.
- IPCC (2007) *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Cambridge.
- Jeltsch, F., Weber, G.E. & Grimm, V. (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree–grass coexistence. *Plant Ecology*, **150**, 161–171.
- Maranz, S. (2009) Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change. *Journal of Biogeography*, **36**, 1181–1193.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.
- Mayaux, P., Bartholomé, E., Fritz, S. & Belward, A. (2004) A new land-cover map of Africa for the year 2000. *Journal of Biogeography*, **31**, 861–877.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powrie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.
- Moisen, G.G. & Frescino, T.S. (2002) Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling*, **157**, 209–225.
- Nicholson, S.E., Tucker, C.J. & Ba, M.B. (1998) Desertification, drought, and surface vegetation: an example from the West African Sahel. *Bulletin of the American Meteorological Society*, **79**, 815–829.
- Norris, K., Asase, A., Collen, B., Gockowski, J., Mason, J., Phalan, B. & Wade, A. (2010) Biodiversity in a forest–agriculture mosaic – The changing face of West African rainforests. *Biological Conservation*, **143**, 2341–2350.

- Pearce, J. & Ferrier, S. (2000) An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling*, **128**, 127–147.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pompe, S., Hanspach, J., Badeck, F.-W., Klotz, S., Bruehlheide, H. & Kühn, I. (2010) Investigating habitat-specific plant species pools under climate change. *Basic and Applied Ecology*, **11**, 603–611.
- R Development Core Team (2010) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org>
- Ramirez, J. & Jarvis, A. (2008) *High resolution statistically downscaled future climate surfaces*. International Centre for Tropical Agriculture, CIAT, Cali, Colombia.
- Ramirez, J. & Jarvis, A. (2010) *Downscaling global circulation model outputs: the delta method*. International Center for Tropical Agriculture, CIAT, Cali, Colombia.
- Rickebusch, S., Thuiller, W., Hickler, T., Araújo, M.B., Sykes, M.T., Schweiger, O. & Lafourcade, B. (2008) Incorporating the effects of changes in vegetation functioning and CO₂ on water availability in plant habitat models. *Biology Letters*, **4**, 556–559.
- Roekner, E., Bäuml, G., Bonaventura, L., Brokopf, R., Esch, M., Giorgetta, M., Hagemann, S., Kirchner, I., Kornbluh, L., Manzini, E., Rhodin, A., Schlese, U., Schulzweida, U. & Tompkins, A. (2003) *The atmospheric general circulation model ECHAM5*. Report No. 349. Max-Planck-Institut für Meteorologie, Hamburg.
- Rosenfeld, D., Rudich, Y. & Lahav, R. (2001) Desert dust suppressing precipitation: a possible desertification feedback loop. *Proceedings of the National Academy of Sciences USA*, **98**, 5975–5980.
- Rothman, D.S., Agard, J. & Alcamo, J. (2007) The future today. *Global Environment Outlook 4 (GEO-4): environment for development* (ed. by M. Schomaker, M. Keating and M. Chenje), pp. 395–454. United Nations Environment Programme (UNEP), Valletta, Malta.
- Ruelland, D., Levvasseur, F. & Tribotte, A. (2010) Patterns and dynamics of land-cover changes since the 1960s over three experimental areas in Mali. *International Journal of Applied Earth Observation and Geoinformation*, **12**, S11–S17.
- Sala, O.E., Chapin, F.S.C., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480–490.
- Sato, H., Itoh, A. & Kohyama, T. (2007) SEIB-DGVM: a new dynamic global vegetation model using a spatially explicit individual-based approach. *Ecological Modelling*, **200**, 279–307.
- Schalldach, R. & Koch, J. (2009) Conceptual design and implementation of a model for the integrated simulation of large-scale land-use systems. *Information Technologies in Environmental Engineering* (ed. by I.N. Athanasiadis, P.A. Mitkas, A.E. Rizzoli and J. Marx-Gómez), pp. 425–438. Springer, Berlin, Heidelberg.
- Schaphoff, S., Lucht, W., Gerten, D., Sitch, S., Cramer, W. & Prentice, I.C. (2006) Terrestrial biosphere carbon storage under alternative climate projections. *Climatic Change*, **74**, 97–122.
- Scheiter, S. & Higgins, S.I. (2009) Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology*, **15**, 2224–2246.
- Scholes, R.J. (1997) *Savanna*. Cambridge University Press, Cambridge.
- Scholze, M., Knorr, W., Arnell, N.W. & Prentice, I.C. (2006) A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Sciences USA*, **103**, 13116–13120.
- Sequist, J.W., Hickler, T., Eklundh, L., Ardo, J. & Heumann, B.W. (2009) Disentangling the effects of climate and people on Sahel vegetation dynamics. *Biogeosciences*, **6**, 469–477.
- Shugart, H.H. (1998) *Terrestrial ecosystems in changing environments*. Cambridge University Press, Cambridge.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.
- Thuiller, W. (2007) Biodiversity: climate change and the ecologist. *Nature*, **448**, 550–552.
- Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T. & Zimmermann, N.E. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.

- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- Tucker, C.J. & Nicholson, S.E. (1999) Variations in the size of the Sahara Desert from 1980 to 1997. *Ambio*, **28**, 587–591.
- Tucker, C.J., Dregne, H.E. & Newcomb, W.W. (1991) Expansion and contraction of the Sahara desert from 1980 to 1990. *Science*, **253**, 299–301.
- Vincke, C., Diedhiou, I. & Grouzis, M. (2010) Long term dynamics and structure of woody vegetation in the Ferlo (Senegal). *Journal of Arid Environments*, **74**, 268–276.
- Wezel, A. & Lykke, A.M. (2006) Woody vegetation change in Sahelian West Africa: evidence from local knowledge. *Environment, Development and Sustainability*, **8**, 553–567.
- White, F. (1983) *The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. UNESCO, Paris.
- Wilby, R.L. & Wigley, T.M.L. (1997) Downscaling general circulation model output: a review of methods and limitations. *Progress in Physical Geography*, **21**, 530–548.
- Wittig, R., König, K., Schmidt, M. & Szarzynski, J. (2007) A study of climate change and anthropogenic impacts in West Africa. *Environmental Science and Pollution Research*, **14**, 182–189.
- Wood, S.N. (2006) *Generalized additive models: an introduction with R*. Chapman and Hall/CRC, Boca Raton, FL.
- Wood, S.N. (2008) Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **70**, 495–518.
- Woodward, F.I., Lomas, M.R. & Kelly, C.K. (2004) Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 1465–1476.
- Yee, T.W. & Mitchell, N.D. (1991) Generalized additive models in plant ecology. *Journal of Vegetation Science*, **2**, 587–602.
- Zeng, N., Neelin, J.D., Lau, K.M. & Tucker, C.J. (1999) Enhancement of interdecadal climate variability in the Sahel by vegetation interaction. *Science*, **286**, 1537–1540.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Model performance for projected West African biomes.

Appendix S2 Response curves relating West African tree cover to climate and disturbance variables.

Appendix S3 Precipitation records and future projections for different West African biomes.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Jonathan Heubes is a PhD student at the Biodiversity and Climate Research Centre, Frankfurt am Main. His doctoral research focuses on climate and land use impact on vegetation patterns in West Africa.

The research group focuses on the dynamics of biocenoses (<http://www.bik-f.de> and <http://www.ufz.de>).

Author contributions: J.H., K.H., R.W. and G.Z. conceived the ideas; K.K. provided environmental data; J.H. performed the statistical analysis, supported by I.K.; J.H. led the writing, in which all authors contributed.

Editor: Miguel Araújo