

# Assessing the suitability of pioneer species for secondary forest restoration in Benin in the context of global climate change

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**Photo 1.**

In the secondary forests of Lama, a stand composed by young trees of *Lonchocarpus sericeus*. On the ground, the invasive exotic *Chromolaena odorata* (L.) R.M.King is shaded by the trees and its biomass is progressively reduced.

Photo A. J. Gbètoho.

## RÉSUMÉ

### ÉVALUATION DE L'APTITUDE D'ESSENCES PIONNIÈRES POUR LA RESTAURATION DE FORÊTS SECONDAIRES AU BÉNIN DANS UN CONTEXTE DE CHANGEMENT CLIMATIQUE

Pour cette étude, des modèles de niches écologiques sont appliqués à la gestion des forêts secondaires au Bénin. Cette étude a consisté à identifier les zones favorables à l'utilisation d'essences pionnières, telles que *Lonchocarpus sericeus* ou *Anogeissus leiocarpa*, pouvant être ciblée pour assurer à faible coût, dans un contexte de changement climatique global, pour restaurer rapidement des forêts secondaires et des écosystèmes dégradés afin de rétablir leur biodiversité. À l'aide des indices de fréquence mis à disposition sur le site Internet du Centre mondial d'information sur la biodiversité (GBIF) et les données environnementales récentes, les facteurs affectant la distribution des espèces sont évalués pour l'ensemble de l'Afrique de l'Ouest. Les modèles développés avec MaxEnt pour les deux essences, en Afrique de l'Ouest uniquement, affichent une bonne prédictivité pour AUC > 0,80 et des ratios AUC dépassant largement 1,5. Les résultats, intégrés dans des scénarios climatiques rcp4.5 et rcp8.5 à l'horizon 2055 basés sur les données AfriClim suggèrent une petite réduction de l'aire de distribution de *L. sericeus* et quelques variations pour *A. leiocarpa*. Cette distribution potentielle future des deux essences permet d'envisager leur utilisation pour la restauration du couvert végétal dès maintenant et jusqu'aux années 2050. Des améliorations sont nécessaires en utilisant des données complémentaires, en l'étendant à d'autres espèces et en évaluant les incertitudes liées à ces prédictions.

**Mots-clés :** *Lonchocarpus sericeus*, *Anogeissus leiocarpa*, modèle de distribution d'espèces, entropie maximum, modèle linéaire généralisé, aire favorable, écologie.

## ABSTRACT

### ASSESSING THE SUITABILITY OF PIONEER SPECIES FOR SECONDARY FOREST RESTORATION IN BENIN IN THE CONTEXT OF GLOBAL CLIMATE CHANGE

In this study, species distribution modelling (SDM) was applied to the management of secondary forests in Benin. This study aims at identifying suitable areas where the use of candidate pioneer species, such as *Lonchocarpus sericeus* and *Anogeissus leiocarpa*, could be targeted to ensure at low cost, currently and in the context of global climate change, fast reconstitution of secondary forests and disturbed ecosystems and the recovery of their biodiversity. Using occurrence records from the Global Biodiversity Information Facility (GBIF) website and current environmental data, the factors that affected the distribution of the species were assessed in West Africa. The models developed in MaxEnt and R software for West Africa only, for both species, showed good predictive power with AUC > 0.80 and AUC ratios well above 1.5. The results were projected in future climate at the horizon 2055, using AfriClim data under rcp4.5 and rcp8.5 and suggested a little reduction in the range of *L. sericeus* and any variation for *A. leiocarpa*. The potential distribution of the two species indicated that they could be used for vegetation restoration activities both now and in the mid-21st century. Improvement are needed through the use of complementary data, the extension to others species and the assessment of uncertainties related to these predictions.

**KEYWORDS:** *Lonchocarpus sericeus*, *Anogeissus leiocarpa*, species distribution modelling, maximum entropy, generalized linear model, favourable area, ecology.

## RESUMEN

### EVALUACIÓN DE LA APTITUD DE ESPECIES PIONERAS PARA LA RESTAURACIÓN DE BOSQUES SECUNDARIOS EN BENÍN EN UN CONTEXTO DE CAMBIO CLIMÁTICO

En este estudio se aplicaron modelos de distribución de especies al manejo de bosques secundarios en Benín. Este estudio tuvo como objetivo identificar áreas adecuadas donde el uso de especies pioneras candidatas, como *Lonchocarpus sericeus* y *Anogeissus leiocarpa*, pudiera ser dirigido a asegurar a bajo costo, actualmente y en el contexto del cambio climático global, la reconstitución rápida de bosques secundarios y ecosistemas perturbados y la recuperación de su biodiversidad. Utilizando los registros de ocurrencias del sitio web del *Global Biodiversity Information Facility* (GBIF) y los datos ambientales actuales, se evaluaron los factores que afectaron la distribución de las especies en África Occidental. Los modelos desarrollados con MaxEnt para ambas especies, únicamente para África Occidental, muestran una buena capacidad predictiva con una AUC > 0.80 y razones AUC muy por encima de 1.5. Los resultados se proyectaron en el clima futuro en el horizonte 2055, usando los datos de AfriClim bajo rcp4.5 y rcp8.5 y sugirió una pequeña reducción del área de distribución de *L. sericeus* y cualquier variación para *A. leiocarpa*. La distribución potencial de ambas especies indica que podrían usarse para restaurar la cubierta vegetal desde ahora y hasta mediados de este siglo. Se necesitan mejoras mediante el uso de datos complementarios, la extensión a otras especies y la evaluación de las incertidumbres relacionadas con estas predicciones.

**Palabras clave:** *Lonchocarpus sericeus*, *Anogeissus leiocarpa*, modelo de distribución de especies, entropía máxima, modelo lineal generalizado, área favorable, ecología.

## Introduction

Secondary forests are growing in many parts of the world due to anthropic disturbances, but the issue of their management and restoration to primary forest is of great concern because the critical knowledge to guide that management is lacking (Makana and Thomas, 2008; Gbètoho *et al.*, 2016). Depending on the level of degradation, Lamb (1994) suggested that reforestation may be done through substitution of the natural forest by plantation, rehabilitation, restoration or natural succession. The recovery of biodiversity is the highest for natural succession, and the lowest for plantation. However, natural succession may take long due the ecological processes involved in forest succession and human intervention may be necessary to speed up the process of recovery (Scheffer *et al.*, 2001; Makana and Thomas, 2008). Ecological restoration of a forest therefore requires that the intervention be in line with the pathways of forest succession with a careful choice of the species to be used (Bongers *et al.*, 2006). Yet, climate change is a source of uncertainty for the survival of both species used for restoration and on-site species and a great challenge to the long-term stability of natural ecosystems (IPCC, 2007; Hounkpèvi *et al.*, 2016). Climate change is likely to reduce the physiological abilities of species, and may alter forest composition by modifying the distribution of species and by increasing invasion of forest ecosystems by exotic species (Araújo *et al.*, 2011; Fandohan *et al.*, 2015). Human responses should therefore be time-dependent adaptive strategies to conserve the biodiversity, the composition of forests and to ensure its good functioning.

However, in West Africa, cultivation of tree species to restore degraded areas is usually recommended to forest managers (Hounkpèvi *et al.*, 2016; Adjahossou *et al.*, 2016) without any consideration of the species life-history and of natural pathways of forest succession in the area. As a result, species used in enrichment of degraded areas in Benin are faced with competition from on-site species (Djodjouwin *et al.*, 2011). At the onset of forest recovery, the establishment of pioneer species, which are known to be fast growing, enhances forest recovery by out-competing exotic weeds, attracts a community of dispersers and then enhances the quick establishment of late-successional species (Hooper *et al.*, 2005). Therefore, they are very important in forest rehabilitation and recovery processes. Promoting the use of pioneer species, that are well adapted to local ecological conditions, may be a successful approach to ensure, at low cost, the restoration of secondary forests in Benin and in West Africa. However, the geographical space where the environmental requirements of such species are fulfilled and their response to the changing climate are generally not well known.

Assessing species distribution at a large scale is in general constrained by the lack of quantitative field-based data. Species distribution modelling (SDM) allows the use of some known occurrences of the species with environmental and habitat variables to model the eco-geographic distribution of that species. SDM has frequently been used to assess the

spreading ability of invasive alien species (Peterson, 2003; Fandohan *et al.*, 2015), the conservation status of threatened species and underutilized agroforestry species (Bowe and Haq, 2010; Blach-Overgaard *et al.*, 2010; Adjahossou *et al.*, 2016), and the impact of climate change on species distribution and biodiversity of protected areas (Araújo *et al.*, 2011; Houehanou *et al.*, 2013). Using climatic scenarios and climate models with specific algorithms, these researchers have predicted the variation in species range due to global changes. When climate and habitat variables are used, then the fundamental niche is modelled and the result projected in a geographical space corresponds to the potential distribution (Pearson and Dawson, 2003). The fundamental niche represents the global cultivation potential of a species (Cuni-Sanchez *et al.*, 2010) and is very relevant for forest management.

In this paper, SDM was used to address a key management issue, the restoration of secondary forests in Benin. We assessed the vulnerability to climate change of two pioneer species, widely distributed through Africa: *Anogeissus leiocarpa* (DC.) Guill. & Perr., and *Lonchocarpus sericeus* (Poir.) DC. They have a great and quick ability in standing biomass production (Gbètoho *et al.*, 2016) and could be used in reforestation. These species correspond to the ecology of Benin that is drier than the guineo-congolian area due to the Dahomey gap. They appear naturally in successional pathways of forests in Benin (Gbètoho *et al.*, 2016). The key research questions of our investigation were as follows:

- 1) What are the determinants of the distribution and ecological niche of the targeted tree species in West Africa?
- 2) Could the species be used in the short, medium and long term for the ecological restoration of protected areas in Benin?



**Photo 2.**

In the secondary forests of Lama, a stand composed by trees of *Anogeissus leiocarpa*. On the ground, the invasive exotic *Chromolaena odorata* (L.) R.M.King was eliminated and the shade allow shade-tolerant species to progressively establish in the forest.  
Photo A. J. Gbètoho.



**Photo 3.**  
Trees of *Anogeissus leiocarpa* marked at the breast height and numbered with red paint for periodic inventories in the framework of the study of the dynamics of the forests. Photo A. J. Gbètoho.

## Methods

### Species description

*L. sericeus* is a species of the Sudano-Guinean to Guinean zones that grows along rivers, in forest galleries, in coastal secondary forests and semi-deciduous forests, and on swampy soils (Burkill, 1995). In these areas, it is exposed to an annual rainfall of 1,200 to 1,900 mm and more. The tree could reach 13 m or more at maturity. It is an ornamental tree which is also harvested as a medicinal plant, and for timber (Akoègninou *et al.*, 2006). *A. leiocarpa*, the African Birch, has a large ecological amplitude and is highly adapted to drought; it is a Sudanian species that could grow from the border of the Sahelian zone to the margins of wetter forests with an annual rainfall of 600 to 1200 mm (Couteron and Kokou, 1997). The trees can grow up to 30 m in height, and the species is highly regarded for its quality wood and its many medicinal properties (Akoègninou *et al.*, 2006).

### Input Data

#### Collection and cleaning of species occurrence data

In total, 2,051 and 681 occurrence records were downloaded respectively for *L. sericeus* and *A. leiocarpa* from the Global Biodiversity Information Facility (GBIF) website<sup>1</sup>. They included digitized herbarium records, and locations of species recorded using a Global Positioning System (GPS) during field surveys in Africa. The data from field surveys in Benin (already published on the GBIF website) include our long-term data collected in Lama forest, other presence points from the databases of our institution and of other institutions in the country.

1 [www.gbif.org](http://www.gbif.org)

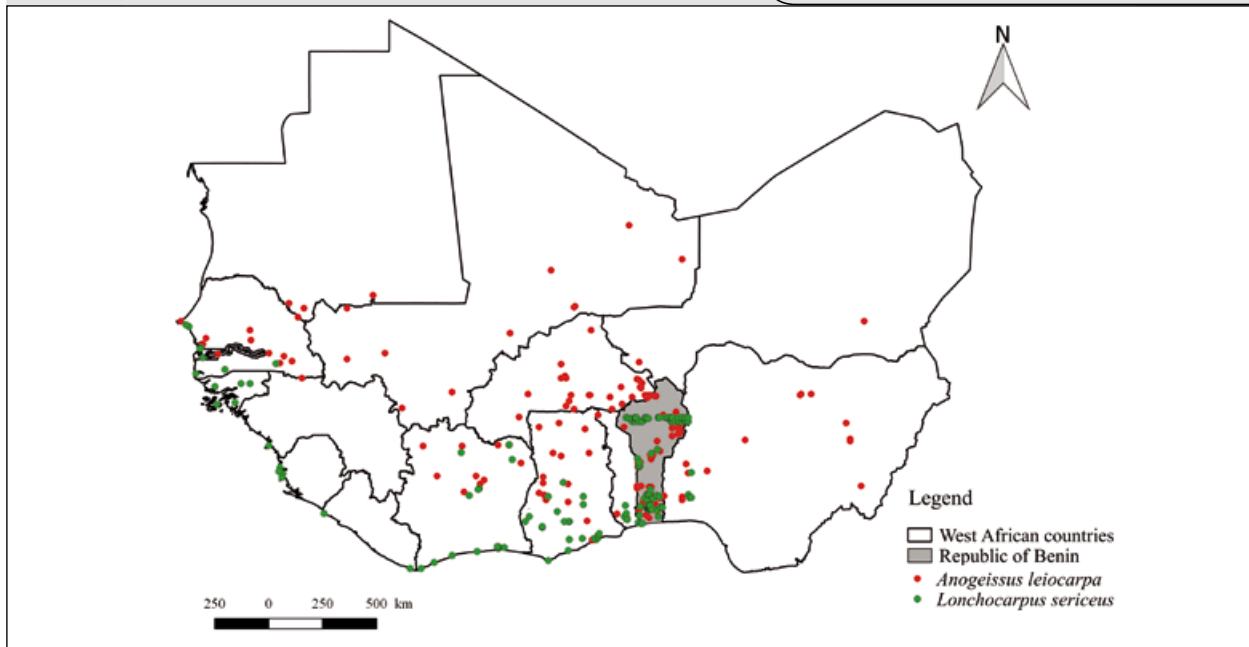
For species with broad distributions, large distances between occurrence localities could lead to high variability in environmental factors due to non-analogue climate or spatial non-stationarity (Peterson and Holt, 2003; Bowe and Haq, 2010), thus resulting in the elaboration of a model with weak predictive power (Murphy and Lovett-Doust, 2007). By doing a regional partition of occurrences of a species with large distribution in Africa, Gouwakinnou (2011) demonstrated that the climate is analogue in West-Africa. Therefore, the modelling was carried out at West African level. Records that fell outside West Africa were removed. West Africa included Benin, Burkina Faso, Cape Verde, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, and Togo (figure 1). The records prior to 1950 were also removed from the datasets, to match the time period of the environmental datasets which covered the period 1950-2000. Furthermore, the geographic coordinates of occurrence records are mandatory to model the distribution of the respective species. However, herbarium collection data were frequently lacking geographic coordinates. GEOlocate<sup>2</sup> was therefore used to assign the coordinates to records on the basis of locality information. Georeferencing of records with coordinates was verified by checking that information on locality and country matched in QGIS: those points that fell outside their geographic range or in the sea were checked and corrected if enough description of the locality was made; but records with erroneous coordinates without information on location were removed.

### Climatic data

The species' distributions were analysed using a set of environmental data. At a large scale, the distribution of a species depends mainly on climate (Vayreda *et al.*, 2013). We selected "a priori" four variables that we found to be the most biologically relevant in plant ecology in tropical West Africa and easy to interpret: annual precipitation (bio12), annual temperature (bio1), temperature seasonality (bio4) and precipitation seasonality (bio15). These variables were downloaded for the current climate (1950-2000, version 1.4) (Hijmans *et al.*, 2005) in 2.5° grids from WorldClim. For future climate, the AFRICLIM ensemble-mean bvar (bioclimatic variables) at the horizon 2055 were downloaded online<sup>3</sup>. Indeed, the global circulation models (GCM) and their resolutions provided by IPCC are not suitable for Africa where the climatic gradients are steep and much more localized (Platts *et al.*, 2015). Therefore, AFRICLIM which came from the combination of eight global circulation models (GCM), downscaled using two regional circulation model (RCM: RCA4 from the Swedish Meteorological and Hydrological Institute, SMHI; and CanRCM4 from the Canadian Centre for Climate Modelling and Analysis, CCCma), and four observation baselines (CRU, WorldClim, TAMSAT and CHIRPS) is now the best model for ecological applications in Africa (Platts *et al.*, 2015). AFRICLIM was elaborated under two representative concentration pathways (rcp): rcp4.5 and rcp8.5. The rcp were developed by the IPCC fifth assessment report (AR5) in 2014. They described four possible climates futures, by considering greenhouse gas (GHG) emissions with or without

2 [www.museum.tulane.edu/geolocate](http://www.museum.tulane.edu/geolocate)

3 <https://webfiles.york.ac.uk/KITE/AfriClim/>



**Figure 1.** Spatial distribution of the presence records of *Lonchocarpus sericeus* and *Anogeissus leiocarpa* in West Africa. *L. sericeus* presence points are distributed in coastal countries while *A. leiocarpa* is well spread through West Africa.

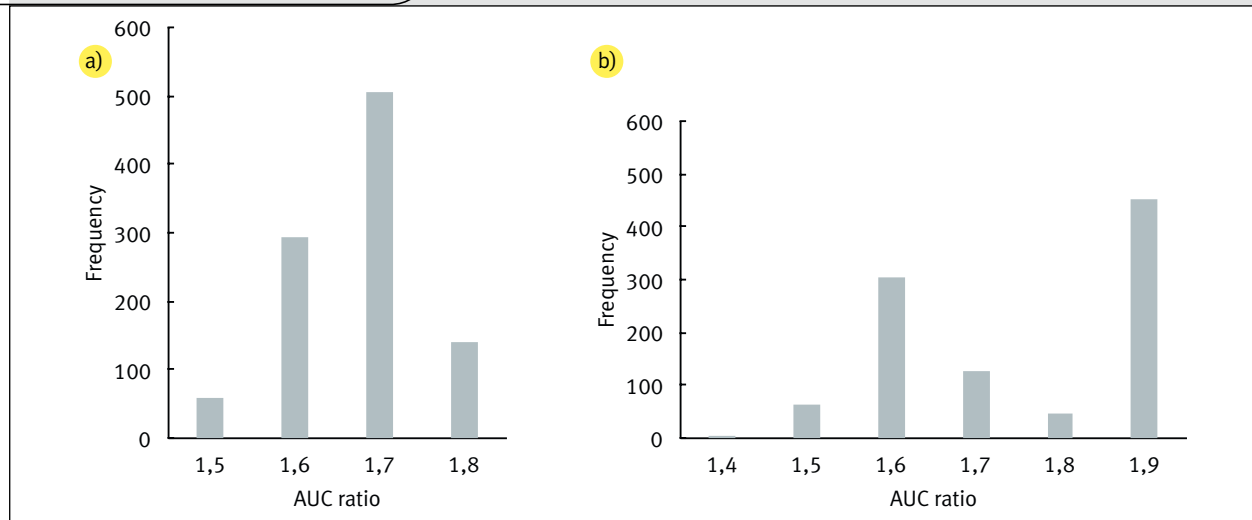
mitigation strategies. The rcp4.5 and rcp8.5 projected respectively the lowest and the highest increase in temperature (1.4°C and 2°C) by the mid-21<sup>st</sup> century, and are very suitable for capturing the range of uncertainties (Harris *et al.*, 2014).

#### Data processing and analysis

The presence data for *L. sericeus* were located only in coastal countries, while those of *A. leiocarpa* were located in the whole West Africa. Therefore, the geographic background for the modelling of *L. sericeus* distribution was clipped to coastal countries, while the whole West Africa was considered for *A. leiocarpa*. This was necessary because geographic background has a strong impact on species distribution models. Indeed, a geographic background that is too large does not take into account fine scale conditions and the model may over fit the occurrences provided (Lobo *et al.*, 2010). Modelling of the distribution of the two species was carried out using a combination of two algorithms: the “Maximum Entropy”, a machine-learning algorithm implemented in MaxEnt v3.3.3k and the “general linear model” (GLM), a regression method using “Maximum likelihood” implemented in R software. MaxEnt is a good algorithm to analyse “presence-only” data and on small to medium scale of modelling (Philips *et al.*, 2006). Due to the recent criticism on MaxEnt: “black-box” processing, the non-use of absence data in the analysis, and its incapacity to check the significance of the variables and statistical indexes computed (Royle *et al.*, 2012), other statistical methods have been used in SDM. We choose GLM due to the relationships between Maximum Entropy and Maximum Likelihood (Guisan *et al.*, 2002; Renner and Warton, 2013). These methods performs statistical inference on data that did not come from random sampling. Therefore, the modelling were achieved under the assumptions of random sampling and that of constant probability of species detection (Royle *et al.*, 2012).

Some collection biases were generally linked to the concentrations of the sampling effort on some sites during fieldwork (Stockwell and Peterson, 2002). To avoid pseudoreplication of local environment due these biases, duplicate records in 2.5° grids were removed. Respectively, 214 and 237 georeferenced occurrences were retained for *L. sericeus* and *A. leiocarpa* (figure 1). Then, the best regularization multiplier (beta) was determined through the computation of Akaike Information Criterion (AIC) on models run using beta from 1 to 10; beta of the model with the lowest AICc was chosen (Warren and Seifert, 2011). The default value in MaxEnt is 1 while a larger regularization multiplier will give a more spread out, less localized prediction (Elith *et al.*, 2010), which is preferable when projecting in new time series.

Respectively, 147 (69%) and 163 (69%) points were used for modelling in MaxEnt and R, while the 31% points that remain were used in further step as evaluating data. In MaxEnt, models were calibrated using “Crossvalidate” run type with 5 replicates., Crossvalidate performs k-folds subdivision of the data: one fold is used to test the prediction of the model trained using the other folds during each replicate. While doing the analyses, a jackknife procedure was performed to determine the contribution of the variables to the model. In R, we selected pseudoabsence points following Senay *et al.* (2013) and we got respectively 1,123 and 651 points for *L. sericeus* and *A. leiocarpa*. These points were selected from the geographical space of the presence points but were environmentally different to those points. The presence and pseudo absence points were randomly partitioning in 5 folds, with one fold use for auto-evaluation during modelling. We perform the regression using the Gaussian function, an approximation of the binomial function (presence, absence) for large dataset and test the significance of the bvar. For the two species, we only retained the less correlated variables that are really significant to the model and the two algorithms were run using the same variables.



**Figure 2.**

AUC ratio computed for evaluation of (a) *Lonchocarpus sericeus* and (b) *Anogeissus leiocarpa* models. The histograms showed that the ratios are in general higher than 1.5.

The results were imported into QGIS 2.18 as raster maps where the cells contain the probability distribution values, ranging gradually from 0 (predicted absence) to 1 (with  $0 < \text{predicted presence} \leq 1$ ), as a measure of the presence likelihood of the species. The predictions from the two algorithms were averaged and the cells were classified into favourable and unfavourable area using the 10 percentile training presence. The distributions of the two species were done at a regional West African level, but the management strategies were done at country-level for Benin. Therefore, the results were clipped to the boundaries of Benin. The current and future distributions were then overlaid on the network of Benin's protected areas. For each species the favourable areas currently and at the horizon 2055 were computed in QGIS. Then, 130 random points were generated at the whole country level to compare the current values of the bvar to their future values under the two rcp using a Wilcoxon one sample p rank. At these points, the values of the bvar were collected using point sampling tool in QGIS for the comparison.

During model validation, the average value of the area under curve (AUC) of the receiver operating characteristic (ROC) curve was used to assess the predictive ability of each model: in practice,  $\text{AUC} > 0.75$  means a model with good prediction (Araújo *et al.*, 2005). But, the predictive power of these models was tested with Partial Roc, using the 31% of the occurrence data set apart for evaluation. Partial ROC (Peterson *et al.*, 2008) is a new and efficient approach that assesses model performance by evaluating specificity and sensitivity using test points (evaluation data). We computed AUC with 95% of the evaluation data (AUCpartial) and AUC with 50% of evaluation points (AUCrandom) and compared them using Bootstrap after 1,000 iterations. Then, AUC ratio (AUCpartial/AUCrandom) was computed and its distribution over the 1,000 iterations was achieved using histograms. In practice, the prediction map of a good model must well predict the occurrences of evaluation data. We looked for AUC ratio above 1.5 (0.75 for good prediction/0.5 for random prediction). These analyses were carried out online with the *Niche tool box*<sup>4</sup>.

<sup>4</sup> <http://shiny.conabio.gob.mx:3838/nichetoolb2/>

## Results

### Determinants of the distribution of the targeted species

The model of *L. sericeus* has a good predictive ability with an AUC of 0.88 ( $\pm 0.12$ ). The Bootstrapping gave a probability of 0 ( $< 0.05$ ). This indicates that the model has better predictive abilities than a null model. Furthermore, the AUC ratio was well above 1.5 with a distribution mode of 1.7 and a positive skew (0.92) (figure 2). The model of *A. leiocarpa* also had good predictive ability with a mean AUC of 0.92 ( $\pm 0.04$ ). The AUC ratio was well above 1.5 with a distribution mode of 1.9 and a positive skew (1.05) (figure 2). Therefore, the two models had good predictive power.

The temperature seasonality (bio4) contributed most to the model of *L. sericeus* (table I). However, the annual precipitation (bio12) gave the highest gain when used in isolation and decreased the most the gain and the AUC value when omitted (figure 3). The importance of the third variable, annual temperature (bio1) was not negligible as all these variables reduce the gain and the AUC value when omitted (figure 3). The last observation was also consistent for the variables that determine the distribution of *A. leiocarpa*. The annual precipitation (bio12) contributed the most to the model (table I). It gave the highest gain when used in isolation and decreased the most the gain and the AUC value when omitted. The results of the GLM showed these variables had great significance in the distribution of the species ( $p < 0.000$ , table I) and therefore, could really be used to achieve the modelling. The correlation between the environmental variables and the presence points was 0.67 for *L. sericeus* and 0.94 for *A. leiocarpa*.

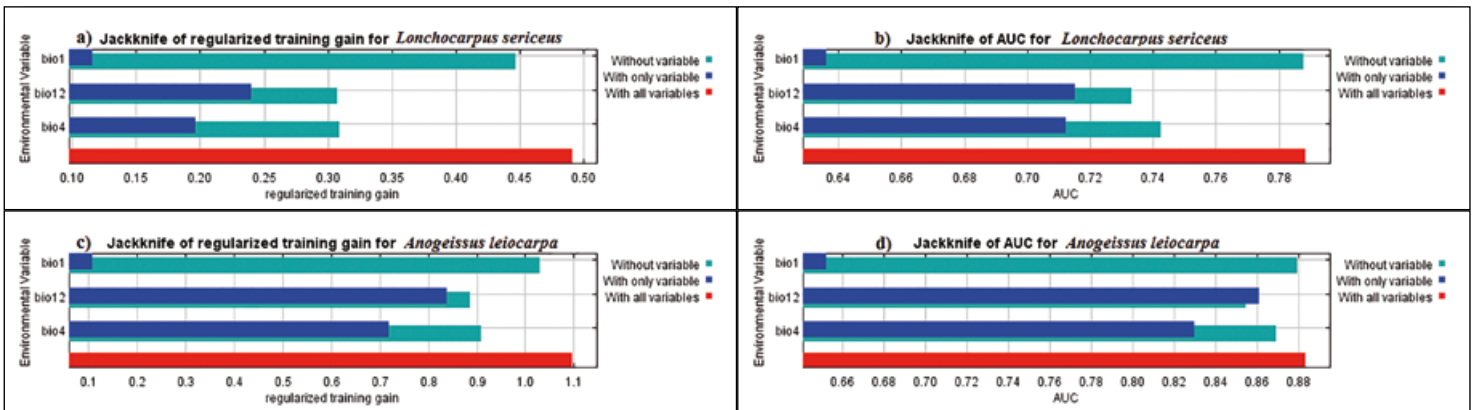
The response curve of *L. sericeus* to bio12 was bell-shaped, with an increase from 750 to 1,100 mm and then a sharply decline, but was generally above the suitability threshold between 750 mm and 2,500 mm (red line and interval of variation in blue; figure 4a). The logistic prediction was highest for bio1 between 26 and 28°C and for bio4  $< 2^\circ\text{C}$  (figure 4b and c). The response curve of *A. leiocarpa* to bio12 (figure 4d) was also bell-shaped between 500 and

**Table 1.**

Bioclimatic variables (bvar) predictors of (a) *Lonchocarpus sericeus* and (b) *Anogeissus leiocarpa* distributions. bio12 = Annual Precipitation (mm); bio1 = Mean Annual Temperature (°C); bio4 = Temperature Seasonality (standard deviation \*100, °C).

Bvar	WorlClim Definition	Estimate	Contribution (%)	Permutation importance (%)
<b>a) <i>Lonchocarpus sericeus</i></b>				
bio12	Annual Precipitation (mm)	-3.388e-04***	33.8	39
bio1	Mean Annual Temperature (°C)	4.932e-03***	13.8	9.6
bio4	Temperature Seasonality (°C)	-5.167e-04***	52.4	51.4
<b>b) <i>Anogeissus leiocarpa</i></b>				
bio12	Annual Precipitation (mm)	-4.450e-04***	68.3	20.5
bio1	Mean Annual Temperature (°C)	1.507e-02***	4.8	6
bio4	Temperature Seasonality (°C)	-3.937e-04***	27	73.5

\*\*\*: Probability < 0.000, very high level of significance of the variable; Contribution means how the variable contributed to the increase of the gain of the model, during the modelling. Permutation importance is linked to how the variable decrease the AUC, and therefore how the model is heavily dependent to that variable.



**Figure 3.**

Jackknife of regularized training gain (a and c) and of AUC (b and d) respectively for *Lonchocarpus sericeus* (a and b) and *Anogeissus leiocarpa* (c and d). The three variables are very important in the model as they could decrease the gain and the AUC when omitted.

1,300 mm, with the highest prediction at 1,200 mm. In response to bio1 (figure 4e), the prediction was above the suitability threshold between 24°C and 30°C and was the highest for bio1 = 28°C. The response curve of *A. leiocarpa* to bio4 was bell-shaped between 1 and 3°C were the prediction was above the suitability threshold, with the highest prediction at 1.4°C (figure 4f).



**Photo 4.**

The trunk of a tree of *L. sericeus*, covered by Lianas and surrounded by the exotic invasive *Chromolaena odorata* (L.) R.M.King. Photo A. J. Gbètoho.

**Table II.**

Potential habitat suitability for *Lonchocarpus sericeus* and *Anogeissus leiocarpa* distributions and climate characteristics under current and future climatic scenarios.

bio12 = Annual Precipitation (mm); bio1 = Mean Annual Temperature (°C); bio4 = Temperature Seasonality (standard deviation \*100, °C).

Bvar/Area	Current	rcp4.5	rcp8.5
bio12 (mm) <sup>a</sup>	1,061 – 1,090	1,045 – 1,077	1,064 – 1,097
bio1 (°C) <sup>a</sup>	27.0 – 27.3*	29.3 – 29.5†*	29.2 – 29.5†*
bio4 (°C) <sup>a</sup>	15.84 – 17.34*	17.0 – 18.5†*	18.0 – 19.0†*
<b>a) <i>Lonchocarpus sericeus</i></b>			
Whole country (km <sup>2</sup> ) <sup>b</sup>	83,687	79,185 (-4%)↓	76,962 (-8%)↓
Protected areas (km <sup>2</sup> ) <sup>b</sup>	16,312	15,483 (-3.4%)↓	14,654 (-10.2%)↓
<b>b) <i>Anogeissus leiocarpa</i></b>			
Whole country (km <sup>2</sup> ) <sup>b</sup>	101,241	101,241 (+0.2%)↓	101,241 (+0.2%)↓
Protected areas (km <sup>2</sup> ) <sup>b</sup>	24,279	24,486 (+0.8%)↓	24,486 (+0.8%)↓

Climatic values computed by choosing 130 random points in the whole country, and comparison of the values of the bvar for current climate to values for future climate; a: Confidence interval (CI) estimated with Wilcoxon rank for one sample; b: suitability area computed in QGIS, variation trend in brackets; † : increase; ↓ : decrease; \*: significantly different from the other values.

### Current and potential distribution for the horizon 2055

Under current conditions, at least 74% of the whole country was suitable to *L. sericeus*, which included 67% of the protected areas (forest reserves and the national park) from south to north (figure 5a-b; table II). Under future climate, both scenarios suggested a decrease of 3% to 7% of suitability area in the protected areas for that species. Almost the whole country (88.0%), including 89.2% of the national protected areas, was found to be currently suitable to *A. leiocarpa* (figure 5d-f). Both rcp suggested a substantial increase of the suitability area in the protected areas under future climate for that species (table II). The Wilcoxon test showed that bio12 was not significantly different between current climate and the two rcp, while there was a significant increase of bio1 and bio4 between current values and future projections. For each of these variables, the current climate had the lowest value, rcp4.5 was intermediate, and the rcp8.5 had the highest value.

## Discussion and Conclusion

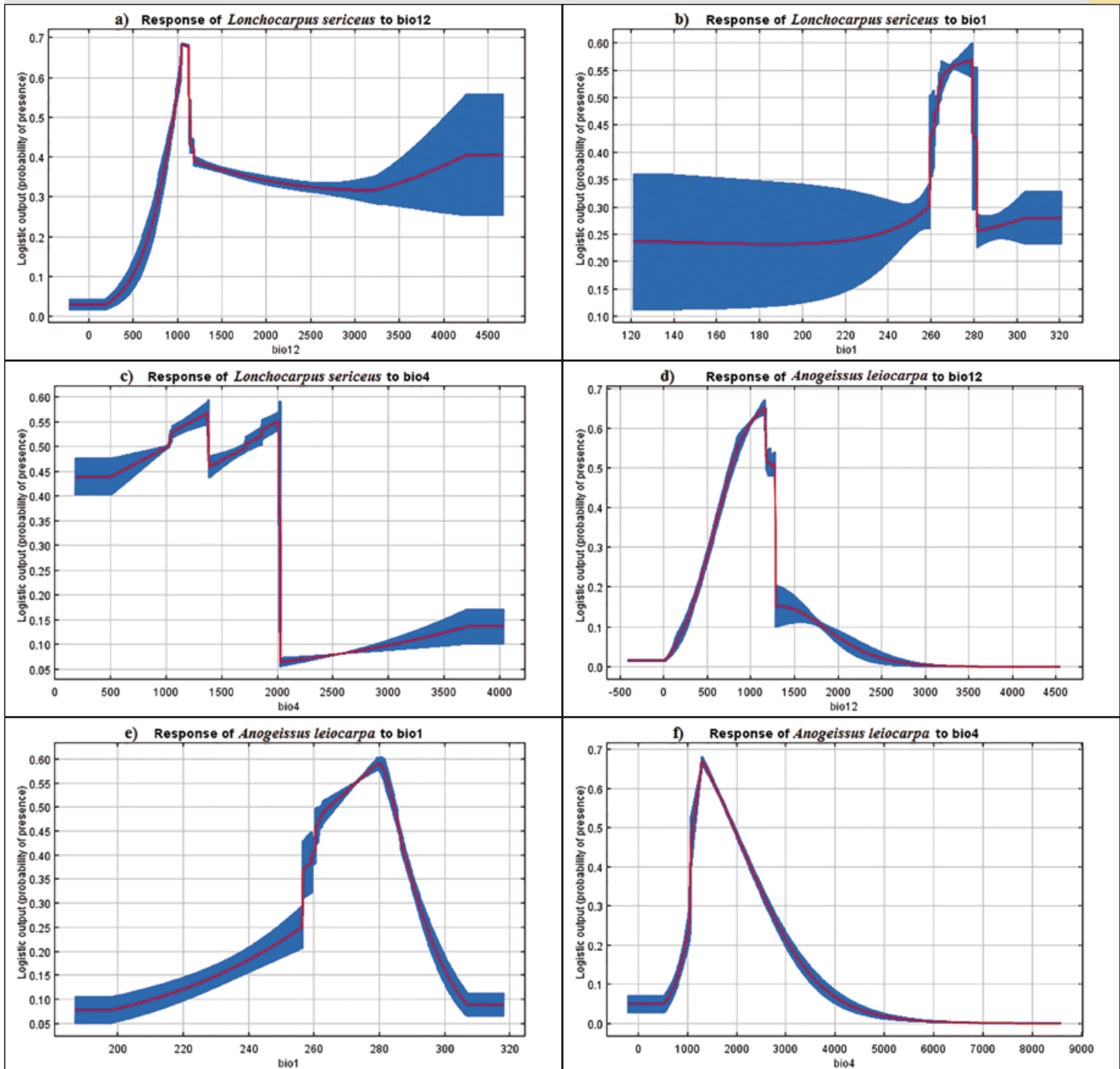
Tree pioneer species represent a great opportunity for forest managers who can plant them actively to accelerate plant succession and forest restoration. The knowledge of the niche of pioneer species could help to identify the best areas where particular species can be used with success. We identified the ecological requirements of two multi-purpose pioneer species with broad geographical distributions, using geographical spaces where the environmental conditions could be considered homogeneous. For the West African sub-region, which includes Benin, models were built to identify the areas where they can be used in ecological restoration for now and into the mid-century.

### Determinants of *L. sericeus* and *A. leiocarpa* distributions across West Africa

The distribution of a plant species in a geographic space is determined by complex interactions of biotic and abiotic factors. These factors include climate, soil characteristics, inter- and intra-specific competition, anthropic disturbances, and dispersal limitation (Blach-Overgaard *et al.*, 2010). The environmental factors are the main determinants of the living conditions of the species, while dispersal limitations and biotic interactions may further modify the distribution (Soberón and Peterson, 2005). Good knowledge of the environmental requirements of a species is therefore important to assess the broad geographic space where it could survive and its potential response to climate change for conservation and management purposes (Bowe and Haq, 2010).

At a large scale, the distribution of a species depends mainly on climate especially on factors related to water (Vayreda *et al.*, 2013). Annual precipitation is among the first contributors of the targeted species distribution. According to our models, annual rainfall between 750 and 2,500 mm was found to be suitable for the range of *L. sericeus* while it grows in area with annual rainfall from 1,200 to 1,900 mm. Indeed, the deficit could be compensated as that species is found along rivers, in forest galleries, in coastal secondary forests and semi-deciduous forests, and on swampy soils (Burkill, 1995). Furthermore, it is well adapted to hydromorphic soil and could support flooded (Gbêtoho *et al.*, 2016). The distribution of *L. sericeus* was already related to edaphic conditions by Burkill (1995). An annual precipitation between 500 and 1,300 mm is found to be suitable for *A. leiocarpa*, and those values are close to the 600 to 1,200 mm stated by Couteron and Kokou (1997). The species is well adapted to drought with annual



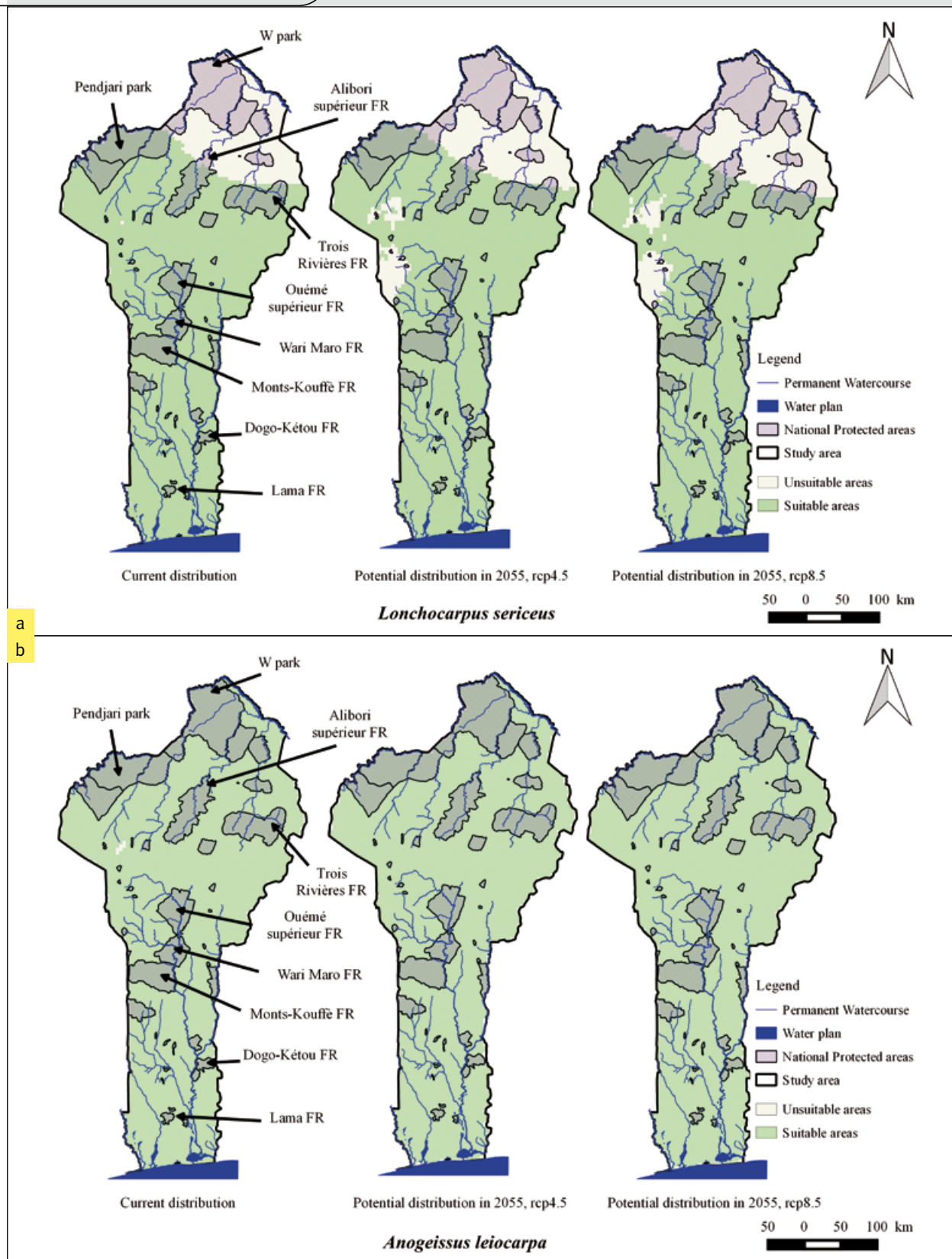


**Figure 4.**

Response curves of *Lonchocarpus sericeus* (a, b and c) and *Anogeissus leiocarpa* (d, e, f) distributions showing how logistic predictions varied with only the environmental variable considered. bio12 = annual rainfall (mm); bio1: annual temperature (°C) and bio4: temperature seasonality (°C \*100). bio12 between 750 mm and 2,500 mm, bio1 between 26 and 28°C and bio4 < 2°C are suitable for *L. sericeus*. bio12 between 500 and 1,300 mm, bio1 between 24°C and 30°C and bio4 between 1 and 3°C were suitable for *A. leiocarpa*.

temperature between 24°C and 30°C. Edaphic conditions in forest galleries and periodically flooded soils may allow *A. leiocarpa* to grow in severe drought conditions (Couteron and Kokou, 1997). Gouwakinnou (2011) also found drier

conditions and higher temperature for *Sclerocarya birrea* subsp. *birrea*, species of Sudano-sahelian Africa that had broader distributions in Africa and therefore, larger ecological amplitude as *A. leiocarpa*.

**Figure 5.**

Distribution of *Lonchocarpus sericeus* (a) and *Anogeissus leiocarpa* (b) under current and future climate conditions in Benin. *L. sericeus* distributions cover a great part of the country, but will decrease a little under future climate scenarios. The whole country is favourable to *A. leiocarpa* currently and under the future climate scenarios. As the species are found, in forest galleries and near water, the network of watercourses and water plan is also projected on the maps to show that even if rainfall is not enough, the species could get water from soils.

The edaphic conditions favourable to our pioneer species where the rainfall is limiting are related to soil moisture. Soil moisture may be an important factor that determines the distribution of the two species. However, soil related variables was not taken into account due to the scale of the modelling (> 2,000 km; Pearson and Dawson, 2003), the inexistence of adequate projections for soil hydrology, and because we are concerned with the impact of climate change on the range of the species. Furthermore, the isohyets of rainfall in Benin that showed a current lowest rainfall of 900 mm at the country level, and the well distribution of watercourse and water plan indicated that these species may not experience a water deficit at our country level.

### Current and potential distributions of the two species at the mid-century

Fundamental niche and potential distributions are convenient when the purpose of the modelling is introduction, as it represents the global cultivation potential (Cuni-Sanchez *et al.*, 2010). Therefore, assessing the potential distribution of our two species is relevant to support ecological restoration of degraded areas and secondary forests. The significance of the bvar and the high correlation of the modelling points to these bvar indicated that our variables were very suitable to achieve the distribution of the species. However, the “a priori” selection of these bvar, instead of retained variables using only Jackknife test could lead to difference in the results, which should be assessed by ensemble forecasting models (Araújo and New, 2007). AUC values and ratios showed that the models have good predictive power and could be used to predict the distributions of the species under current and future conditions.

Both the species may not experience water deficit, but, *A. leiocarpa* is more adapted to drought than *L. sericeus*, and we can see that *L. sericeus* is only distributed in coastal countries, while *A. leiocarpa* occurrences were also found in the sahelian zone. Therefore, the whole Benin is currently suitable for *A. leiocarpa*. But, the area located over the latitude of 11°N (north of Alibori Superieur Forest reserve and W park; figure 5a) where the temperature could exceed 30°C is not currently suitable for *L. sericeus*.

The current distribution of *A. leiocarpa* was very different to the result of Adjahossou *et al.* (2016) for that species in the same study area. The differences may be linked first to the low number of occurrences they used, the resolution of the environmental data and also to the consideration of the variable “soil” in their model. Indeed, the precision of the model increases with the number of training points, but the bias linked to the availability of presence-points could lead to overfitting when using environmental data with high resolution. For example, in a grid of 2.5' (150", ≈ 5 km) they are about 25 grids of 30" (≈ 1 km); even if they were presence points in each of these 25 grids of 30", they will represent only one occurrence after the removal of duplicates in the 150" grid. Climate is projected to become hotter and drier in West Africa under the rcp of AFRICLIM (Platts *et al.*, 2015). At Benin level, we found an increase of the precipitation and of the temperature at the horizon 2055. However, the

variations are still in the ranges of the values suitable for *A. leiocarpa* and very little increase in the favourable areas was not noticed. The two rcp give the same result for *A. leiocarpa*. Hounkpèvi *et al.* (2016) also found an increase of the potential area of *Vitex doniana* Sweet, which had also a large ecological amplitude with a rainfall requirement (700 mm to 2000 mm). However, the increase of temperature in the north will reduce a little the suitable area of *L. sericeus*. The decrease of the favourable area for *L. sericeus* is higher under rcp8.5 than under rcp4.5 (lower increase of temperature compare to rcp8.5). At all, the species should not be vulnerable to climate change.

### Implications for restoration policies

Ecological niche modelling had largely been used to inform relevant policies for species of interest such as agroforestry species, threatened species, invasive species, and pests (Bowe and Haq, 2010; Blach-Overgaard *et al.*, 2010) and the effectiveness of conservation through the network of protected areas. However, some protected areas are already threatened by unsustainable use of the existing resources (Houehanou *et al.*, 2013; Adjahossou *et al.*, 2016). The management of disturbed forests should consist of stopping the degradation in order to promote succession and to use ecological knowledge and practical experiences to rebuild forest ecosystems (Bongers *et al.*, 2006).

Forest managers usually prefers to ensure reforestation with good timber (commercial) species in order to make profitable the costs associated to the timber production. However the means are not generally available, and the natural forest in Benin are in general under integral protections and such operations could not be profitable economically, but only in the consideration of the intrinsic importance of biodiversity. Pioneer tree species are established first at the beginning of the succession, are gregarious and ensure the restoration of site quality for good recovery (Hooper *et al.*, 2005). At canopy closure, they will progressively be replaced by late successional species. This work shows our species represent a great opportunity in forest management and could be used to achieve forest restoration in the short and mean terms. However, can we plan large restoration actions with these two species?

The use of MaxEnt is subjected to some uncertainties. These uncertainties resulted from the non-use of absence data, the selection of non-biological variables, and the potentiality of overfitting data (Royle *et al.*, 2012). Some of these uncertainties could be solved through the choice of the good regularization multiplier (Warren and Seifert, 2011), the good choice of the extent of modelling (Lobo *et al.*, 2010), the visual analysis of the ecological meaning of the predictions map, and the combination of MaxEnt results to other statistical methods, of which the general linear models (Guisan *et al.*, 2002; Renner and Warton, 2013). However, the source of variations in SDM could also be linked to the statistical methods, the variables selected, the climate data used..., and only ensemble forecasting models are able to achieve these uncertainties (Araújo and New, 2007).



**Photo 5.**

In the secondary forests of Lama, a stand composed by trees of *Lonchocarpus sericeus*. On the ground, the biomass of the invasive exotic *Chromolaena odorata* (L.) R.M.King is increasing due to tree gaps.

Photo A. J. Gbètoho.

At this step, managers could associate our results to the composition and successional pathways of their forests and plante the species in the forests where they are relatively important (importance value index) in the canopy composition, such as Lama forest (Gbètoho *et al.*, 2016). Therefore, the seeds of the species could be collected in order to produce seedlings that will be planted in degraded areas, fallows, and secondary forests of protected areas. Human dispersion of the seeds in forest areas followed by light silvicultural treatments such as weed suppression may also be done. With the principle of participatory management, the local people should be associated in the production of the seedlings or in their dispersion in the vegetation, to get some incomes for their livelihoods. Further studies are needed to assess the least expensive but most successful method, among planting of seedlings and human dispersal of seeds, and the best techniques to achieve forest restoration through facilitated establishment of pioneer species in degraded forest areas.

The present work should be extended to several pioneer species, and should include abundance data to get more precision, to examine biotic interactions, environmental non climatic variables importance in order to really put at the disposal of forest managers a good set of species to be used to ensure restoration at low cost of protected areas in Benin.

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