



# Ecological niche information supports taxonomic delimitation of *Irvingia gabonensis* and *I. wombolu* (Irvingiaceae)

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## ABSTRACT

African bush mango trees (Irvingiaceae) are priority food trees in West and Central Africa. There are bitter- and sweet-fruited species, which are difficult to distinguish based on morphological characters. This has led to a debate about their correct taxonomic status. Furthermore, it is unclear whether they are native to the Dahomey Gap, the dry and hot area, separating the two West African forest blocks. This study evaluates the ecological differences between bitter- and sweet-fruited species in tropical Africa, and the nature (wild vs. cultivated) of the occurrences in the Dahomey Gap, in order to discuss the current taxonomical opinions. *Irvingia gabonensis* and *I. wombolu* occurrence data were combined with climate and soil data in MaxEnt to produce environmental niche models. Environmental niche identity tests were carried out in ENM-Tools. Wild sweet-fruited trees were predicted in the Guineo–Congolian phytogeographical region, while the predicted occurrence of bitter-fruited trees extended to the Guineo–Congolia/Sudania and Lake Victoria transition zones. The related niche difference is significant, supporting the taxonomical opinion that bitter- and sweet-fruited species are two different taxa. We also conclude that bitter-fruited trees occur naturally in the Volta forests (Dahomey Gap). Moreover, our results support that *I. gabonensis* is not native to the Dahomey Gap. In historical times, they were probably introduced from Nigeria.

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## 1. Introduction

African bush mango trees (ABMTs) belong to the Irvingiaceae and occur in evergreen and semi-deciduous forests in West and Central Africa (Harris, 1996; Lowe et al., 2000). They are priority food tree species (Franzel et al., 1996) because they produce two major non-timber forest products: the edible mesocarp of their mango-like fruit (eaten when it has a sweet taste), and the kernels inside the seed (which are used to thicken and flavor sauces) (Tchoundjeu and Atangana, 2007). Two species of ABMTs are recognized: the sweet and edible fruited species, and the one that bears extremely bitter and totally inedible fruit pulp (Harris, 1996; Lowe et al., 2000). The taste of the fruit pulp is a reliable criterion that easily discriminate between the two species throughout their geographical distribution range. Attempts to separate them using morphological characters are unsatisfactory (Okafor, 1975; Harris, 1996; Vihotogbé et al., 2013) in separating these species taxonomically. Okafor (1975) regarded the difference in fruit pulp taste as

weak character and merely recognized the different taxa at variety level: *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. var. *gabonensis* and *I. gabonensis* var. *excelsa* (Mildbr.) Okafor for the sweet- and bitter-fruited trees respectively. However, Harris (1996) recognized them at species level as *I. gabonensis* and *I. wombolu* Vermoesen, respectively, although he admitted the weak morphological dissimilarity between them. Lowe et al. (2000) and Vihotogbé et al. (2014a) supported the species level opinion based on Random Amplified Polymorphic DNA (RAPDs) markers and phenological data. However, because of low reproducibility of RAPDs, and despite the low probability for hybridization between *I. gabonensis* and *I. wombolu* (Lowe et al., 2000; Vihotogbé et al., 2014a), this taxonomic opinion is still controversial. The uncertainty about ABMTs taxonomic position hinders breeding and genetic resources conservation programs (Austen et al., 2016).

ABMTs occur in the Guineo–Congolian phytogeographical region, and also throughout the Guineo–Congolian/Zambezian zone and Guineo–Congolia/Sudania Transition zone (White, 1979). The Guineo–Congolian region is divided into the Upper and Lower Guinean rain forest blocks (White, 1979; Droissart et al., 2018) that are interrupted by a

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savannah corridor known as the Dahomey gap (Maley, 1996). The ecoregion of the Dahomey Gap is hotter and dryer than the Upper and Lower Guinean forest blocks, and extends from Accra, in Ghana across Togo and Benin to Badagry, in Nigeria (Sowunmi, 2004). In their distribution range the significance of ecological factors that govern differences between both taxa have never been discussed.

From the taxonomic revision of Harris (1996) it is clearly shown that sweet- and bitter-fruited ABMTs have different distribution ranges. According to Harris (1996), while *I. gabonensis* is confined to the Lower Guinean forests, *I. wombolu* occurs from Upper Guinea to the northern half of the Lower Guinean regions and the Guineo–Congolia/Sudania Transition zone east to Lake Victoria (Uganda). The latter distribution pattern is typical for species with a preference for sub-humid and semi-deciduous forest habitats, while the first is typical for species with a preference for humid evergreen forests. According to the ecological species concept (Van Valen, 1976) species are to be regarded as a set of organisms exploiting a single niche (Ridley, 1996; Aldhebiani, 2018). So, when two sets of closely related organisms occupy different niches, this can be seen as evidence for genetic differences between them (Templeton, 1991). In other words, the two sets seem to conserve their genetic integrity and therefore exchange of genetic material does probably not take place (Ridley, 1996). Thus, they most likely show reproductive isolation and also act as species under the biological species concept (Mayr, 1963). This shows that niche preference may be interpreted as an additional character set to be used as criterion for species distinction and hence for taxonomic purposes.

The increased market demand of bush mango kernels causes an over-exploitation in natural habitats. This results in poor regeneration of ABMTs across their distribution range (Lowe et al., 2000). Therefore, cultivation initiatives are increasing throughout their distribution range, with the higher domestication level in the Dahomey Gap (Vihotogbé et al., 2013), where Vihotogbé et al. (2018) assessed the geographical distribution of cultivable lands. Thus, clarification of the conflicting nature of occurrences (Harris, 1996; Vihotogbé et al., 2018) is needed, for a better ecological and taxonomical knowledge of these taxa.

Ecological niche modeling (ENM) relates known occurrences of a species with environmental predictors related to the species niche to generate the probability of its presence for any point within the geographic area under investigation (Guisan and Zimmermann, 2000; Franklin, 2009). Given their ability to identify areas where species should be able to successfully complete their life cycle, ENM is a powerful tool for agro-biodiversity conservation (Miller and Knouft, 2006; Sanchez et al., 2010). Numerous algorithms have been designed to refine ENM techniques. In the case of presence-only data, the maximum entropy approach (MaxEnt; Phillips et al., 2006) was identified as the more accurate, even when the set of known occurrences is limited (Elith et al., 2006; Pearson et al., 2007; Wisz et al., 2008; Leaché et al., 2009). Testing for significance of an ENM was developed by Raes and ter Steege (2007) applying a null-model approach (Gotelli and McGill, 2006). Furthermore, the ENM-Tools package was developed (Warren et al., 2008) to quantify niche differences between taxa (McCormack et al., 2010). We used all three methods to address the following two main research questions:

1. Are the environmental niches of bitter- and sweet-fruited ABMTs significantly different?
2. Is the Dahomey Gap included in the environmental niche of sweet- and/or bitter-fruited ABMTs?

## 2. Materials and methods

### 2.1. Presence data

Using different sources, we obtained 101 occurrence records for *I. wombolu* and 262 for *I. gabonensis* (Table 1). In this study, we used occurrences that are engaged in the conflicting taxonomical opinions of

**Table 1**

Data sources and sample size for both *Irvingia* species used in the study.

| Species                    | Occurrence data source              | Total sample size | Unique records |
|----------------------------|-------------------------------------|-------------------|----------------|
| <i>Irvingia wombolu</i>    | Naturalis Biodiversity Center Brahm | 14                | 76             |
|                            | GBIF Data Portal (2018)             | 37                |                |
|                            | Lowe et al. (2000)                  | 28                |                |
|                            | Harris (1996)                       | 22                |                |
| <i>Irvingia gabonensis</i> | Naturalis Biodiversity Center Brahm | 88                | 174            |
|                            | GBIF Data Portal (2018)             | 98                |                |
|                            | Lowe et al. (2000)                  | 76                |                |

these taxa. The records were collected across tropical Africa, based on their unequivocal description, regarding the fruit pulp taste: (i) edible sweet fruit pulp for *I. gabonensis*, and (ii) extremely bitter and totally unpalatable mesocarp for *I. wombolu* (Harris, 1996; Lowe et al., 2000). Any record suspected to represent a cultivated specimen, or with no consistent description regarding fruit pulp taste, was discarded. Additionally, herbarium specimens used by Harris (1996) were georeferenced and the sample location maps of Lowe et al. (2000) were digitized to extract ABMTs' geographic positions. Data obtained from the in-house database of the Naturalis Biodiversity Center (GBIF Data Portal, 2018), were checked critically and used as an occurrence record, only if the identification was sufficiently trustworthy. Duplicate records (from the different sources) were removed and the data was resampled to 5 arc-minute ( $\sim 9.3 \times 9.3$  km) to yield a total of 250 unique presence records, 76 for *I. wombolu* and 174 for *I. gabonensis* (Table 1).

### 2.2. Environmental factors

Consistent conclusions can be drawn from ENMs based on climatic variables only (Scheldeman et al., 2007). But, because climatic data often have limited power to capture small scale variations in a landscape and can display important spatial autocorrelations, additional environmental factors, notably soil properties, are often required to improve the predicted outcomes of an ENM. This is particularly important when assessing environmental differences between closely related species that geographically co-occur (McCormack et al., 2010). Moreover, it has been shown that a combination of soil and climate variables play a key role in higher plant species distribution pattern in tropical Africa (Linder et al., 2005). We used both climatic and soil data as environmental factors to produce our ENMs. Nineteen 5-arc-minutes bioclimatic variables were obtained from the WorldClim database (<http://www.worldclim.org/current>), and soil data were collected from the ISRIC World Soil Information database (ISRIC-WISE version 1.2; <http://www.isric.org/>). We defined our study area being West and Central Africa, limited by 2° S to 15° N latitude and 15° W to 35° E longitude, and cropped all environmental parameter layers for this area. Then, bioclimatic variables were tested for multicollinearity using Pearson's correlation, and only those with  $|r| < 0.70$  were retained (Dormann et al., 2007). Soil data were tested for multicollinearity using Spearman rank correlation, to overcome issues related to differences in units (i.e. pH, density, ratio), and soil variables with Spearman's  $|\rho| < 0.70$  were retained. For groups of correlated variables, we used a PCA analysis to select the ones with the highest information content (highest factor loading on axes one or two) combined with ecological interpretation. The topsoil salinity (although showing complete independence against all other variables) was not retained because it holds negligible information within the ranges of ABMTs. In total, 14 environmental layers (8 climatic and 6 soil layers) were used in the ENM (Table 2).

### 2.3. Environmental niche modeling

Using MaxEnt with default parameters, a model for each of the two taxa was produced, based on the 14 environmental layers. The

**Table 2**

Contribution of abiotic variables to environmental niche models.

| Abiotic variables |                                      | Contribution (%)     |                   |
|-------------------|--------------------------------------|----------------------|-------------------|
| Code              | Description                          | <i>I. gabonensis</i> | <i>I. wombolu</i> |
| Bio1              | Annual mean temperature              | 2.0                  | 0.4               |
| Bio2              | Mean diurnal range                   | 50.0                 | 2.3               |
| Bio4              | Temperature seasonality              | 3.8                  | 0.8               |
| Bio6              | Minimal temperature of coldest month | 9.0                  | 6.6               |
| Bio14             | Precipitation of driest month        | 0.1                  | 59.9              |
| Bio15             | Precipitation seasonality            | 15.1                 | 0.3               |
| Bio16             | Precipitation of wettest quarter     | 16.8                 | 6.7               |
| Bio19             | Precipitation of coldest quarter     | 0.4                  | 17.1              |
| BULK              | Bulk soil density                    | 0.1                  | 1.0               |
| CFRAG             | Coarse fragments                     | 1.2                  | 2.7               |
| CNrt              | C/N ratio                            | 0.5                  | 0.9               |
| ESP               | Exchangeable Na percentage           | 0.2                  | 0.0               |
| PHAQ              | pH measured in water                 | 0.5                  | 1.5               |
| TOTN              | Total nitrogen                       | 0.4                  | 0.0               |

projection of the obtained models in the geographical space provides the potential distribution area of the corresponding taxon. Model accuracy was assessed using the area under the curve (AUC) of the Receiver Operating Characteristic (ROC) plot (Fielding and Bell, 1997). This statistic describes the relationship between the percentage of correctly predicted presences against that of incorrectly predicted absences and ranges from 0.5 (random prediction) to 1 (high model consistency). Since MaxEnt is a presence-only modeling technique and absences are replaced by pseudo-absences or a background sample (Phillips et al., 2006), the maximum AUC is no longer 1 and can therefore not be used. Raes and ter Steege (2007) recognized this problem and developed a null-model approach to test whether the obtained AUC value is significantly better than a random expectation. We developed two null-distributions by modeling 99 sets of respectively 74 and 176 presence localities randomly drawn from the study area. This yielded 99 AUC values for each niche model and 100 when the AUC values of *I. wombolu* and of *I. gabonensis* were added. All AUC values were ranked and when the AUC value of the true taxon was ranked above the 95th AUC value of the series, the chance that a random set of localities produces an equally good model is less than 5%, hence it is significantly different from random expectation. The method is described in more detail by Raes and ter Steege (2007).

## 2.4. Environmental niche overlap and identity testing

This analysis aims to evaluate the difference between the niche models of bitter- and sweet-fruited trees. The models produced by MaxEnt were used in ENM-Tools to calculate the Schoeners *D* and Hellinger *I* similarity indices (Warren et al., 2008) measuring the niche overlap between model pairs. This similarity index ranges from 0 for niches completely disjoint, to 1 for identical niches (Warren et al., 2008). The significance of the niche difference is then assessed by pooling the occurrences from both taxa and subsequently generating 100 pseudo-replicate pairs of 74 and 176 occurrences by randomly sampling from the pooled dataset. Actual niche overlap between the two *Irvingia* taxa was compared with those of the 100 randomly obtained sets. If the Schoener *D* and Hellinger *I* values between the two models of the *Irvingia* taxa are lower than the values of the 100 pseudo-replicate pairs, niche overlap is less than random chance, and hence the difference is significant.

## 3. Results

### 3.1. Potential distribution areas

Figs. 1 and 2 provide the environmental niche models of *I. gabonensis* and *I. wombolu*. With an AUC value of 0.968 for *I. gabonensis* and 0.922 for *I. wombolu*, respectively, both models are significantly better than the random expectation ( $p < .01$ ). Figs. 3 and 4 show the null-distributions of the AUC values for 174 and 76 records. In both cases, the AUC value of the models of *I. gabonensis* and *I. wombolu* are larger than the 95% upper confidence interval values. *Irvingia gabonensis* is predicted to occur in western Central African forest regions coinciding well with the Lower Guinea forest block. Some high occurrence probabilities are concentrated close to the coasts of West Africa, west of the Dahomey Gap and so within the Upper Guinean forests, although no occurrence data (i.e. actual observations) from this area are known. The Dahomey Gap is excluded from the potential distribution range of the species, apart from two very small areas in western Togo (Volta forest region) and the southernmost tip of Benin (Fig. 5). The potential distribution of *I. wombolu* partly overlaps with that of *I. gabonensis*, notably in Nigeria, Cameroon and narrow strips in West Africa, but extends both to sub-humid areas (Sierra Leone, northern Ivory Coast, Central African Republic, etc.). Part of the Dahomey Gap is also included. The spatial

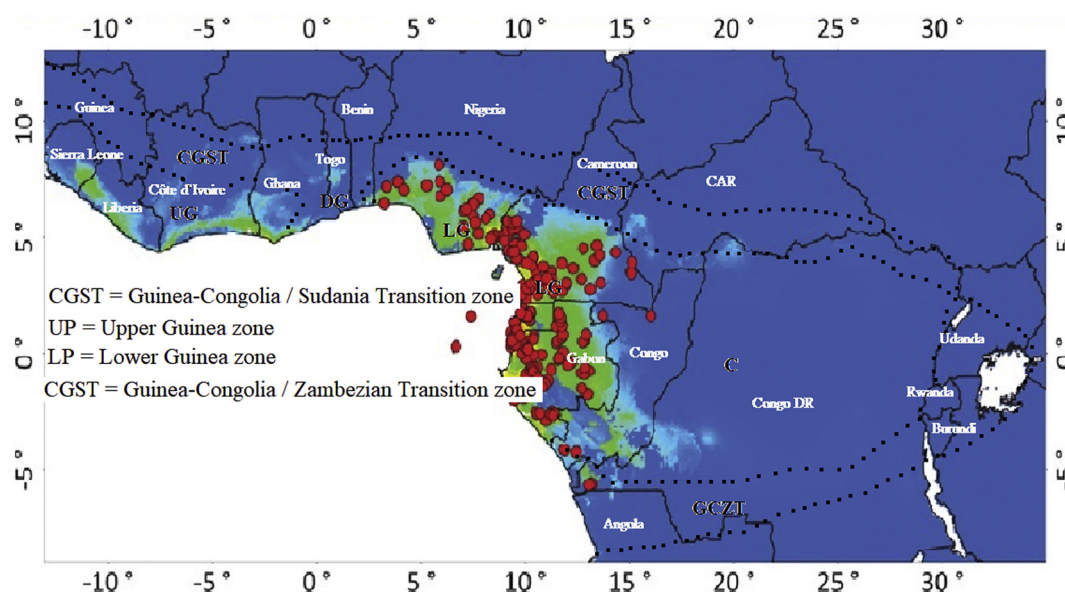


**Fig. 1.** Species distribution model of *Irvingia gabonensis*. Red dots indicate actual occurrence data points used. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

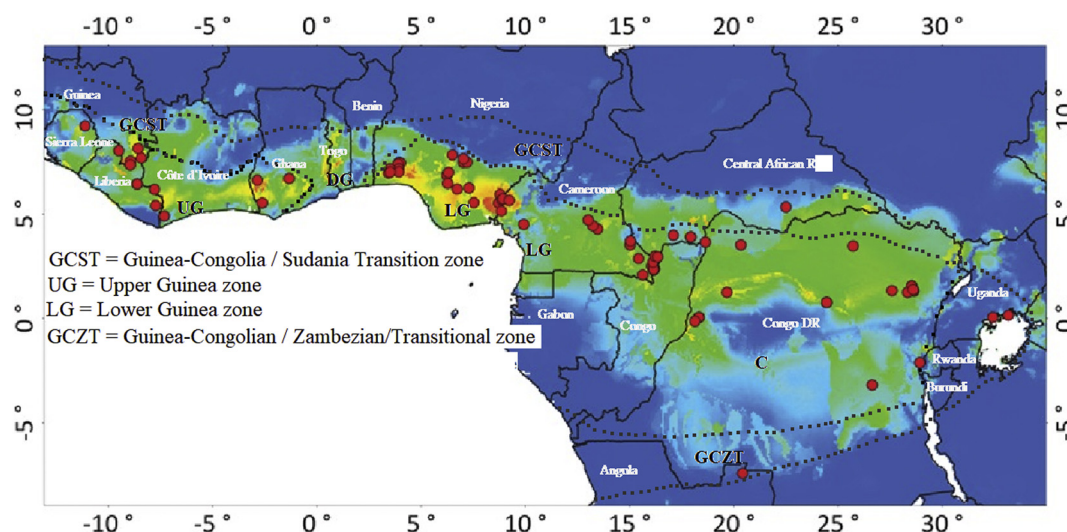


**Fig. 2.** Species distribution model of *Irvingia wombolu*. Red dots indicate actual occurrence data points used. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

overlap between the two MaxEnt models is shown in Fig. 5, for which the probability of occurrence values was converted to discrete presence-absence maps using the 10-percentile presence threshold prior to mapping.

### 3.2. Environmental niche differences

From Table 2 it is clear, and as expected from Figs. 1 and 2, that the predictions of the two ENMs are driven by different environmental factors. The occurrence of *I. gabonensis* is most highly associated with the mean diurnal range (50%), precipitation in the wettest quarter (16.8%) and precipitation seasonality (15.1%), while that of *I. wombolu* is determined by precipitation in the driest month (59.9%) and precipitation in the coldest quarter (17.1%). Remarkable is that none of the soil variables seems to have a high influence on the potential distributions. Figs. 6 and 7 show niche overlap expressed by the Schoener *D* and Hellinger *I* statistic and indicate that the model pair similarity fell far out of the range of values from 100 randomly sampled sets. Thus, it can be concluded that the natural habitats populated by *I. gabonensis* and *I. wombolu* are significantly different.

## 4. Discussion

### 4.1. Ecological and taxonomic differences between bitter and sweet ABMTs

The difficulty to distinguish between bitter- and sweet-fruited trees based on morphological characters was the key argument of Okafor (1975) to opt for the taxonomic level of variety instead of species. However, the fairly striking difference in distribution of the two taxa as provided by Harris (1996) led us to investigate their respective niches and possible differences. Our study has now demonstrated that indeed the two taxa populate significantly different environmental niches. This is in line with Vihotogbé et al. (2018) who demonstrated significant differences in cultivable lands, meaning different ecological adaptability between both taxa. Since the occupation of a distinct niche is most likely caused by a genetic difference, we may conclude that most likely the two *Irvingia* taxa maintain a distinct genetic integrity, and as such should best be regarded as distinct taxa at the species level. The existence of a genetic difference is corroborated by the genetic and phenological studies of Lowe et al. (2000) and Vihotogbé et al. (2014a), respectively. However, a recent morphological study of bark, leaf and

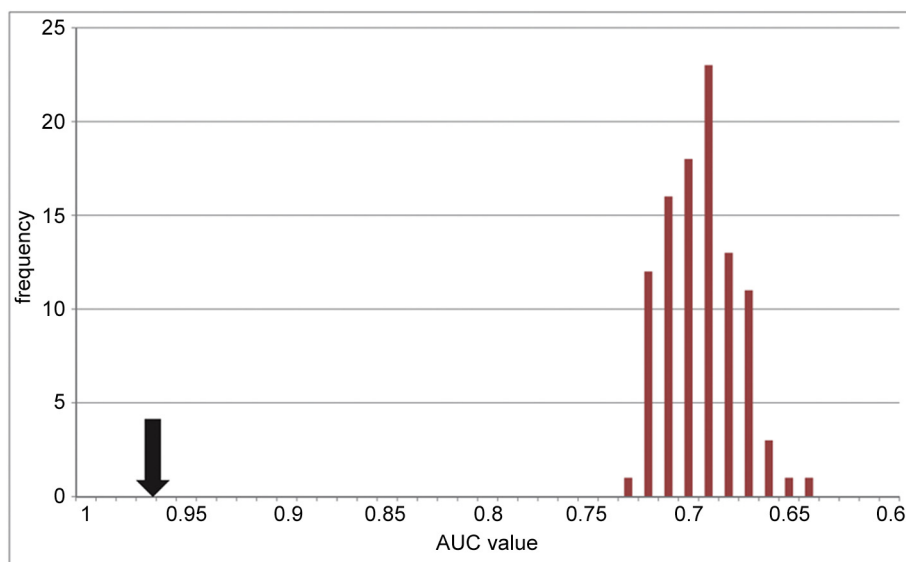


**Fig. 3.** Distribution of the niche model AUC values for 99 sets of 174 randomly drawn localities. Arrow indicates AUC value of *I. gabonensis*.

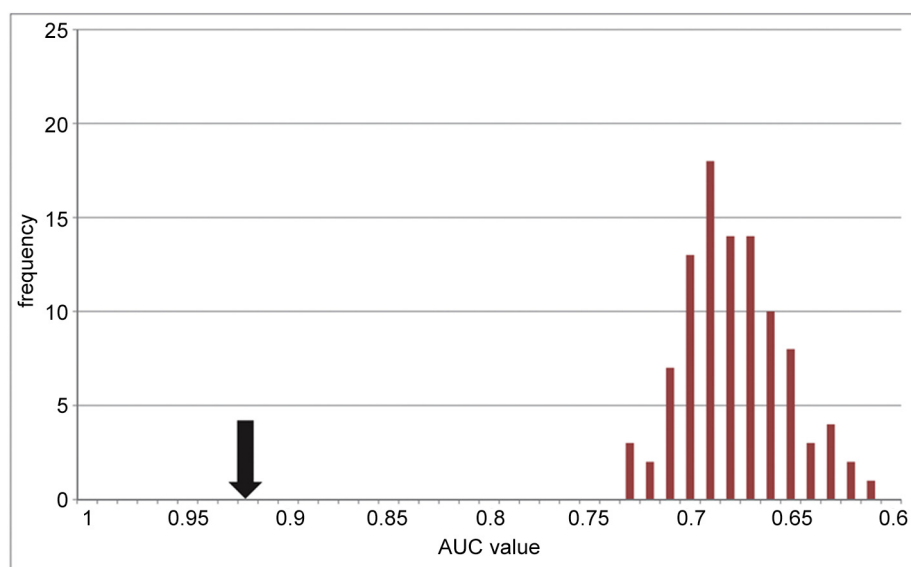


Fig. 4. Distribution of the niche model AUC values for 99 sets of 76 randomly drawn localities. Arrow indicates AUC value of *I. wombolu*.

fruit characteristics (Vihotogbé et al., 2013) did not yield any consistent differentiating characters, apart from unequivocal dissimilarity in fruit pulp taste and fibrosity. Therefore, we strongly recommend additional morphological and molecular analysis to arrive at a final verdict on this taxonomic issue.

The potential distribution of *I. gabonensis* is restricted to the wetter parts of the Guineo–Congolian phytocorion. This is consistent with findings of Kang et al. (1994), which indicated better growth and fruiting performances in Port Harcourt (south-eastern Nigeria, annual rainfall 2400 mm) than in Ibadan (south-western Nigeria, annual rainfall 1300 mm). The contrasting extension of bitter-fruited trees to sub-humid climatic conditions (Ndoye et al., 1997) was also confirmed by our models with optimum habitat suitability at relatively low levels of precipitation in the driest month. This is consistent with higher fruiting levels for bitter-fruited trees compared to sweet-fruited trees in the sub-humid south-western Nigeria (Kang et al., 1994). As such, bitter-fruited trees display a higher ecological variability than sweet-fruited ones. Therefore, the much larger area of cultivatable land found for *I. gabonensis* in the Dahomey Gap might be a purely human-driven process (Vihotogbé et al., 2018).

Lowe et al. (2000) postulated the presence of genetic diversity centres of *I. wombolu* to be in southern Nigeria and south-eastern Cameroon. Especially the first coincides with our predicted highest occurrence probabilities (Fig. 2). Additionally, our results also suggest high occurrence probabilities of *I. wombolu* in the Upper Guinean forest block (Harris, 1996). The Dahomey Gap isolates the Upper Guinean from the Lower Guinean forest block, and thus forms a barrier against the natural exchange of genetic material (Giresse, 2008). Therefore, the study of Lowe et al. (2000) should preferably be extended to include material of *I. wombolu* from the Upper Guinean forests to validate their conclusions for its entire distribution range.

Although there is a significant geographical overlap of their ecological niche models, *I. gabonensis* and *I. wombolu* are known as rainy season and dry season bush mango trees, respectively (Tchoundjeu et al., 2005; Alonge and Idung, 2015). Furthermore, it was demonstrated that totally different fruiting periods consistently distinguish *I. gabonensis* from *I. wombolu* in sympatric areas of the Volta forest region (Vihotogbé et al., 2014a) and Lowe et al. (2000) calculated low probability for hybridization between these taxa.

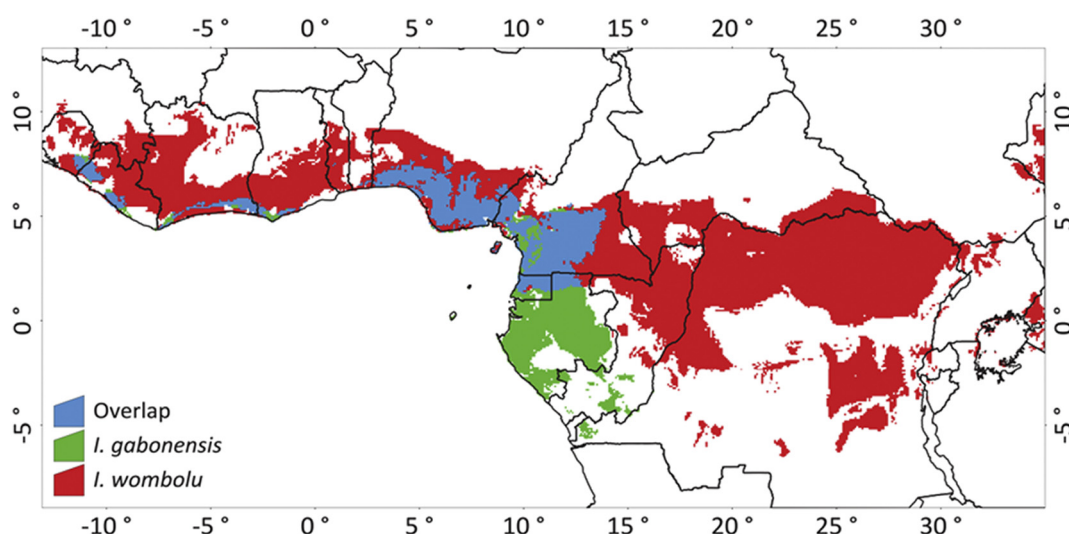


Fig. 5. Overlap in species distribution models of both *Irvingia* species in this study. Models converted to discrete presence/absence maps with a 10-percentile presence threshold.

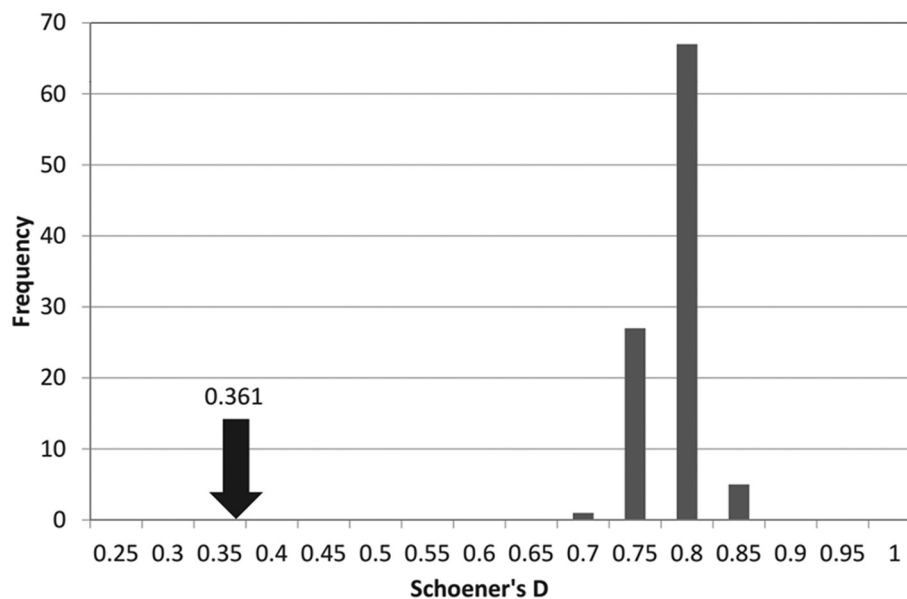


**Fig. 6.** Significance test on niche similarity – 1. Schoener *D* similarity index between the two *Irvingia* niche models (black arrow), compared with those between 100 paired sets of localities randomly drawn from the pooled data (for a more detailed description, see text).

#### 4.2. Occurrence and origin of ABMTs in the Dahomey Gap

This study shows that the Volta forest zone in western Togo, the wettest area in the Dahomey Gap, is part of the predicted environmental niche of *I. wombolu* (Fig. 2). In this area, bitter-fruited trees are known as “the never cultivated ABMTs” or “wild only ABMTs”, while in the rest of the Dahomey Gap local communities are not familiar with this taxon (Vihotogbé et al., 2018). In the Volta forest, *I. wombolu* is found in secondary forests often under direct influence of the surrounding villages. Other species are even deliberately planted in these forests, which is why such an agroforestry system is referred to as a forest garden (Wiersum, 2004). Because of the uncertainty about its natural occurrence there, no *I. wombolu* occurrence data from the Volta zone were entered in our original data set. It is now clear from the niche model (Fig. 2) that this environment is highly suitable for this species and that, most likely, its presence originates from a natural occurrence

(Vihotogbé et al., 2018). Local communities in the Volta forest region confirmed that sweet-fruited trees have been introduced and are cultivated primarily for their sweet mesocarp, but the seed of any ABMT has no place in their diet and is even not yet completely accepted by many sociocultural groups outside the Volta forest region in Togo. Therefore, apart from a general use as timber, bitter-fruited trees have no direct value for local communities in the Volta region, the mesocarp being inedible. Also, local knowledge about social and medicinal use of ABMTs is very poor (Vihotogbé et al., 2014b). We confirm here that bitter ABMTs are native to the Volta forest zone and are passing from a wild status within natural forest to a situation with scattered individuals preserved in agricultural productive spaces, notably forest gardens and farms. Thus, intensive cash crop production and increasing market value for the wood of *I. wombolu*, are causing decline of regenerations and species' population size (Vihotogbé et al., 2018). Therefore, the local distribution range of *I. wombolu* is likely to decline over time (Posner, 2008).

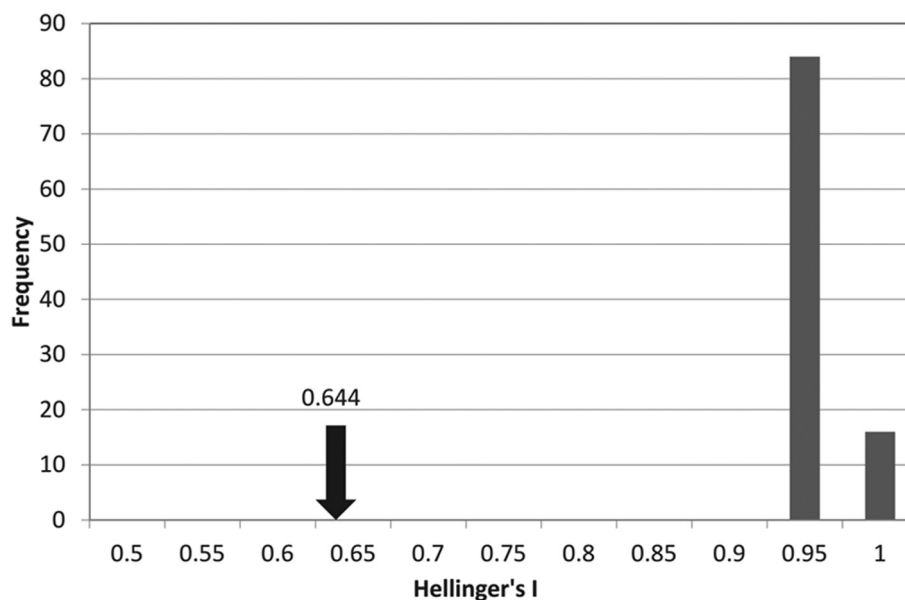


**Fig. 7.** Significance test on niche similarity – 2. Hellinger *I* similarity index between the two *Irvingia* niche models (black arrow), compared with those between 100 paired sets of localities randomly drawn from the pooled data (for a more detailed description, see text).

The Dahomey Gap is an ecological zone where *I. gabonensis* occurs, but outside of its natural environmental niche (Fig. 1). During extensive fieldwork in this ecoregion, no wild sweet-fruited trees were recorded, not even in forest relicts preserved throughout the Dahomey Gap, including the comparatively wetter Volta forest in western Togo (Vihotogbé et al., 2018). Ethnobotanical data suggest the introduction of sweet-fruited trees into the Dahomey Gap from the Lower Guinean forest block through migration of the Nigerian Yoruba communities and their subsequent settlement in south-eastern Benin. From there, material seems to have spread to other parts of Benin and Togo (Vihotogbé et al., 2014b). This is consistent with the conclusion of Ude et al. (2006) who suggest that sweet-fruited trees dispersed from the Lower Guinean forests to sub-humid ecological areas in the Guinea–Congo/Sudania Transition zone. Therefore, we postulate that the occurrence of sweet-fruited trees in the Dahomey Gap is solely due to cultivation activities (Harris, 1996; Tchoundjeu and Atangana, 2007) and the market-led domestication process has created high ecological adaptation and economically profitable plant material (Vihotogbé et al., 2013, 2018). Sayer (1992) postulated that in the Dahomey Gap the expected natural vegetation under the current climate would consist of semi-deciduous forest interspersed with tracts of denser vegetation types such as riverine forest as well as patches of swamp forest and lowland evergreen forest. Nagel et al. (2004) and Tossou et al. (2008) claimed that this implies that the present-day savannah vegetation was humans-induced, while Salzmann and Hoelzmann (2005) demonstrated that, before its establishment, the Dahomey Gap was occupied by evergreen forests with typical Guineo–Congolian forest trees species. This past climatic phase plays an important role in explaining present-day tree species distributions (Linder et al., 2005; Waltari et al., 2007). Therefore, hindcasting their potential distribution with past climatic data could be particularly useful to indicate habitat suitability for sweet ABMTs in the past in order to infer the true origin of the Dahomey Gap trees, or a possible extinction event in Upper Guinea.

#### 4.3. ENM as a new taxonomic hypothesis testing tool

We have argued above that the niche of a specific taxon should be treated as a distinct characteristic and can be used as a diagnostic tool to at least support or contradict a presumed taxonomic distinction, similar to morphological or molecular data. Now that ENM becomes easier to apply and techniques are being further improved and refined, and at the same time digitized natural history collection data are increasingly becoming available, ENMs open up a new toolbox to test taxonomic hypotheses.

#### Declaration of Competing Interest

This research was conducted with significant contribution of all authors, who all agree upon its submission to *South African Journal of Botany*. The authors declare that they have no conflict of interest.

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#### References

- Aldhebiani, A.Y., 2018. Species concept and speciation. *Saudi J. Biol. Sci.* 25, 437–440.
- Alonge, A.F., Idung, M., 2015. Development of a bush mango (*Irvingia gabonensis*) Nut-cracker. *Agric. Eng. Int.* 17, 191–199.
- Austen, G.E., Bindemann, M., Griffiths, R.A., Roberts, D.L., 2016. Species identification by experts and non-experts: comparing images from field guides. *Sci. Rep.* 6, 33634. <https://doi.org/10.1038/srep33634>.
- Dormann, C.F., McPherson, J.M., Araújo, M., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Droissart, V., Dauby, G., Hardy, O.J., Deblauwe, V., Harris, D.J., Janssens, S., Mackinder, B.A., Blach-Overgaard, A., Sonké, B., Sosef, M.S.M., Stévant, T., Svenning, J.-C., Wieringa, J.J., Couvreur, T.L.P., 2018. Beyond trees: biogeographical regionalization of tropical Africa. *J. Biogeogr.* 45, 1153–1167.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Mc, C., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Franklin, J., 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge.
- Franzel, S., Jaenicke, H., Janssen, W., 1996. Choosing the Right Trees: Setting Priorities for Multipurpose Tree Improvement. ISNAR Research Report No. 8. International Service for National Agricultural Research, The Hague.
- GBIF.org, 12 December 2018. GBIF Occurrence Download. <https://doi.org/10.15468/dl.s9nvm>.
- Giresse, P., 2008. Tropical and Sub-Tropical West Africa: Marine and Continental Changes during the Late Quaternary. Elsevier, Amsterdam.
- Gotelli, N.J., McGill, B.J., 2006. Null versus neutral models: what's the difference? *Ecography* 29, 793–800.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.
- Harris, D.J., 1996. A revision of the Irvingiaceae in Africa. *Bull. Jard. Bot. Natl Belg.* 65, 143–196.
- Kang, B.T., Akinnifesi, F.K., Ladipo, D.O., 1994. Performance of selected woody agroforestry species grown on an Alfisol and an Ultisol in the humid lowland of West Africa, and their effects on soil properties. *J. Trop. For. Sci.* 7, 303–312.
- Leaché, A.D., Koo, M.S., Spencer, C.L., Papenfuss, T.J., Fisher, R.N., McGuire, J.A., 2009. Quantifying ecological, morphological, and genetic variation to delimit species in the coast horned lizard species complex (*Phrynosoma*). *PNAS* 106 (30), 12418–12423.
- Linder, H.P., Lovett, J., Mutke, J.M., Barthlott, W., Jürgens, N., Rebelo, T., Küper, W., 2005. A numerical re-evaluation of the sub-Saharan phytochoria of mainland Africa. *Biol. Skrifter* 55, 229–252.
- Lowe, A.J.A., Gillies, C.M., Wilson, J., Dawson, I.K., 2000. Conservation genetics of bush mango from central/West Africa: implications from random amplified polymorphic DNA analysis. *Mol. Ecol.* 9, 831–841.
- Maley, J., 1996. The African rain forest—main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proc. R. Soc. Edin. Edin.* 104, 31–73.
- Mayr, E., 1963. Systematics and the Origin of Species. Columbia University Press, New York.
- McCormack, J.E., Zellmer, A.J., Knowles, L.L., 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. *Evolution* 64, 1231–1244.
- Miller, A.J., Knouft, J.H., 2006. GIS-based characterization of the geographic distributions of wild and cultivated populations of the mesoamerican fruit tree *Spondias purpurea* (Anacardiaceae). *Am. J. Bot.* 93, 1757–1767.
- Nagel, P., Sinsin, B., Peveling, R., 2004. Conservation of biodiversity in a relic forest in Benin — an overview. *Regio Basil* 45, 125–137.
- Ndoye, O., Perez, M.R., Eyebe, A., 1997. The Market of Non-timber Forest Products in the Humid Zone of Cameroon. Rural Development Forestry Network Paper 22cOverseas Development Institute, London.
- Okafor, J.C., 1975. Varietal delimitation in *Irvingia gabonensis* (Irvingiaceae). *Bull. Jard. Bot. Natl Belg.* 45, 211–221.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34, 102–117.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Posner, S., 2008. Biodiversity and Tropical Forest Assessment for Togo. USAID, Washington.
- Raës, N., ter Steege, H., 2007. A null-model for significance testing of presence-only species distribution models. *Ecography* 30, 727–736.
- Ridley, M., 1996. Evolution. 2nd Edition. Blackwell Science, Cambridge.
- Salzmann, U., Hoelzmann, P., 2005. The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene* 15, 190–199.
- Sanchez, A.C., Osborne, P.E., Haq, N., 2010. Identifying the global potential for baobab tree cultivation using ecological niche modelling. *Agrofor. Syst.* 80, 191–201.
- Sayer, J.A., 1992. Benin and Togo. In: Sayer, J.A., Harcourt, C.S., Collins, N.M. (Eds.), *The Conservation Atlas of Tropical Forests Africa*. IUCN, Gland, pp. 97–101.
- Scheldeman, X., Willems, L., Coppens d'Eeckenbrugge, G., Romeijn-Peters, E., Restrepo, M.T., Romero Motoche, J., Jimenez, D., Lobo, M., Medina, C.I., Reyes, C., Rodriguez, D., Ocampo, J.A., Van Damme, P., Goetgebeur, P., 2007. Distribution diversity and environmental adaptation of highland papayas (*Vasconcellea* spp.) in tropical and sub-tropical America. *Biodivers. Conserv.* 16, 1867–1884.
- Sowunmi, A., 2004. Aspects of Nigerian coastal vegetation in the Holocene: some recent insights. In: Battarbee, R.W., Gasse, F., Styckley, C.E. (Eds.), *Past climate variability through Europe and Africa*. 6. Dord Springer, pp. 199–218.
- Tchoundjeu, Z., Atangana, A., 2007. *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. In: van der Vossen, H.A.M., Mkamilo, G.S. (Eds.), *PROTA 14, Vegetable oils/Oléagineux*. PROTA Foundation/Backhuys Publishers/CTA, Wageningen, pp. 95–99.

- Tchoundjeu, Z., Atangana, A.R., Degrande, A., 2005. Indigenous methods in preserving bush mango kernels in Cameroon. *Am. J. Appl. Sci.* 2, 1337–1342.
- Templeton, A., 1991. The meaning of species and speciation: A genetic perspective. In: Ereshefsky, M. (Ed.), *The Units of Evolution. Essays on the Nature of Species* Cambridge. MIT Press, London, pp. 159–183.
- Tossou, M.G., Akouegninou, A., N'dah, D., 2008. Rôle de l'homme dans la mise en place du Dahomey Gap: apports palynologiques et archéologiques. available at: <http://cohesion.rice.edu/centersandinst/safa/emplibary/TossouetalSafa2008.pdf>.
- Ude, G.N., Dimkpa, C.O., Anebe, P.O., Shaibu, A.A., Tenkouano, A., Pillay, M., Tchoundjeu, Z., 2006. Analysis of genetic diversity in accessions of *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. *Afr. J. Biotechnol.* 5, 219–223.
- Van Valen, L.M., 1976. Ecological species, multispecies, and oaks. *Taxon* 25, 233–239.
- Vihotogbé, R., Berg van den, R.G., Sosef, M.S.M., 2013. Morphological characterization of African bush mango trees (*Irvingia* species) in West Africa. *Genetic Resour. Crop Evol.* 60, 1597–1614.
- Vihotogbé, R., Berg van den, R.G., Sinsin, B., Bongers, F., Sosef, M.S.M., 2014a. Does phenology distinguish bitter and sweet African bush mango trees (*Irvingia* spp., Irvingiaceae)? *Trees* 28, 1777–1791.
- Vihotogbé, R., Glèlè Kakai, R., van Andel, T., Berg van den, R.G., Sinsin, B., Sosef, M.S.M., 2014b. Impacts of the diversity of traditional uses and potential economic value on food tree species conservation status: case study of African bush mango trees (Irvingiaceae) in the Dahomey Gap (West Africa). *Plant Ecol. Evol.* 147, 109–125.
- Vihotogbé, R., Idohou, R., Gebauer, J., Sinsin, B., Peterson, A.T., 2018. Estimation of cultivable areas for *Irvingia gabonensis* and *I. wombolu* (Irvingiaceae) in Dahomey-Gap (West Africa). *Agroforest. Syst.* 1–10.
- Waltari, E., Hijmans, R.J., Peterson, A.T., Nyari, A.S., Perkins, S.L., Guralnick, R.P., 2007. Locating Pleistocene Refugia: comparing phylogeographic and ecological niche model predictions. *PLoS One* 2, e563. <https://doi.org/10.1371/journal.pone.0000563>.
- Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62, 2868–2883.
- White, F., 1979. The Guineo-Congolian region and its relationship to other phytocoria. *Bull. Jard. Bot. Natl Belg.* 44, 11–55.
- Wiersum, K.F., 2004. Forest gardens as an intermediate land-use system in the nature–culture continuum: characteristics and future potential. *Agrofor. Syst.* 61, 123–134.
- Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008. Effects of sample size on the performance of species distribution models. *Div. Distrib.* 14, 763–773.