Article

Nationwide Assessment of Population Structure, Stability and Plant Morphology of Two *Mimusops* Species along a Social-Ecological Gradient in Benin, West Africa

Gisèle K. Sinasson S.^{1,2,*} , Charlie M. Shackleton² and Brice Sinsin¹

¹ Laboratoire d'Ecologie Appliquée, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, Cotonou 01 BP 526, Benin; bsinsin@gmail.com

² Department of Environmental Science, Rhodes University, Makhanda 6140, South Africa; c.shackleton@ru.ac.za

* Correspondence: sinasson.gisele@gmail.com

Abstract: Understanding tree species autecology and population structure supports effective conservation actions. Of particular importance are multipurpose trees that provide non-timber forest products (NTFPs). We assessed the population structures and morphologies of two species of NTFP trees in the genus *Mimusops* across bioclimatic zones in Benin by sampling 288 plots within 11 forests. Structural characteristics were compared between species, forests and zones. Correlations were also observed between *Mimusops* tree regeneration density, tree features and ecological characteristics. The density of trees ≥ 5 cm and of regeneration and mean tree height were higher for *M. andongensis* (within more protected forest) than *M. kummel* (in forests with access to people), while the highest mean diameter was observed for *M. kummel*. Tree and regeneration densities and mean height were greatest in the humid zone of Benin, whilst the largest mean diameter was obtained in the sub-humid zone. The results showed significant correlations between regeneration density and soil properties for *M. andongensis* but not for *M. kummel*. The correlations between tree morphology and soil characteristics were weak for both species. Ecological characteristics, along with the species' functional traits and pressures, are important factors related to the observed differences between the species. All diameter classes were represented, and the population seemed more stable in the more protected forest relative to other forests. *Mimusops* trees with a diameter of 5–15 cm represented more than 30% of this species in most forests; this suggests, for *M. kummel*, whose trees flower when quite small (≥ 6 cm dbh), that there are sufficient reproductive trees. Thus, as a long-lived species, its populations could be maintained even with low/episodic recruitment. However, we found no regeneration in many forests and climate change could threaten populations. Therefore, it is important to investigate regeneration growth and dynamics, seed production and germination of the species in relation to the biophysical conditions and disturbances experienced by *Mimusops* stands.

Keywords: climatic conditions; demographic structure; human pressure; NTFPs; regeneration; size class distribution; soil properties

Citation: Sinasson S., G.K.; Shackleton, C.M.; Sinsin, B. Nationwide Assessment of Population Structure, Stability and Plant Morphology of Two *Mimusops* Species along a Social-Ecological Gradient in Benin, West Africa. *Forests* **2021**, *12*, 1575. <https://doi.org/10.3390/f12111575>

Academic Editor: Christel Kern

Received: 12 September 2021

Accepted: 5 November 2021

Published: 16 November 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Forest resources and Non-Timber Forest Products (NTFP) species, in particular, face multiple anthropogenic pressures that include direct threats, due to their exploitation, and indirect ones, through habitat threats [1,2]. Such pressures include overexploitation, changing land use, bushfires, grazing and invasive species [2–4], which can negatively impact natural populations at both the species and community scales [5,6]. Such impacts may be irreversible for some species [7]. In this context, it is important to analyse the current status of NTFP populations in relation to anthropogenic pressures to understand and potentially mitigate the impacts.

Synergistically with human disturbance, environmental factors (such as climate, soil conditions and slope) influence the abundance and observed variability in the functional characteristics of tree species in natural habitats [8,9]. Plant responses to diverse environmental stresses often manifest in their morphological and physiological characteristics [10], which determine their growth, survival and reproduction. Thus, variations in environmental factors typically lead to variations in NTFP population density, vigour and structure. Therefore, understanding ecological correlates and stresses, along with anthropogenic disturbances, is also an important step in the planning of management actions for important NTFPs. This can help to predict the potential for recovery of species populations if pressures are mitigated or removed.

In the face of these different pressures, a comprehensive knowledge of species autecology is needed to understand population characteristics and dynamics due to the different pressures. This is necessary for guiding sustainable conservation strategies [11,12]. In terms of species autecology, population structure (density and size class distribution) and plant morphology are a direct reflection of their health and performance [11]. Thus, the knowledge of population structure, along with plant species' morphologies, is an essential tool in understanding their population ecology and trends in relation to pressures [8].

Mimusops andongensis Hiern and *Mimusops kummel* Bruce ex A. DC are two NTFP tree species naturally occurring in many African countries, including Benin, where they occur mainly in semi-deciduous and riparian forests, respectively. Both species are used for energy, construction and manufacturing, as well as for alimentary and medicinal purposes [13–17]. Additionally, *M. kummel* has been identified as one of the important sources of pollen for honey production in different African countries, although among the least abundant species [18,19]. Thus, *M. andongensis* and *M. kummel* are two important NTFP species that deserve more study [13,20]. Mirroring many countries worldwide, forest resources in Benin face various pressures, including overharvesting, deforestation for cultivation, uncontrolled bushfires, invasive species, etc. [21]. *M. andongensis* and *M. kummel* are subject to such pressures [15] and therefore understanding variation in their population structure and morphology in the context of anthropogenic and ecological stresses will inform conservation options.

Thus, this study assessed (i) the population structure and morphology of *M. andongensis* and *M. kummel* within different bioclimatic zones in Benin, (ii) how ecological factors influence structural and morphological characteristics of both species, and (iii) how anthropogenic disturbances on the species and their habitats shape their population structure.

2. Methods

2.1. Study Area

Benin is located in West Africa between 6°10' and 12°25' north and 0°45' and 3°55' east. The study was realized in different forests within the three bioclimatic zones of Benin (Figure 1). There is a northward climatic gradient across Benin from the Guineo–Congolian (humid) zone in the south to the typical Sudanian (semi-arid) zone in the north, marked by a reduction in the number of rainy months and a decrease in mean annual rainfall and humidity [22] (Table 1). The third (Guineo–Sudanian or sub-humid) zone is a transition between these two. The soils in the humid zone are deep ferrosols and the vegetation is a mixture of relics of dense semi-deciduous forests and Guinean savannas. Soils are mainly ferruginous in the sub-humid zone supporting a mosaic of vegetation including woodlands, dense dry forests, tree and shrub savannas and riparian forests. In the semi-arid zone, well drained ferruginous soils are dominant, with lesser expanses of hydromorphic soils, and the vegetation is mainly composed of savannas and riparian forests with small diameter trees [22]. *M. andongensis* is found in semi-deciduous forests while *M. kummel* occurs in riparian forests. The investigated forests and species have been or are exploited for different human needs (Table 1).

Figure 1. Climatic zones and study site locations and attributes in Benin, W. Africa.

Table 1. Ecological characteristics in the different biogeographical zones and the investigated forests (Adapted from [22]).

Biog. Zones	Phyto-Districts	Climat Types	Rainfall (mm)	IM	Major Soils	Major Plant Formation	Invent. Sites	<i>Mimusops</i> Species	Protection Status	No. Plots	Size of Plots
GC	Plateau	HT	900–1300	3.8–4.9	Ferralitic soils without concretions	Semi-deciduous forest	Lama	<i>M. andongensis</i>	Protected with no/very low access to people	100	50 × 30 m
GS	Bassila	ST	1100–1200	2.7–3.9	Ferruginous soils, Ferralitic soils with concretions	Dry semi-deciduous forest, woodland and riparian forest	Manigri	<i>M. kummel</i>	Non-protected	12	30 × 30 m
GS	Bassila	ST	1100–1200	2.7–3.9	Ferruginous soils, Ferralitic soils with concretions	Dry semi-deciduous forest, woodland and riparian forest	Agoua	<i>M. kummel</i>	Protected with access to people	26	30 × 30 m
GS	Zou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Savè	<i>M. kummel</i>	Non-protected	7	30 × 20 m
GS	Zou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Assanté	<i>M. kummel</i>	Non-protected	10	30 × 20 m
GS	South Borgou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Idadjo	<i>M. kummel</i>	Non-protected	20	30 × 20 m
GS	South Borgou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Aklamkpa	<i>M. kummel</i>	Non-protected	15	30 × 20 m
GS	South Borgou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Monts- Kouffé	<i>M. kummel</i>	Protected with access to people	30	30 × 30 m
GS	South Borgou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Ouémé-Supérieur	<i>M. kummel</i>	Protected with access to people	23	30 × 30 m
GS	South Borgou	ST	1100–1200	2.8	Ferruginous soils on crystalline rocks	Dry forest, woodland and riparian forest	Wari-Marô	<i>M. kummel</i>	Protected with access to people	30	30 × 30 m
TS	Atacora Chain	DT	1000–1200	2.1	Poorly evolved and mineral soils	Riparian forest, dry forest and woodland	Tanougou	<i>M. kummel</i>	Non-protected	15	30 × 20 m

Biog. zones = biogeographical zones; GC = Guineo–Congolian; GS = Guineo–Sudanian transition; TS = typical Sudanian; phytodistricts = phytogeographical districts; HT = humid tropical; ST = sub-humid tropical; DT = dry tropical; I_M = climatic index of Mangenot; invent. sites = inventoried zones; no. plots = number of plots.

2.2. Data Collection

We sampled 288 plots in eleven forests distributed among the three bioclimatic zones. Forests have been selected based on their size and abundance of *Mimusops* species, with one forest (Lama Forest reserve) for *M. andongensis*. Plots were systematically set at least 200 m apart, following the transect lines plotted in the semi-deciduous Lama Forest [4] and along watercourses in the other forests (for *M. kummel*). Details of the ecological characteristics of the investigated forests as well as the sizes and number of the plots are summarized in Table 1.

Within each plot, we sampled and numbered (to avoid confusion in data collection) *Mimusops* trees with dbh (diameter at breast height) ≥ 5 cm and measured their dbh and height using a clinometer. We also sampled ten 5×5 -m (Lama Forest) or five 10×10 -m (other forests) subplots within each plot to assess the regeneration (saplings—dbh < 5 cm and height ≥ 1 m and seedlings—height < 1 m). We also randomly selected ten sexually mature trees per forest (when applicable) and collected 30 leaves from each tree. Leaves were obtained from the bottom, the middle and the top (only for small height individuals) of the canopy. The measured characteristics included the length and width of leaves, and the length of petiole.

For ecological characterization of the forests, we recorded slope in the field and obtained soil layers of soil characteristics (sand, silt, clay, pH, organic carbon, CEC—Cation Exchange Capacity) for five different soil depths from 0 to 60 cm [23] from ISRIC—World Soil Information website [24]. Values were then extracted to plot coordinates, using Spatial Analyst Tools in ArcGIS 10.3. Mean values of soil data were calculated by combining data from the different soil layers.

2.3. Data Analysis

For structural characterization, we determined and compared tree density, mean diameter, basal area and mean height of trees ≥ 5 cm, as well as the density of regeneration between species, forests and climatic zones. To morphologically characterize both species, apart from mean diameter and height, we determined and compared mean values for the lengths and widths of leaves and the lengths of petioles between species and climatic zones. Comparisons were made using t-tests and ANOVA as applicable. In the case of significant differences in the ANOVA, we used pair-wise Tukey multiple comparison to compare means.

Soil characteristics were also compared between forests using ANOVA. To evaluate the effect of ecological factors on the regeneration, we applied multiple regression analysis between slope and soil variables and seedlings and saplings densities. We also analysed the relation between tree-level and soil characteristics, using Pearson correlation.

We established size class distributions (SCD) for each forest by grouping *Mimusops* trees into 5 cm diameter classes. We also performed a log-linear analysis to test if the diameter structures were different between forests. Moreover, we assessed the population stability of the species using the permutation index (P) and Simpson's index of dominance (C) [25,26]. The permutation index measures deviation from a monotonic decline, which would be expected in an "ideal" population. If a size distribution is discontinuous, with more individuals in preceding size classes, P is higher than that of a continuous monotonically declining population with $P = 0$ [27]. Simpson's index of dominance is a measure for the evenness of the occupation of the size classes; values above 0.1 reveal that the size frequency is steeper than would be expected from an exponentially declining population and values below 0.1 show that the size classes are more evenly distributed. We also determined and displayed graphically the quotients between the numbers of trees in successive diameter classes. These quotients approach a constant value in a stable population and fluctuating quotients indicate an unstable population [28].

Log-linear analysis was performed in SAS 9.2 [29] while the other analyses were done using R 3.1.2 [30].

3. Results

3.1. Dendrometric and Leaf Morphological Variations between Species and Bioclimatic Zones

Tree density (29.7 ± 46.7 trees/ha), seedling and sapling density (46.4 ± 96.3 and 8.2 ± 20.5 stems/ha, respectively) and mean tree height (13.3 ± 3.2 m) were higher for *M. andongensis* than *M. kummel*, while the greatest mean diameter (32.1 ± 22.1 cm) was observed for *M. kummel* ($p < 0.05$; Table 2). Adult tree and regeneration (dbh < 5 cm) densities and mean height were highest ($p < 0.05$; Table 2) in the humid zone, relative to the other two zones. However, there were no regeneration individuals in the semi-arid zone. Mean diameter (33.3 ± 22.8 cm) was higher in the sub-humid zone ($p < 0.05$). There was no significant difference in mean basal area between zones ($p > 0.05$), varying between 0.4 ± 0.5 m²/ha and 1.5 ± 5.0 m²/ha.

Table 2. Dendrometric and morphological characteristics (means $\pm$ SD) between species and bioclimatic zones.

Characteristics	Between Species			Between Climatic Zones			
	<i>M. andongensis</i>	<i>M. kummel</i>	<i>p</i> -Value ¹	GC	GS	TS	<i>p</i> -Value ²
Trees (stems/ha)	29.7 ± 46.7	13.7 ± 23.6	0.002	$29.7 \pm 46.7a$	$13.7 \pm 24.0 b$	$13.3 \pm 19.8 b$	0.001
Saplings (stems/ha)	8.2 ± 20.5	0.4 ± 3.1	<0.0001	$8.2 \pm 20.5 a$	$0.4 \pm 3.2 b$	$0.0 \pm 0.0 b$	<0.0001
Seedlings (stems/ha)	46.4 ± 96.3	0.7 ± 4.1	<0.0001	$46.4 \pm 96.3 a$	$0.7 \pm 4.3 b$	$0.0 \pm 0.0 b$	<0.0001
Dbh (cm)	23.1 ± 15.2	32.1 ± 22.1	0.008	$23.1 \pm 15.2 b$	$33.3 \pm 22.8 a$	$20.5 \pm 8.2 c$	<0.0001
Basal area (m ² /ha)	1.04 ± 1.4	1.4 ± 4.8	0.311	1.0 ± 1.4	1.5 ± 5.0	0.4 ± 0.5	0.416
Height (m)	13.3 ± 3.2	11.5 ± 3.6	0.009	$13.3 \pm 3.2 a$	$11.5 \pm 3.6 b$	$2.7 \pm 1.2 c$	<0.0001
Leaf length (cm)	10.3 ± 1.4	12.6 ± 2.6	<0.0001	$10.3 \pm 1.4 c$	$12.6 \pm 2.5 b$	$13.9 \pm 2.8 a$	<0.0001
Leaf width (cm)	3.9 ± 0.6	4.4 ± 1.1	<0.0001	$3.9 \pm 0.6 c$	$4.3 \pm 1.1 b$	$5.3 \pm 1.0 a$	<0.0001
Petiole length (cm)	1.2 ± 0.3	1.6 ± 0.6	<0.0001	$1.2 \pm 0.3 b$	$1.6 \pm 0.6 a$	$1.3 \pm 0.6 c$	<0.0001

Values with same letters are not significantly different; GC = humid zone, GS = sub-humid zone, TS = semi-arid zone; *p*-value ¹ = *t*-test and *p*-value ² = ANOVA; SD = standard deviation.

There was a significant difference between species for the length and width of leaves and the mean length of the petiole ($p < 0.0001$; Table 2). The highest values were obtained for *M. kummel* (12.6 ± 2.6 cm for leaf length, 4.4 ± 1.1 cm for leaf width and 1.6 ± 0.6 cm for petiole length). Similarly, the mean length and width of leaves and the mean length of petiole differed between bioclimatic zones ($p < 0.0001$; Table 2). The highest values for length (13.9 ± 2.8 cm) and width (5.3 ± 1.0 cm) of leaves were obtained in the semi-arid zone (*M. kummel*) and the lowest values in the humid zone (*M. andongensis*). The mean length of petiole was higher in the sub-humid zone (1.6 ± 0.6 cm) in comparison to the other zones. Although the mean of leaf characteristics was higher for *M. kummel* than *M. andongensis*, values for *M. kummel* in some forests were significantly lower than the values for *M. andongensis* (Table 3). The mean leaf length was low (9.2 ± 1.8 cm) in Manigri forest, compared to other forests, while the lowest leaf width (2.2 ± 0.4 cm) was obtained in Assanté forest, both for *M. kummel*. Also, the lowest petiole length (0.7 ± 0.2 cm) was found in Manigri forest.

Table 3. Leaf morphological characteristics (means $\pm$ SD) in the investigated forests.

Forests	Leaf Length (cm)	Leaf Width (cm)	Petiole Length (cm)
<i>Semi-arid zone (M. kummel)</i>			
Tanougou	$13.9 \pm 2.8 ab$	$5.3 \pm 1.0 a$	$1.3 \pm 0.6 efg$
<i>Sub-humid zone (M. kummel)</i>			
Ouémé Supérieur	$13.4 \pm 2.4 abc$	$5.0 \pm 0.9 ab$	$2.1 \pm 0.7 a$
Wari-Maró	$14.3 \pm 0.5 a$	$4.8 \pm 1.0 b$	$2.0 \pm 0.5 a$
Manigri	$9.2 \pm 1.8 g$	$3.6 \pm 0.5 e$	$0.7 \pm 0.2 h$
Monts Kouffé	$12.6 \pm 2.4 cd$	$4.6 \pm 0.9 bc$	$1.6 \pm 0.4 bc$
Idadjo	$12.7 \pm 2.6 cd$	$4.3 \pm 0.9 cd$	$1.7 \pm 0.7 b$

Table 3. Cont.

Forests	Leaf Length (cm)	Leaf Width (cm)	Petiole Length (cm)
Aklamkpa	13.1 ± 1.8 bcd	3.8 ± 1.2 e	1.5 ± 0.4 cde
Agoua	12.1 ± 2.2 de	4.4 ± 0.7 c	1.5 ± 0.4 bcd
Assanté	11.2 ± 2.6 ef	2.2 ± 0.4 f	1.2 ± 0.2 efg
Savè	12.1 ± 2.9 de	4.4 ± 1.2 c	1.4 ± 0.7 cde
<i>Humid zone (M. andongensis)</i>			
Lama	10.3 ± 1.4 f	3.9 ± 0.6 de	1.2 ± 0.3 fg
<i>p</i> -value	<0.0001	<0.0001	<0.0001

Values with same letters are not significantly different; $\alpha = 0.05$, Pair-wise Tukey comparisons; SD = standard deviation.

We found a significant difference between forests in density of trees and regeneration, mean diameter, height and basal area ($p < 0.05$; Figure 2). The lowest tree density was observed in Ouémé Supérieur (2.4 ± 6.7 trees/ha) and Wari-Marou (4.4 ± 10.8 trees/ha) forests in the sub-humid zone, while mean densities of seedlings and saplings were greatest in Lama Forest reserve (humid zone) than in the other forests. The highest mean diameter (73.9 ± 32.8 cm) and basal area (8.7 ± 14.6 m²/ha) were obtained in Aklamkpa forest (sub-humid zone) and the lowest mean height (6.6 ± 1.3 m) in Ouémé Supérieur. There were no regeneration stems in Aklamkpa, Assanté, Ouémé Supérieur, Monts Kouffé and Tanougou forests.

Figure 2. Tree density, basal area, mean diameter (Dg), sapling and seedling density (mean, Standard Deviation, min.–max.) according to forests. TG = Tanougou; OS = Ouémé Supérieur; WM = Wari-Marou; MG = Manigri; MK = Monts Kouffé; ID = Idadjo; AK = Aklamkpa; AG = Agoua; AS = Assanté; SA = Savè; LM = Lama; 1 = semi-arid zone; 2 = sub-humid zone; 3 = humid zone.

3.2. Regeneration Density and Morphological Variation According to Slope and Soil Factors

There was a significant difference in soil characteristics (sand, silt, clay, pH, organic carbon, CEC) between forests ($p < 0.0001$; Table 4). Soils of the Lama Forest reserve (humid zone) contained the highest proportions of clay, organic carbon and CEC but the lowest sand content. The lowest percentages of clay and silt, and the highest sand percentage were obtained in Assanté, Savè, Aklamkpa and Idadjo forests (sub-humid zone). The highest pH was observed in Savè and the lowest organic carbon content in Assanté. We found no significant difference between Tanougou forest, in the semi-arid zone, and one or some of the forest(s) in the sub-humid zone (Ouémé Supérieur, Wari-Marou, Manigri, Monts Kouffé, Agoua, Aklamkpa, Assanté forests) for soil characteristics (except for organic carbon, for which Tanougou forest had the second highest value after Lama Forest reserve, and for pH). There was also a significant difference between some forests in the sub-humid zone in term of soil characteristics. According to silt percentage, Lama Forest reserve was not significantly different from most forests in the sub-humid zone.

Table 4. Soil characteristics (means $\pm$ SD) in the investigated forests.

Forests	Clay (%)	Silt (%)	Sand (%)	OC (g/kg)	CEC (cmolc/kg)	pH (H ₂ O)
Tanougou	24.6 $\pm$ 1.1 b	21.6 $\pm$ 3.1 a	53.9 $\pm$ 4.0 c	14.3 $\pm$ 2.7 b	10.5 $\pm$ 0.5 bc	6.1 $\pm$ 0.0 c
<i>Semi-arid zone</i>						
Ouémé Supérieur	25.1 $\pm$ 0.6 b	19.8 $\pm$ 0.3 ab	55.3 $\pm$ 0.3 c	9.7 $\pm$ 0.4 ef	8.1 $\pm$ 0.2 c	5.9 $\pm$ 0.0 g
Wari-Marou	26.1 $\pm$ 1.6 b	21.2 $\pm$ 0.9 a	52.5 $\pm$ 2.1 c	10.2 $\pm$ 0.7 def	10.3 $\pm$ 0.8 bc	6.1 $\pm$ 0.0 cde
Manigri	26.9 $\pm$ 1.6 b	19.3 $\pm$ 0.4 ab	53.9 $\pm$ 1.9 c	11.1 $\pm$ 1.2 cde	9.8 $\pm$ 0.5 bc	5.9 $\pm$ 0.0 g
Monts Kouffé	26.6 $\pm$ 0.8 b	20.8 $\pm$ 1.0 ab	52.6 $\pm$ 1.5 c	12.2 $\pm$ 0.8 c	10.2 $\pm$ 0.5 bc	6.1 $\pm$ 0.0 e
Idadjo	21.2 $\pm$ 2.7 c	18.1 $\pm$ 1.8 b	61.3 $\pm$ 4.4 b	9.7 $\pm$ 1.5 ef	11.6 $\pm$ 0.3 b	6.2 $\pm$ 0.0 b
Aklamkpa	16.8 $\pm$ 1.7 d	18.9 $\pm$ 1.6 ab	64.5 $\pm$ 1.9 b	8.4 $\pm$ 0.6 f	9.2 $\pm$ 0.4 bc	6.2 $\pm$ 0.0 b
Agoua	26.1 $\pm$ 0.9 b	19.9 $\pm$ 1.8 ab	54.1 $\pm$ 1.8 c	11.8 $\pm$ 1.0 cd	10.8 $\pm$ 0.7 bc	6.1 $\pm$ 0.1 de
Assanté	20.7 $\pm$ 0.5 c	15.2 $\pm$ 0.3 c	71.7 $\pm$ 0.3 a	5.6 $\pm$ 0.4 g	9.6 $\pm$ 1.4 bc	6.1 $\pm$ 0.0 cd
Savè	16.4 $\pm$ 1.0 d	15.3 $\pm$ 1.9 c	68.2 $\pm$ 2.9 a	10.7 $\pm$ 1.4 cde	11.6 $\pm$ 0.9 b	6.3 $\pm$ 0.1 a
<i>Humid zone</i>						
Lama	46.6 $\pm$ 2.8 a	20.2 $\pm$ 1.5 ab	33.2 $\pm$ 3.8 d	19.8 $\pm$ 1.2 a	29.6 $\pm$ 2.8 a	6.0 $\pm$ 0.0 f
<i>p</i> -value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Values with same letters are not significantly different; $\alpha = 0.05$, Pair-wise Tukey comparisons; OC = organic carbon; SD = standard deviation.

The results from the multiple regression analysis showed a significant relationship between slope and soil characteristics, and both seedling and sapling density for *M. andongensis* ($p < 0.05$; Table 5). However, for seedlings, only the individual relationships with silt and sand (both negative) were significant ($p < 0.05$). For saplings, only the relationship with slope (positive) was significant ($p < 0.05$). In the case of *M. kummel*, there was no significant relationship between soil properties and the density of seedlings and saplings ($p > 0.05$; Table 5).

Table 5. Multiple regression coefficients between slope, soil characteristics and regeneration density.

	<i>Mimusops andongensis</i>				<i>Mimusops kummel</i>			
	Seedlings		Saplings		Seedlings		Saplings	
	Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>
Model	-	0.04	-	0.02	-	0.35	-	0.80
Intercept	13,156.2	0.10	-859.5	0.63	97.6	0.97	23.0	0.25
Clay	-133.3	0.05	7.6	0.60	-3.7	0.87	-13.6	0.26
Silt	-146.1	0.04	1.9	0.90	8.5	0.70	-14.3	0.21
Sand	-143.3	0.04	6.4	0.66	3.4	0.88	-14.0	0.23
OC	0.14	0.99	0.5	0.89	8.7	0.10	0.4	0.85
CEC	-12.6	0.08	-0.7	0.67	4.1	0.50	1.5	0.58
pH	204.3	0.67	41.3	0.69	-76.5	0.57	-42.0	0.51
Slope	7.9	0.61	13.1	<0.0001	-8.7	0.41	4.0	0.43

OC = organic carbon.

The correlation analysis highlighted weak, albeit significant relationships between morphological characteristics (diameter, height, leaf length and width, and petiole length) and soil properties for both species ($p < 0.05$; Table 6). Some correlations were consistent among the two species, such as the negative relationship between tree size and slope or CEC, while others were opposite, such as correlations between tree size variables and the clay or sand content of soils. Consistent correlations (positive) were also observed among the two species with regards to the relationship between leaf size (length and width) and OC, while opposite correlations were obtained with clay or sand content of soil.

Table 6. Pearson correlation coefficients between tree and soil characteristics.

Tree Characteristics	Clay	Silt	Sand	OC	CEC	pH	Slope
<i>Mimusops andongensis</i>							
Diameter	0.05	−0.02	−0.03	−0.09	−0.12 *	0.03	−0.17 *
Height	0.14 *	0.15 *	−0.16 *	0.11 *	−0.26 *	0.12 *	−0.18 *
Leaf length	−0.08	0.07	0.08	0.09	−0.10	−0.11 *	−
Leaf width	−0.02	−0.06	0.02	0.01	−0.01	0.001	−
Petiole length	0.27 *	0.15 *	−0.27 *	−0.25 *	0.24 *	0.21 *	−
<i>Mimusops kummel</i>							
Diameter	−0.36 *	−0.07	0.20 *	−0.20 *	−0.24 *	0.19 *	−0.13
Height	−0.13	−0.20 *	0.15 *	−0.19 *	−0.01	0.09	−0.04
Leaf length	0.03	0.13 *	−0.10 *	0.14 *	−0.14 *	−0.03	−
Leaf width	0.30 *	0.24 *	−0.35 *	0.44 *	0.09 *	−0.10 *	−
Petiole length	0.12 *	0.09 *	−0.14 *	0.03	−0.00	−0.01	−

OC = organic carbon; *: Significant at 5%.

3.3. Size Class Distribution (SCD)

The SCDs were significantly different between the studied forests ($\chi^2 = 78.31$, $p = 0.02$). All dbh classes (dbh 5 cm to dbh > 50 cm) were represented in Lama Forest (for *M. andongensis*), while, in other forests (for *M. kummel*), there some classes were missing (Figure 3). Trees with dbh of 5–10 cm were the most abundant in Lama Forest as well as in Manigri, Savè and Idadjo forests, while the dbh class of 10–15 cm was the most abundant in Monts Kouffé, Agoua, Wari-Marou and Tanougou forests. In Assanté, trees with a dbh of 25–30 cm were the most abundant, those with a dbh of 20–25 cm in Ouémé Supérieur, while the most abundant in Aklamkpa were individuals > 50 cm. Trees in the smallest dbh classes (5–15 cm) represented more than 30% of individuals for both species (except in Ouémé Supérieur and Aklamkpa). These classes formed 20% of trees in Ouémé Supérieur, while they were absent in Aklamkpa (Table 7).

Table 7. Permutation and Simpson indices and percentage of smallest size classes in the investigated forests.

Forests	Permutation Index (P)	Simpson Index (C)	% dbh 5–15 cm
<i>Semi-arid zone (M. kummel)</i>			
Tanougou	14	0.19	55.6
<i>Sub-humid zone (M. kummel)</i>			
Ouémé Supérieur	22	0.10	20.0
Wari-Marou	18	0.17	53.8
Manigri	33	0.12	33.3
Monts Kouffé	12	0.13	31.3
Idadjo	29	0.09	30.8
Aklamkpa	37	0.50	0
Agoua	16	0.10	33.3
Assante	17	0.25	45.4
Savè	14	0.10	46.7
<i>Humid zone (M. andongensis)</i>			
Lama	2	0.17	49.8

Figure 3. Size class distribution for *M. kummel* (a–j) and *M. andongensis* (k) in the study forests.

The Permutation index calculated for the different forests was greater than zero (Table 7). However, the index value was very low in Lama Forest reserve ($P = 2$), showing a more monotonically declining reverse-J structure than in the other forests. Based on the Simpson index, size classes were more evenly distributed in Idadjo, Savè, Agoua and Ouémé Supérieur ($C = 0.1$), while, in the other forests, SCDs were steeper than would be expected from an exponentially declining population ($C > 0.1$). The quotients obtained between numbers of trees in successive size classes fluctuated widely, potentially indicating unstable populations of *Mimusops* species; but the fluctuation was less pronounced in Lama Forest reserve (Figure 4).

Figure 4. Quotients between numbers of trees in successive size classes; Lama, for *M. andongensis*, and the other forests for *M. kummel*.

4. Discussion

Population structure and morphology were different between *M. andongensis* and *M. kummel*. The density of trees with dbh ≥ 5 cm, regeneration stems, and mean height of trees were higher for *M. andongensis* than *M. kummel*. The first explanation for this difference may be attributed to them being two different species that may have specific functional traits and thus different performance in response to ecological conditions and competition [31,32]. However, habitat is an important factor which might also account for the difference between the two species [33]. For instance, the two species occur under different climatic conditions with *M. andongensis* in the most humid part of the country and *M. kummel* in the sub-humid and semi-arid parts [22]. We also found a significant difference between the forests based on soil characteristics, which may explain the differences between the two species. Indeed, soils in Lama Forest reserve have the highest clay (47% with 33% of sand and 20% of silt), organic carbon content and CEC in comparison to other forests, indicating that this forest is more fertile and more suitable for growth and development [34,35]. Fertile soils reflect a higher capacity to hold nutrients due to higher exchangeable base cations and higher organic matter content with a healthy pH [34]. However, other factors, including soil structure, climate and parent material, as well as physiochemical and biological properties, can influence soil fertility [36]. Also, tree morphology and the abundance of a species are a result of its performance in response to changes in ecological conditions through time [10].

Considering the structural characteristics, however, we found no significant difference (except for regeneration density) between Lama Forest reserve and some of the other forests, while there were significant differences between forests in the same climatic zone and under similar soil conditions. There was also no significant relationship between *M. kummel* regeneration densities and soil characteristics. Indeed, regeneration individuals were lacking in many forests. Therefore, the difference, here, between *M. andongensis* and *M. kummel* may be due to other factors. Such differences between the two species' characteristics might be mainly imputed to the difference in the levels of human pressures that the species, as well as their habitats faced [37]. For instance, *M. andongensis* was found in Lama Forest reserve, one of the most important protected areas and probably the most preserved forest in Benin, while *M. kummel* occurs in riparian forests, in and out of

protected areas that are exploited by local people. Furthermore, mean diameter was higher for *M. kummel* than *M. andongensis*, a result of an abundance of small-diameter trees in Lama Forest reserve relative to the riparian forests, where people (and animals) using the forest may impede natural regeneration or recruitment to larger size classes.

The relationships between soil characteristics and regeneration of *M. andongensis* were mostly negative or non-significant, highlighting the probable existence of other factors that influence its regeneration density [38]. Competition with invasive species and seed predation are some factors that affect the regeneration of the species in Lama Forest reserve [4]. Similarly, there was no significant influence of soil conditions on seedling and sapling abundance for *M. kummel* (in fact, regeneration lacks in several forests) and this could be due to predation of fruits and seeds [39]. Fire is also often an important factor influencing species regeneration [40] and this could be the case for both species in Benin. In fact, it has been shown that riparian forests in Benin face several human pressures such as fire, farm encroachment and timber extraction [41]. Lama Forest reserve sometimes experiences accidental fires [42], which might impact *M. andongensis* seeds. Although data indicate that the soil in Lama Forest reserve is more fertile and suitable for growth, the mean values for leaf morphological characteristics were higher for *M. kummel* than *M. andongensis*. The mean value in only one forest where *M. kummel* occurs was significantly lower than value in *M. andongensis*. Moreover, correlations between the morphological characteristics of both species and soil properties were weak. This suggests functional characteristics to be more responsible for variation in leaf morphology between the species.

All diameter classes were represented in Lama Forest reserve, while in other forests there were missing classes. Added to this, the permutation and Simpson indices, as well as the quotients determined between successive diameter classes, indicated the population of *M. andongensis* to be more stable than the populations of *M. kummel* [27,43]. This may be due to differences in the levels of anthropogenic disturbance between Lama Forest reserve and the other forests. There were missing diameter classes in the populations of *M. kummel* and this might be a result of the impact of anthropogenic pressures followed by failures in regeneration and recruitment. However, populations of both species showed good proportions of trees with dbh 5–15 cm (>30 %) except two (Ouémé Supérieur and Aklamkpa), suggesting good recruitment. However, tree size is rarely a direct function of age, especially for long-lived species, and trees with dbh 5–15 cm might be older than they seemed [44,45]. This is confirmed in the case of *Mimusops* species, for which trees with dbh 10 cm and 6 cm for *M. andongensis* and *M. kummel* respectively, exhibited flowers [46], indicating the reproductive maturity of relatively small trees. This means that populations of *M. kummel*, within most forests, have sufficient reproductive trees but lack regeneration and recruits. For many long-lived species, populations can be maintained with a low or episodic recruitment [47,48]. However, this should be considered with caution especially in the context of climate change, which may threaten the species [48]. We found no or very low regeneration in many forests and climate change could alter the hydrologic regime, potentially causing the death of adult trees, particularly in less humid parts of the range [49]. Therefore, it is important to assess the mortality process of the species and factors likely to influence it.

Our results show that the population in the most protected forest in the country is more stable than populations in the other forests, with no missing diameter classes. This suggests the full protection of Lama Forest reserve to be beneficial for the preservation of *M. andongensis* populations, although the long-term benefits of protection might be mitigated by competition with invasive species, especially on regenerative stems [15,50]. The advantages of protecting forests for species conservation are well known [51] and this management strategy has been applied for different vegetation types, with other forms of harvesting regulations [52]. However, the full restriction of access to forests by local people (like in the case of Lama Forest reserve) might result in the loss of local knowledge/cultural heritage and therefore increase local people's vulnerability during difficult times [53]. Therefore, exploitation methods likely to limit negative impacts on the

remaining populations of both species should be considered for sustainable management and conservation of both species and the biodiversity in general.

A limitation of this study is the short period of data collection. Indeed, only long-term investigation of population structure, in relation to the different ecological conditions and anthropogenic disturbances, will allow for observation of important changes for an effective understanding of the dynamics there between. This is also useful for prioritizing informed efficient management and conservation strategies [54]. Thus, the species' populations should be monitored for long-term data collection. For that, repeat monitoring in the installed plots is recommended at intervals of one or two years so that the necessary changes may be detected [55]. Furthermore, the stands with regeneration failure should be studied further and prioritized for restoration purposes.

5. Conclusions

This study showed a significant difference between the population structures and morphologies of *M. andongensis* and *M. kummel* in Benin. Significant difference was also found between bioclimatic zones, while there was no significant difference between forests in different bioclimatic zones. Although the difference between the two species may be attributed to their specific functional characteristics, the results from this study also highlighted the influence of climate. Nonetheless, the two species occur under different soil conditions and this might contribute to the differences observed between them. However, we found no significant difference between forests with different soil characteristics, while there was significant difference between some forests in the same climatic zone and under similar soil conditions. This suggests plant-scale analysis to be the most sensitive, mainly because of the interference of anthropogenic pressures, which influence the observed effects of climate and soil. Thus, further investigation on the growth and demographic dynamics of both species, in relation to the different threats, could be useful to inform sustainable management options.

The relationships revealed between both species' regeneration densities and soil characteristics were mostly negative or non-significant. Regeneration and recruits were also lacking in many forests, for *M. kummel*. This suggests the existence of other factors (e.g., fruit/seed predation, fire) that may affect regeneration in both species. Success in the regeneration and recruitment of plant species ensures population survival. Thus, for conservation purposes, further research would be welcomed to elucidate seed germination and development dynamics of regeneration as well as the influencing factors. Several soil properties (e.g., individual nutrient concentrations) were not considered in the analyses and it would be useful to have such information to assess how soil properties influence abundance of seedlings and saplings.

According to our results, the protection of forests is the key to sustaining species populations. However, the full protection of forests is at odds with the needs of local people for NTFPs, especially in the current context of climate change, which is likely to worsen rural peoples' vulnerability in times of hardship. Also, the full protection of forests might lead to the loss of local knowledge on different useful species that are important for domestication purposes, and the cultural heritages and identities of many people. Therefore, exploitation strategies that are likely to limit the negative impacts on existing populations, of not only the target species but other species in demand, should be encouraged. Also, assessing the assisted germination or vegetative propagation of useful species should be investigated for species' reintroduction.

Author Contributions: G.K.S.S. designed the study; G.K.S.S. conducted fieldwork; G.K.S.S. did the data-analysis and wrote the manuscript; C.M.S. and B.S. supervised design and implementation of the research; C.M.S. and B.S. reviewed the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the International Foundation for Science, grant D/5467-1. The APC was funded by the South African Research Chairs Initiative of the Department of Science and Innovation and the National Research Foundation of South Africa, grant no. 84379.

Data Availability Statement: The data presented in this study are openly available in Dryad Repository at <https://datadryad.org/stash/share/2h0PNk3w-KR9iYgkSgth3Nk7bpgpD2oPXX1kefCGKMA>, accessed on 12 September 2021.

Acknowledgments: We thank Organization for Women in Science for the Developing World and Swedish International Development Cooperation Agency (grant no. 3240266463, 2013), and the Ministry of Higher Education of Benin through Postgraduate scholarships to K.G.S.S. Idea Wild Foundation also provided some fieldwork materials. The contribution of C.M.S. was supported by the South African Research Chairs Initiative of the Department of Science and Innovation and the National Research Foundation of South Africa (grant no. 84379). Any opinion, finding, conclusion or recommendation expressed in this material is that of the authors and the NRF does not accept any liability in this regard. Huge thanks go to Cyrus Binassoua, Christian Affoukou, Hervé Kanlissou, Michaël Hounsa, and local guides in the different sites for field assistance.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

References

- Selwood, K.E.; McGeoch, M.A.; Mac Nally, R. The effects of climate change and land-use change on demographic rates and population viability. *Biol. Rev.* **2015**, *90*, 837–853. [\[CrossRef\]](#)
- Sá, D.; Scariot, A.; Ferreira, J.B. Effects of ecological and anthropogenic factors on population demography of the harvested *Butia capitata* palm in the Brazilian Cerrado. *Biodivers. Conserv.* **2020**, *29*, 1571–1588. [\[CrossRef\]](#)
- World Wide Fund. Saving Forests at Risk. In *WWF Report 2015: Living Forests Report*; WWF—World Wide Fund for Nature (Formerly World Wildlife Fund): Gland, Switzerland, 2015; pp. 1–45.
- Sinasson, S.G.K.; Shackleton, C.M.; Glèlè Kakai, R.L.; Sinsin, B. Forest degradation and invasive species synergistically impact *Mimulus andongensis* (Sapotaceae) in Lama Forest Reserve. *Biotropica* **2017**, *49*, 160–169. [\[CrossRef\]](#)
- Noulekoun, F.; Birhane, E.; Chude, S.; Zenebe, A. Characterization of *Faidherbia albida* (Del.) A. Chev. population in agroforestry parklands in the highlands of Northern Ethiopia: Impact of conservation, environmental factors and human disturbances. *Agrofor. Syst.* **2017**, *91*, 123–135. [\[CrossRef\]](#)
- Mantyka-Pringle, C.S.; Visconti, P.; Di Marco, M.; Martin, T.G.; Rondinini, C.; Rhodes, J.R. Climate change modifies risk of global biodiversity loss due to landcover change. *Biol. Conserv.* **2015**, *187*, 103–111. [\[CrossRef\]](#)
- Herrero-Jauregui, C.; Guariguata, M.R.; Cardenas, D.; Vilanova, E.; Robles, M.; Licona, J.C.; Nalvarte, W. Assessing the Extent of “Conflict of Use” in Multipurpose Tropical Forest Trees: A Regional View. *J. Environ. Manag.* **2013**, *130*, 40–47. [\[CrossRef\]](#) [\[PubMed\]](#)
- Ticktin, T. The ecological sustainability of non-timber forest products: Principles and methods. In *Ecological Sustainability for Non-Timber Forest Products: Dynamics and Case Studies of Harvesting, People and Plants International Conservation*; Shackleton, C.M., Pandey, A.K., Ticktin, T., Eds.; Routledge: London, UK; Taylor & Francis Group: New York, NY, USA, 2015; ISBN 1317916123, 9781317916123. pp. 31–52.
- You, J.; Qin, X.; Ranjitkar, S.; Loughheed, S.C.; Wang, M.; Zhou, W.; Ouyang, D.; Zhou, Y.; Xu, J.; Zhang, W.; et al. Response to climate change of montane herbaceous plants in the genus *Rhodiola* predicted by ecological niche modelling. *Sci. Rep.* **2018**, *8*, 5879. [\[CrossRef\]](#) [\[PubMed\]](#)
- Maharjan, K.S.; Poorter, L.; Holmgren, M.; Bongers, F.; Wieringa, J.J.; Hawthorne, D.W. Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica* **2011**, *43*, 552–561. [\[CrossRef\]](#)
- Herrero-Jauregui, C.; Sist, P.; Casado, M.A. Population structure of two low-density neotropical tree species under different management systems. *For. Ecol. Manag.* **2012**, *280*, 31–39. [\[CrossRef\]](#)
- Mota-Vargas, C.; Rojas-Soto, O.R. The importance of defining the geographic distribution of species for conservation: The case of the Bearded Wood-Partridge. *J. Nat. Conserv.* **2012**, *20*, 10–17. [\[CrossRef\]](#)
- Lemmens, R.H.M.J.; Omino, E.A.; Bosch, C.H. *Bois d’Oeuvre de l’Afrique Tropicale. Conclusions et Recommandations Basées sur PROTA 7(1): “Bois d’Oeuvre 1”*; Fondation PROTA: Nairobi, Kenya, 2010.
- Soro, D.; Kone, M.W.; Kamanzi, K. Evaluation des Activités Antimicrobiennes et Anti-Radicaux Libres de Quelques Taxons Bioactifs de Côte D’Ivoire. *Eur. J. Sci. Res.* **2010**, *40*, 307–317.
- Sinasson, S.G.K.; Shackleton, C.M.; Assogbadjo, A.E.; Sinsin, B. Local Knowledge on the Uses, Habitat and Change in Abundance of Multipurpose *Mimulus* Species in Benin. *Econ. Bot.* **2017**, *71*, 105–122. [\[CrossRef\]](#)
- Abdelmohsen, G.; Dawoud, G.T.M.; Mohamed, M.S.M. Investigation of the biochemical and ultrastructural mechanisms underlying the antimicrobial activity of *Mimulus* spp. extracts. *Baghdad Sci. J.* **2020**, *17*, 452–462. [\[CrossRef\]](#)

17. Alemneh, D. Ethnobotany of wild edible plants in Yilmana Densa and Quarit Districts of West Gojjam zone, Amhara region, Ethiopia. *Ethnobot. Res. Appl.* **2020**, *20*, 47. [\[CrossRef\]](#)
18. Tossou, G.M.; Yédomonhan, H.; Adomou, A.C.; Demènou, B.B.; Akoègninou, A.; Traoré, D. Caractérisation pollinique des miels d'un élevage apicole dans l'arrondissement de Manigri en zone soudano-guinéenne au Bénin. *Ann. Bot. Afr. Ouest* **2011**, *7*, 42–58.
19. Ismail, M.Y.; Leonard, T.; Tarimo, J.F.; Kayombo, C.J. Beekeeping Potential, Richness, and Distribution of Plant Species Foraged by Stinging Honey Bee (*Apis mellifera* L.) in West Kilimanjaro Tanzania Forest Service Agency (TFS) Plantation. *Int. J. Adv. Res.* **2021**, *3*, 33–54. [\[CrossRef\]](#)
20. Teketay, D.; Senbeta, F.; Maclachlan, M.; Bekele, M.; Barklund, P. *Edible Wild Plants in Ethiopia*; Addis Ababa University Press: Addis Ababa, Ethiopia, 2010.
21. Food and Agriculture Organization (FAO). *Global Forest Resources Assessment 2015: Main Report*; Food and Agriculture Organization of the United Nations: Rome, Italy, 2015.
22. Adomou, A. Territoires phytogéographiques au Bénin. In *Atlas de la Biodiversité de l'Afrique de l'Ouest*; Sinsin, B., Kampmann, D., Eds.; BIOTA: Cotonou, Benin; Frankfurt, Germany, 2010; Volume 1, pp. 120–143. Available online: <https://www.uni-frankfurt.de/47671063/BJ-Atlas> (accessed on 1 April 2016).
23. Wigley, B.J.; Coetsee, C.; Hartshorn, A.S.; Bond, W.J. What do ecologists miss by not digging deep enough? Insights and methodological guidelines for assessing soil fertility status in ecological studies. *Acta Oecol.* **2013**, *51*, 17–27. [\[CrossRef\]](#)
24. Hengl, T.; Heuvelink, G.B.M.; Kempen, B.; Leenaars, J.G.; Walsh, M.G.; Shepherd, K.D.; Sila, A.; MacMillan, R.A.; Mendes de Jesus, J.; Tamene, L.; et al. Mapping Soil Properties of Africa at 250 m Resolution: Random Forests Significantly Improve Current Predictions. *PLoS ONE* **2015**, *10*, e0125814. [\[CrossRef\]](#)
25. Wiegand, K.; Ward, D.; Thulke, H.-H.; Jeltsch, F. From snapshot information to long-term population dynamics of acacias by a simulation model. *Plant Ecol.* **2000**, *150*, 97–114. [\[CrossRef\]](#)
26. Botha, J.; Witkowski, E.T.F.; Shackleton, C.M. A comparison of anthropogenic and elephant disturbance on *Acacia xanthophloea* (fever tree) populations in the lowveld, South Africa. *Koedoe* **2002**, *45*, 9–18. [\[CrossRef\]](#)
27. Venter, S.M.; Witkowski, E.T.F. Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda, South Africa. *For. Ecol. Manag.* **2010**, *259*, 294–300. [\[CrossRef\]](#)
28. Shackleton, C.M.; Guthrie, G.; Main, R. Estimating the potential role of commercial over-harvesting in resource viability: A case study of five useful tree species in South Africa. *Land Degrad. Dev.* **2005**, *16*, 273–286. [\[CrossRef\]](#)
29. Statistical Analysis Software. *SAS/STAT® 9.2 User's Guide*; SAS Institute Inc.: Cary, NC, USA, 2008.
30. R Development Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria; Available online: <http://www.R-project.org> (accessed on 1 May 2018).
31. Gallagher, R.V.; Randall, R.P.; Leishman, M.R. Traits differences between naturalized and invasive plant species independent of residence time and phylogeny. *Conserv. Biol.* **2015**, *29*, 360–369. [\[CrossRef\]](#)
32. Lebrija-Trejos, E.; Reich, P.B.; Hernandez, A.; Wright, S.J. Species with greater seed mass are more tolerant of conspecific neighbours: A key driver of early survival and future abundances in a tropical forest. *Ecol. Lett.* **2016**, *19*, 1071–1080. [\[CrossRef\]](#) [\[PubMed\]](#)
33. Li, L.; Ye, W.H.; Wei, S.G.; Lian, J.Y.; Huang, Z.L. Spatial patterns and associations between species belonging to four genera of the Lauraceae family. *PLoS ONE* **2014**, *9*, e111500. [\[CrossRef\]](#)
34. Mairura, F.S.; Mugendi, D.N.; Mwanje, J.I.; Ramish, J.J.; Mbugua, P.K. Assessment of farmers' perceptions of soil quality indicators within smallholder farms in the central highlands of Kenya. In *Advances in Integrated Soil Fertility Management in Sub-Saharan Africa: Challenges and Opportunities*; Bationo, A., Ed.; Springer: Berlin/Heidelberg, Germany, 2007; pp. 1035–1046.
35. Berrill, J.-P.; O'Hara, K.L. How do biophysical factors contribute to height and basal area development in a mixed multi-aged coast redwood stand? *Forestry* **2016**, *89*, 170–181. [\[CrossRef\]](#)
36. Benton, J.J., Jr. *Plant Nutrition and Soil Fertility Manual*, 2nd ed.; CRC Press, Taylor and Francis Group: Boca Raton, FL, USA, 2012.
37. Chaturvedi, R.K.; Raghubanshi, A.S.; Tomlinson, K.W.; Singh, J.S. Impacts of human disturbance in tropical dry forests increase with soil moisture stress. *J. Veg. Sci.* **2017**, *28*, 997–1007. [\[CrossRef\]](#)
38. Berrill, J.-P.; Dagley, C.M. Regeneration and recruitment correlate with stand density and composition in long-unburned aspen stands undergoing succession to conifer in the Sierra Nevada, USA. *For. Res.* **2014**, *3*, 119. [\[CrossRef\]](#)
39. Mendes, C.P.; Ribeiro, M.C.; Galetti, M. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. *Ecography* **2016**, *39*, 465–475. [\[CrossRef\]](#)
40. Chazdon, R.L. Tropical reforestation pathways. In *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*; University of Chicago Press: Chicago, IL, USA, 2014; pp. 245–427.
41. Ceperley, N.; Montagnini, F.; Natta, A. Significance of sacred sites for riparian forest conservation in Central Benin. *Bois For. Trop.* **2010**, *303*, 5–23. [\[CrossRef\]](#)
42. ONAB (National Office of Wood). *Plan Directeur d'Aménagement et de Gestion du Noyau Central de la Forêt Classée de la Lama 2011–2020*; Ministère de l'Environnement et de la Protection de la Nature: Cotonou, Benin, 2011; 98p.
43. Botha, J.; Witkowski, E.T.F.; Shackleton, C.M. The impact of communal harvesting on *Warburgia salutaris* ('pepper-bark tree') in Mpumalanga, South Africa. *Biodivers. Conserv.* **2004**, *13*, 1675–1698. [\[CrossRef\]](#)
44. Worbes, M.; Staschel, R.; Roloff, A.; Junk, W.J. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. *For. Ecol. Manag.* **2003**, *173*, 105–123. [\[CrossRef\]](#)

45. Kalliovirta, J.; Tokola, T. Functions for estimating stem diameter and tree age using tree height, crown width and existing stand database information. *Silva Fenn.* **2005**, *39*, 227–248. [[CrossRef](#)]
46. Sanny, S.G.K.; Shackleton, C.M.; Sinsin, B. Reproductive phenology of two *Mimusops* species in relation to climate, tree diameter and canopy position in Benin (West Africa). *Afr. J. Ecol.* **2018**, *56*, 323–333. [[CrossRef](#)]
47. Condit, R.; Sukumar, R.; Hubbell, S.P.; Foster, R.B. Predicting population trends from size distributions: A direct test in a tropical tree community. *Am. Nat.* **1998**, *152*, 495–509. [[CrossRef](#)]
48. Wickens, G.E.; Lowe, P. *The Baobabs: Pachycauls of Africa, Madagascar and Australia*; Springer Science and Business Media: Berlin/Heidelberg, Germany, 2008; 498p.
49. Maranz, S. Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change. *J. Biogeogr.* **2009**, *36*, 1181–1193. [[CrossRef](#)]
50. Ticktin, T.; Ganesan, R.; Paramesha, M.; Setty, S. Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *J. Appl. Ecol.* **2012**, *49*, 774–784. [[CrossRef](#)]
51. Gray, C.L.; Hill, S.L.L.; Newbold, T.; Hudson, L.N.; Börger, L.; Contu, S.; Hoskins, A.J.; Ferrier, S.; Purvis, A.; Scharlemann, J.P.W. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat. Commun.* **2016**, *7*, 12306. [[CrossRef](#)]
52. Ruwanza, S.; Shackleton, C.M. Density and regrowth of a forest restio (*Ischyrolepis eleocharis*) under harvest and non-harvest treatments in dune forests of Eastern Cape Province, South Africa. *Econ. Bot.* **2015**, *69*, 136–149. [[CrossRef](#)]
53. Brockington, D.; Wilkie, D. Protected areas and Poverty. *Philos. Trans. R. Soc. B* **2015**, *370*, 20140271. [[CrossRef](#)]
54. Lindenmayer, D.B.; Likens, G.E.; Andersen, A.; Bowman, D.; Bull, C.M.; Burns, E.; Dickman, C.R.; Hoffmann, A.A.; Keith, D.A.; Liddell, M.J.; et al. Value of long-term ecological studies. *Austral Ecol.* **2012**, *37*, 745–757. [[CrossRef](#)]
55. Wheeler, C.E.; Mitchard, E.T.A.; Nolasco Reyes, H.E.; Iñiguez Herrera, G.; Marquez Rubio, J.I.; Carstairs, H.; Williams, M. A New Field Protocol for Monitoring Forest Degradation. *Front. For. Glob. Chang.* **2021**, *4*, 655280. [[CrossRef](#)]