



Proximity to natural forests failed to rescue a declining agroforestry tree species

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ABSTRACT

The conservation of species in human-modified landscapes such as agroforestry systems is central to global conservation and sustainable use of biodiversity. Understanding the dynamics of key species in agroforestry systems is important for predicting the sustainability of these systems. However, the population dynamics of agroforestry tree species are often unknown, and planning for the management of these systems is generally grounded on the untested assumption that the tree component will persist over time. Here, we developed an integral projection model for *Vitellaria paradoxa* (Sapotaceae), one of the most important tree species in traditional agroforestry systems in West Africa. We collected three years of demographic data from six populations around the Pendjari Biosphere Reserve in Benin to parameterize this model and test the effect of populations' proximity to natural habitats on the short- and long-term dynamics of *V. paradoxa*. However, models suggest that *V. paradoxa* populations are projected to decline at a yearly rate of 10.6% and within the next two decades, this tree will be locally extinct. We found a significant positive effect of proximity to natural forest on the long-term population dynamics, but this failed to save populations from decline. Elasticity analyses show that the best strategy to slow down such a decline includes preserving the largest mature trees. However, traditional management systems that protect shea butter trees in agroforestry systems are now replaced by increasing tree cutting to produce firewood, charcoal and carve out mortars and pestles. The decline of this key agroforestry tree poses a broader threat to long-term sustainability of agroforestry systems.

1. Introduction

Agroforestry systems are the basis for crop production and the livelihood of millions of people in the tropics (Jose, 2009; Nair, 2007). Local people living from farming these lands are some of the poorest in the world, and particularly around protected areas, this activity does not necessarily protect them from food insecurity (Brockington and Wilkie, 2015; Duffy et al., 2021; Gardner et al., 2013; Waldron et al., 2017). In addition to various crops that are produced on the limited lands often conceded by park management to local people for strictly controlled farming activities, wild plants and animals found in traditional agroforestry systems remain valuable sources of food (Kessler, 1992; Schreckenberg, 1999). Hence, the sustainability of food production around these protected areas is intimately linked to the long-term

dynamics of key tree species that are integral to the structure and productivity of agroforestry systems. These key tree species (e.g., *Vitellaria paradoxa*, *Parkia biglobosa*, *Acacia senegal*, *Balanites aegyptiaca*, *Faidherbia albida*) provide food, medicine, wood but also provide nursing effects or nutrient to the crop component (Bayala et al., 2015; Verbree et al., 2014). However, decades of studies on tropical agroforestry systems failed to critically examine the dynamics of these important tree species (Choungou Nguenkeng et al., 2021). Management of agroforestry parklands are often based on the assumption that the tree component, despite numerous reports of decline (Aleza et al., 2015; Dimobe et al., 2020; Pienaaah et al., 2024; Tom-Dery et al., 2018), is bound to persist over time (Maranz, 2009). However, the limited recruitment and increasing mortality of adult reproductive trees (Baziari et al., 2019; Ræbild, 2012; Schreckenberg, 1999; Tougiani et al., 2021) suggest a long-term decline

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and local tree extinction in these agroforests.

The population dynamics of agroforestry tree species has rarely been studied, perhaps due to the assumptions that the long-term persistence of species in such human-modified system is rarely guaranteed. Most studies have focused on describing the communities that constitute the agroforestry systems, how these communities have been shaped by human and the ecosystem services they provide (Lovett and Haq, 2000; Maranz and Wiesman, 2003; N'Woueni and Gaoue, 2021). Recently, numerous studies focused on the productivity of key agroforestry tree species using linear regressions to estimate fruit production, tree size, population structure (Aleza et al., 2015; Djossa et al., 2008; Elias, 2013), the variation of carbon sequestration across different management systems (Aleza et al., 2018; Bondé et al., 2019; Dimobe et al., 2019; Glèlé Kakaï et al., 2011). Further studies examined functional trait variation (Gwali et al., 2012; Sanou et al., 2006) and developed climate suitability models to project the spatial variation of agroforestry tree species (Dimobe et al., 2020). However, these models do not provide insights into landscape changes or demographic variations over time. Understanding of the temporal dynamics of these tree species has direct implications for the sustainability of this tree-crop coexistence and is critical to the management of agroforestry systems.

Demographic models are commonly used to investigate plant population dynamics but rarely are they used to assess the viability of tropical species (Salguero-Gomez et al., 2010 but see; Gaoue, 2016; Gaoue et al., 2011; Groenendijk et al., 2012; Kouassi et al., 2014). Furthermore, studying the dynamics of species in human-modified landscapes such as agroforestry parklands is often rare because species in these systems tend to have low population size, subsequent of human activities, which may limit the use of matrix projection models (Caswell, 2001). Matrix projection models are stage-structured models that require that individuals within the study population to be classified into discrete life stages for which demographic transition rates are estimated (e.g., survival, growth, and fertility). The accuracy of estimates for each demographic process for a given life stage is dependent on the sample size for that specific stage. For rare species or systems with low density, these estimates often carry large uncertainties that can directly affect predictions and ecological conclusions. Instead of discretizing continuous demographic traits such as individual size, survival, growth and fertility, integral projection models (Ellner and Rees, 2006), unlike matrix projection models, consider size as a continuous variable. Thus, it is unnecessary to estimate demographic transitions for each life stages, allowing one to use (non)linear regressions to estimate size-dependent demographic rates. Recent studies show that integral projection models are more accurate than matrix models particularly for rare species with small population size (Ramula et al., 2009). For agroforestry tree species, which are often in low density, integral projection models are suitable to investigate their population dynamics. Further, this approach allows one to directly test the effect of continuous covariates measured at the individual plant level on population dynamics (Dahlgren and Ehrlén, 2011).

One particularity of agroforestry systems is that they are often surrounded by either other parklands or natural vegetation from which plants and animals are dispersed into the systems. Recently, the role that agroforestry systems proximity to natural habitats plays in shaping species assemblages in agroforestry systems has received increasing attention from applied ecologists and foresters (Delaney et al., 2020; N'Woueni and Gaoue, 2021; Pardon et al., 2019). In short, consistent with predictions from the theory of island biogeography (MacArthur and Wilson, 1963), the closer agroforestry systems are to nearby natural habitats, the more likely are species from the latter going to disperse into the agroforestry systems. Furthermore, consistent with the environmental filtering hypothesis (Kraft et al., 2015), species that disperse from nearby natural habitats are expected to be filtered by abiotic factors and then by biotic interactions and human influence. It is expected that these novel biotic interactions will have both negative (herbivory, parasitism) and positive (pollination, and biotic defense) effects on

resident agroforestry species.

Shea butter tree, *Vitellaria paradoxa*, is endemic to agricultural areas and the main tree species on which local people relies in traditional agroforestry systems in the Sudanian regions of West Africa (Aleza et al., 2018; Bondé et al., 2019; Dimobe et al., 2020; M'Woueni et al., 2019; N'Woueni and Gaoue, 2021). Studying the drivers of the dynamics of this key agroforestry tree species is important for the resilience of the agroforestry systems and for the conservation of global biodiversity (Franklin and Lindenmayer, 2009). We studied the population dynamics of *V. paradoxa* in the Pendjari Biosphere Reserve (Benin) and how this is affected by the distance that separates agroforestry systems from nearby natural habitats. We examined the transient dynamics of the study species to predict how its population size might change over the next 50 years. Previous studies suggest that species assembly in agroforestry systems is affected by the regional pool of species but also by human niche construction processes whereby they add and remove species to maximize their livelihood. Thus, we hypothesized that *V. paradoxa* populations that are closer to natural habitats will benefit from more pollinators visits which will migrate from these habitats. Thus, proximity to natural habitat can improve fertility. Furthermore, due to more arrival of diverse colonies of arthropods from nearby habitats, populations closer to these habitats will experience more herbivory and potential negative effects on growth and survival. Hence, we hypothesized that distance from natural habitats will predict demographic processes and population dynamics. We hypothesized that over time, populations closer to natural habitats are more likely to have higher proportion of *V. paradoxa* seedlings and juveniles from seeds dispersed from nearby habitats than those far away which are hypothesized to be dominated by old *V. paradoxa* plants with high mortality rates. Given the recurrent human pressure on agroforestry systems, we hypothesized that the overall population growth rate for the study species, which is a long-lived species, will be negative and most sensitive to changes in the survival rate of adult individuals.

2. Material and Methods

2.1. Study system

We studied the dynamics of Shea butter tree, *Vitellaria paradoxa* C.F. Gaertn. (Sapotaceae), in the Pendjari Biosphere Reserve, West Africa. *Vitellaria paradoxa* is a light-demanding tree species which can reach up to 20 m in height and 50 cm diameter at breast height. The species is distributed widely from Senegal to Uganda and represents the most important economic tree species in traditional agroforestry systems in West Africa (Bouvet et al., 2004). *V. paradoxa* trees produce fruits that are prized and harvested by local people for direct consumption and sale. The kernels are harvested by local people who break them to remove the endocarp (when dry) which is then used to produce shea butter either for local consumption or sold internationally to the cosmetic industry (Boffa, 2015). The flowers are hermaphroditic and usually cross-pollinated mostly by bees but can be self-pollinated (Orwa et al., 2009). The flowering period spans 30–75 days. The fruits are 5–8 cm long and 3–4 cm wide and can take 4–6 months to develop. However, fruits do not reach maturity before the start of the rainy season.

The Pendjari Biosphere Reserve is in the Sudanian region and the northwest part of Benin between 10°30' - 11°30'N and 0°50' - 2°00' E. Annual rainfall ranges from 1000 to 1100 mm with two climatic seasons: the rainy season from mid-May to October followed by a dry season from November to February. The area is characterized by an average annual temperature of 27°C. The minima and maxima are respectively 21°C and 40°C (ASECNA, 2010). The soils are tropical ferruginous and hydro-morphic (Faure and Volkoff, 1998). The Pendjari Biosphere Reserve is dominated by open forests and wooded savannas, tree, shrub, and grassy savannas. These habitats are increasingly degraded by a rapidly growing human population and land encroachment by local populations trapped

in a narrow land strip between the reserve and the *Atacora* chain of mountains which are not appropriate for farming (M'Woueni et al., 2019). These natural habitats, including forest and savannas, are sources of arthropods that can be beneficial or pest for *V. paradoxa*. These habitats can also be source of *V. paradoxa* seeds that can disperse into the agroforestry systems and subsidize existing populations. The probability of dispersal of arthropods or seeds is predicted to be a function of the distance that separates the agroforestry systems from these natural habitats.

2.2. Demographic data

We identified and selected six populations of *V. paradoxa* in the agroforestry parklands in the Pendjari Biosphere reserve. These populations were within 1–15 km of natural habitats. The distance between agroforestry systems and nearby natural habitats was measured using a Garmin's GPSMAP 64sc Global Positioning System (GPS). Only seedlings were present in one of the populations, and we removed this population from our analysis. In each population, one 30 m x 30 m permanent plot was installed. In each plot, all *V. paradoxa* individuals were identified and then tagged using numbered aluminum tags. The diameter at breast height (DBH) of all adults and young individuals and the basal diameter of seedlings were measured each year for three years (2018–2020). At each census, we identified individual plants that died and counted the total number of fruits that remains in the population, and which has not been harvested by local people. The number of fruits per plant could not be obtained because of the frequency at which ripe fruits were dropping and because local populations collect fruits daily as they fall on the ground. Fruits were harvested at such a rate that we cannot accurately estimate the number of fruits that was produced. Instead, we used size dependent fruit production data collected by Aleza et al. (2018) in the study system. We counted the number of new seedlings at each re-census and tag them to estimate population fertility.

2.3. Integral projection modeling

We used three-year (2018–2020) demographic data to develop a size-dependent continuous integral projection model (Ellner and Rees, 2006) to project the long-term dynamics of *V. paradoxa* populations growing in agricultural and natural landscapes of the Pendjari Biosphere Reserve. The integral projection model (IPM) which includes the probabilities of survival, growth, and fertility is of the form:

$$n(y, z, t + 1) = \int_L^U K(x, y, z)n(x, z, t)dx, \tag{1}$$

where $n(y, z, t + 1)$ represents the vector of the number of individuals of size y at time $t + 1$ at the distance z from nearby natural forests. $[L, U]$ is the possible variation of all possible sizes (i.e., $\log(\text{DBH})$ at time t , $L = 0.9 \times \text{minimum size}$ and $U = 1.1 \times \text{maximum size}$ (Miller and al. 2009). The vector $n(x, z, t)$ represents the number of individuals of *V. paradoxa* size x , located at the distance z from natural forests at time t . The kernel $K(x, y, z)$ is a non-negative surface of all possible transitions (i.e. survival, growth and fertility) of individual plant of size x at time t located at the distance z from natural habitat to size y at time $t + 1$, which is composed of two functions, survival-growth function $P(y, x, z)$ and fertility function $f(y, x)$. The survival-growth function is the product of the survival function $s(x, z)$ and the growth function $g(y, x, z)$:

$$P(y, x, z) = s(x, z)g(y, x, z). \tag{2}$$

We parameterized these functions (Table 1) for each of the combinations of our study environment from 2018 to 2020, i.e., three years, using the coefficients estimated from the statistical modeling of the raw demographic data (Table 2).

Survival function, $s(x, z)$

The probability of survival at time $t + 1$ was modeled as a logistic

Table 1
Functions and notation used for the integral projection model.

Functions and notations	Definition
t	Time at starting point for transition assess
$t + 1$	Time after a year
x	Diameter at time t (cm)
y	Diameter at time $t + 1$ (cm)
z	Distance to natural habitats (km)
$s(x, z)$	Survival from time t to time $t + 1$
$g(y, x, z)$	Size growth
$P(y, x, z)$	Survival-growth
$f_n(y, x)$	Number of fruits
p_e	Probability of seedling establishing
$f_d(y)$	Size distribution of new seedling
$n(x, z, t)$	Population state at time t
$n(y, z, t + 1)$	Population state at time $t + 1$
$f(y, x)$	Fertility (Fruiting)
λ	Population growth rate

Table 2
Statistical models describing the demography of *Vitellaria paradoxa* in agroforestry parklands including the effects of agroforests distance from nearest natural habitats on the probability of survival, growth, the number of fruits, the size distribution of seedling and probability of seed germination and establishment. The probabilities of survival $s(x, z)$ and growth $g(y, x, z)$ were modeled as function of individual size x , and distance from natural habitat, z . Size dependent fruit production $f_n(y, x)$ was modeled without including distance because this was not included in the dataset used Aleza et al. (2018). For each model, we estimated the Akaike Information Criterion (AIC) and reported the estimated values, standard error (SE), associated Z-values (Z) and p-values (p) for each regression parameter. *** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$.

Process and equation	Parameters	Estimates (SE)	Z	p	AIC
Survival $s(x, z)$: (n = 60) $\text{logit}(p_s) = a_s + b_s x + c_s z + d_s xz$					70.1
	a_s	3.56 (3.52)	1.01	0.31	
	b_s	-0.59 (0.87)	-0.68	0.49	
	c_s	-1.80 (1.06)	-1.71	0.08	
	d_s	0.46 (0.26)	1.76	0.07	
Growth $g(y, x, z)$: (n = 44) $\mu_g = a_g + b_g x + c_g z + d_g xz$					-151.2
	a_g	0.27 (0.05) ***	5.23	<0.0001	
	b_g	0.94 (0.01) ***	70.59	<0.0001	
	c_g	-0.02 (0.007) **	-2.59	0.009	
	d_g	0.004 (0.002) *	2.29	0.022	
	σ_g^2	0.0014			
Fruiting $f_n(y, x)$: (n = 120) $\text{log}(p_f) = a_f + b_f x$					62934.57
	a_f	4.28 (0.05) ***	93.15	<0.0001	
	b_f	0.71 (0.01) ***	64.81	<0.0001	
Seedling size distribution (n = 61)					
	μ_s	0.53			
	σ_s^2	0.35			
Seed germination and establishment					
	p_e	0.0005 (0.0006)			

function of the size x and the distance z from nearby natural habitats:

$$s(x, z) = \frac{\exp(a_s + b_s x + c_s z + d_s xz)}{\exp(a_s + b_s x + c_s z + d_s xz)}. \tag{3}$$

To estimate the regression coefficients a_s, b_s, c_s and d_s in the function $s(x, z)$, we developed four candidate linear mixed effect models with a binomial error structure using the R package glmmTMB (Brooks et al., 2017) in R version 4.1.1 (R Core Team, 2018). We included population as a random effect and size at time t and population distance from nearby natural habitats as fixed effects. Candidate models included all one way, additive and interactive combinations of size and distance. The best model was selected using Akaike Information Criterion (AIC). The

model which includes the interaction of size and distance was the best-supported model (AIC = 70.12) and was therefore used to estimate the regression coefficients. We also included a quadratic term for distance in our model to test for the positive (e.g., longer distances limit invasion by weeds) and negative (e.g., longer distance limit pollinators immigration) effects of proximity to natural forests. This worsened our model by more than 3 AIC units (from AIC= 70.12–73.34). Thus, we kept the model without a quadratic term for distance.

Growth function, $g(y, x, z)$

We developed four candidate linear mixed effect models with population as a random effect and size x at t (log-transformed) and population distance to nearest natural habitat z as fixed effects using the R package glmmTMB. Because we did not detect heteroscedasticity (Fligner test, $\chi^2 = 27.33$, $df = 35$, $p = 0.82$), we did not model the variance of these models as function of size. We used model selection based on AIC to select the best candidate model. We modeled the growth function $g(y, x, z)$ as a normal distribution with the mean, μ_g , and the standard deviation σ_g , x and y are the size at time t , and $t + 1$, and z , is population distance from natural habitats:

$$g(y, x, z) = \frac{1}{\sigma_g \sqrt{2\pi}} \exp \left\{ -\frac{1}{2} \left(\frac{y - \mu_g}{\sigma_g} \right)^2 \right\}. \quad (4)$$

We estimated the regression coefficients a_g , b_g , c_g and d_g such that $\mu_g = a_g + b_g x + c_g z + d_g x z$ and σ_g is the standard deviation of plant size. We included the interactive effect of size and distance because the model which includes this interaction was the best-supported model (AIC = -151.16).

Fertility function, $f(x, z)$

The fertility function $f(x, z)$ includes fruit production $f_n(x)$, the probability of seed germinating and establishing p_e and seedling size distribution $f_d(y)$:

$$f(y, x) = f_n(x) p_e f_d(y). \quad (5)$$

Fruit production, $f_n(x)$ was modeled as a Poisson model with a mean and variance equal to:

$$f_n(x) = \exp(a_f + b_f x), \quad (6)$$

where the regression coefficients a_f and b_f were estimated using a generalized linear mixed effect model with a Poisson error structure and only plant size x as predictor. Data on individual fruit production was not available because harvesting happened fast before we could count them on the trees. Thus, we used data from the literature provided by Aleza et al. (2018) on the same system. Here we did not include site distance from nearby natural habitat because this detail was not available from the data. However, we included in the mixed models a random effect of soil type. We used the R package glmmTMB.

We calculated the probability of germination and establishment p_e by dividing the number of new seedlings at time $t + 1$ (2019 and 2020) by the number of fruits not harvested at time t (2018 and 2019 respectively). To obtain the seedling size distribution, $f_d(y)$, we measured the basal diameter of new seedlings across sites and estimated the mean μ_s and standard deviation σ_s of seedling sizes. The mean and variance of sizes were used to parametrize a normal distribution for seedling size:

$$f_d(y) = \frac{1}{\sigma_s \sqrt{2\pi}} \exp \left\{ -\frac{1}{2} \left(\frac{y - \mu_s}{\sigma_s} \right)^2 \right\}. \quad (7)$$

2.3.1. Population growth rate, damping ratio and elasticity

The numerical integration of the kernel K in Eq. (1) across the size range yields a big square matrix, whose dominant eigenvalue represents the long-term population growth rate, λ . The second highest eigenvalue of matrix K represent the short-term or transient population growth rate, λ_1 . The damping ratio which is equal to $\rho = |\lambda_1|/\lambda$ is a measure of the distance that separates current observed population size structure from

that of the equilibrium state (Caswell, 2001). The dimension of the big matrix was selected by simulating the effect of varying the size of the matrix on λ and selecting the highest dimension that stabilizes λ . We used a 100 by 100 big matrix. To project the size of *V. paradoxa* populations over time, t , we used the solution:

$$n(t) = K^t n(0), \quad (8)$$

where $n(0)$ represents the current size distribution at time $t = 0$. Given the limited number of years for which we sampled the demographic transitions for our study species, we simulated the dynamics for $t = 50$ years. In addition, we conducted elasticity analysis to identify the demographic processes for which λ is most elastic to (Caswell, 2001).

2.3.2. Simulating the effect of distance from natural habitats

To simulate the effects of the distance from nearby natural habitat on the population dynamics of *V. paradoxa*, we varied the mean of the distribution of distance, z , in the integral projection model (Eq. 1) and estimated the long-term population growth rates for each iteration. From our field data, we estimated the mean distance of *V. paradoxa* populations from nearby natural habitats as 5.03 km, ranging from 1.37 to 13.50 km with a standard deviation of 4.50 km. We built 30 different normal distributions of distance z for mean distance varying from 1 to 14 km, to stay slightly outside of the observed range of distances. However, we kept the observed SD of 4.50 km for each normal distribution. The dataset and R script used for these analyses are available on FigShare (Gaoue, 2022).

3. Results

The probability of survival decreased with individual size (Fig. 1a) and with distance from natural habitats (Fig. 1b), but these trends were not statistically significant (Table 2). However, individual growth rate was significantly affected by size at t and distance (Fig. 2a, b, Table 2). The growth of *V. paradoxa* individuals decreased with distance from natural habitats (Fig. 2b, Table 2), indicating a positive influence of agroforestry proximity to natural habitats. Fruit production increased significantly with individual size with most individuals producing less than 3000 fruits/tree (Fig. 3a, Table 2). However, the seedling to fruit ratio was extremely low ($p_e = 0.0005 \pm 0.0006$) with most new seedlings smaller than 0.5 cm basal diameter (Fig. 3b).

Our model showed that populations of *V. paradoxa* in agroforestry systems around Pendjari Biosphere reserve are projected to decline at a decay rate of 10.6% but with a population structure that is close to equilibrium structure (damping ratio, $\rho = 0.92$; Fig. 4a), suggesting that we can interpret the estimated long-term population growth rate of $\lambda = 0.89$ (Fig. 4a) as representative of current observed dynamics. At equilibrium, the stable size distribution showed that *V. paradoxa* populations are projected to be dominated by seedlings with limited chances to transition into sapling and by large adults (Fig. 4a). The elasticity patterns are dominated by the survival of large reproductive trees (Fig. 4b), indicating that maintaining the current crop of adults *V. paradoxa* is the best way to limit population decline over the long term. *V. paradoxa* population growth rates significantly decreased with distance from natural habitats ($\beta = -0.009 \pm 0.002$, $p = 0.003$, Fig. 5a) suggesting that the species benefit from proximity to natural habitats. However, even for populations that are the closest to natural habitats, simulated long-term population growth rates are less than 1, indicating that proximity to natural habitats could not rescue these populations from decline. Furthermore, consistent with the 10.6% population decline rate, future projection showed that these *V. paradoxa* populations are projected to disappear by the next 20 years (Fig. 5b).

4. Discussion

Conserving biological diversity in human-modified landscapes is an

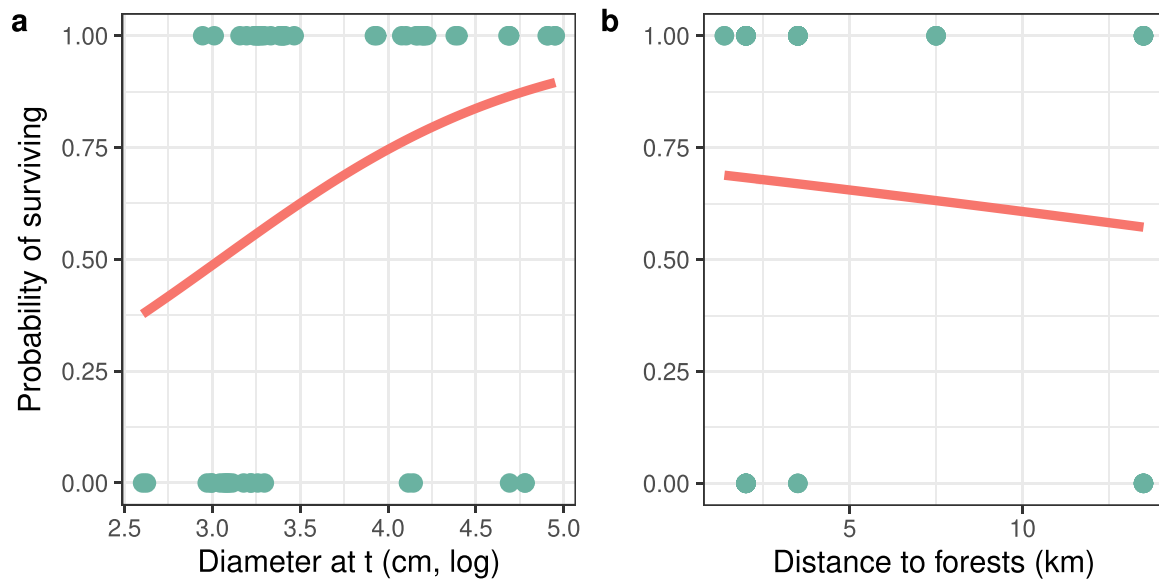


Fig. 1. Effect of (a) individual plant size (log-transformed diameter at breast height) and (b) distance of agroforestry systems from nearby natural habitat on the probability of survival of *Vitellaria paradoxa*. Data points represent observed survival and size for three years (2018–2020). The effect of size and distance on survival probabilities were not significant.

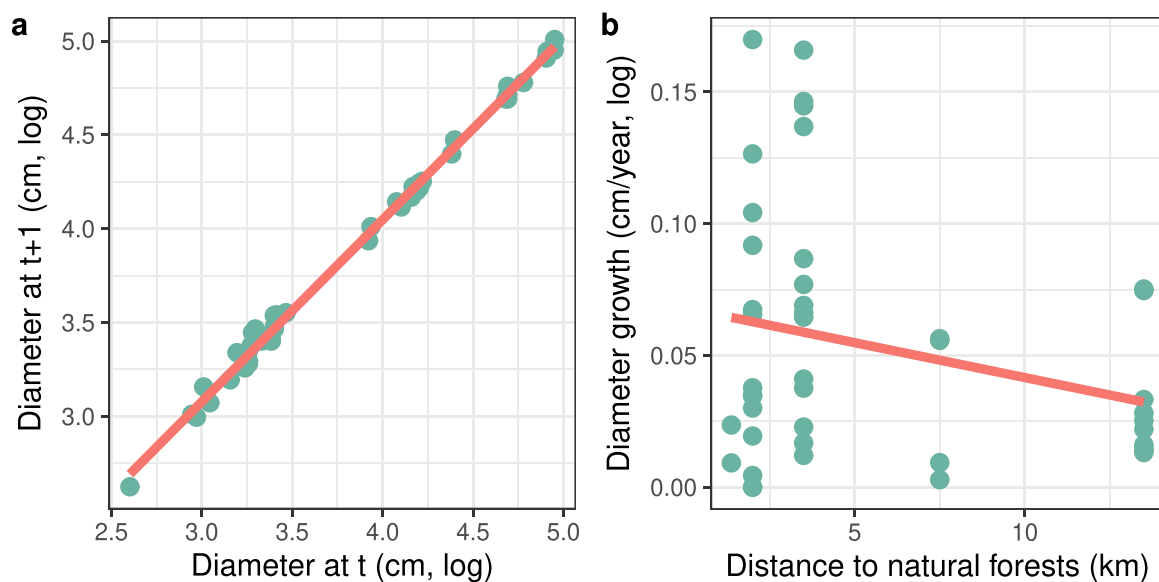


Fig. 2. (a) Size (diameter at breast height log-transformed) growth between t and $t+1$ for *Vitellaria paradoxa* and (b) effect of distance of agroforestry systems from nearby natural habitat on the growth rate.

important strategy for the conservation of biodiversity in natural habitats (Franklin and Lindenmayer, 2009; Koh and Gardner, 2010). Agroforestry systems represent the steppingstone and migration corridors for wildlife across fragments of intact habitats. In addition, agroforestry systems play significant role in providing the basis for agricultural production and offer non-timber forest products to ensure food security in rural regions (Jemal et al., 2018; Leroux et al., 2022). The value of these agroforestry systems is demonstrated to be influenced by the degree of proximity to natural habitats (Mahata et al., 2019; Ratto et al., 2021). In our study, we investigated the population dynamics of a key agroforestry tree species, *Vitellaria paradoxa*, using an integral projection models (Ellner and Rees, 2006). We tested the effect of population proximity to natural habitats on the demography of *V. paradoxa* and the implications for the short- and long-term dynamics of the species and its persistence in the landscape. Because *V. paradoxa* is the most important

tree species in these traditional agroforestry systems in West Africa (Boffa, 2015; N'Woueni and Gaoue, 2021), our study has direct practical implications for the future of sustainable agriculture in the region.

We hypothesized that agroforestry systems close to natural habitats are more likely to have juvenile *V. paradoxa* than those far away which are hypothesized to be dominated by old *V. paradoxa* trees with high mortality rates. We found that increasing the distance from natural habitats had a negligible effect on the probabilities of survival but negative effect on tree growth. The lack of significant effect of proximity on survival is expected particularly because most individuals in the studied populations are adults that are less likely to die unless they were directly logged by farmers. Logging of *V. paradoxa* is not uncommon despite its high utilitarian value. Local people often log the species for firewood and to make charcoal (Choungou Nguenkeng et al., 2021). Increasing logging of food trees such as *V. paradoxa* has become

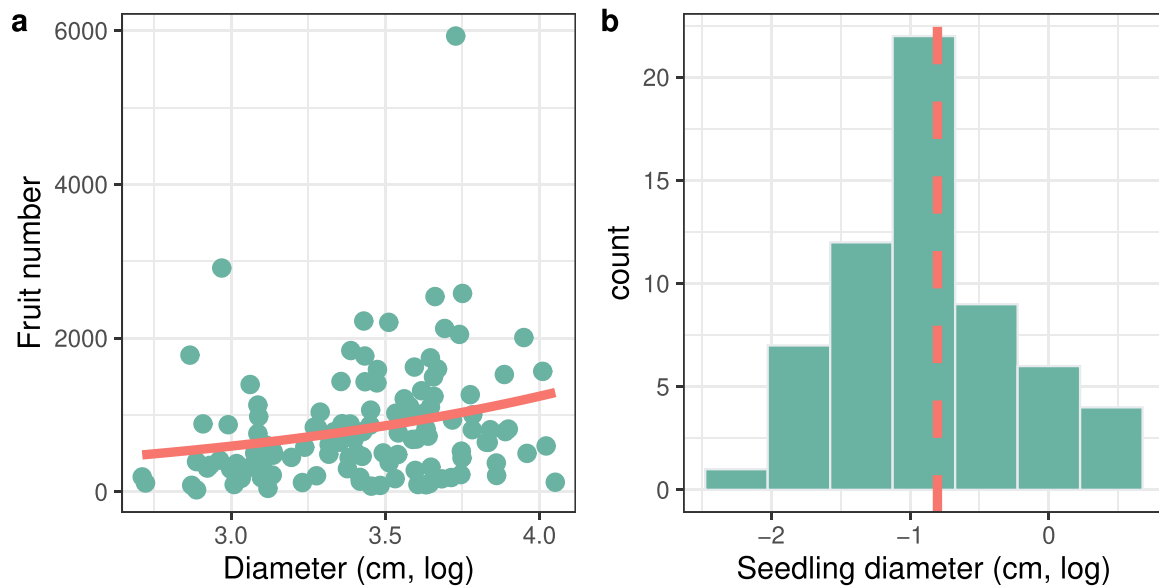


Fig. 3. Effect of (a) individual plant size (log-transformed diameter at breast height) on the number of fruits produced using data from Aleza et al. (2018) in the same study system. Red curve was obtained from a Poisson model fitted to the data. (b) Frequency distribution of new seedling basal diameter indicating a mean size as the dashed red line.

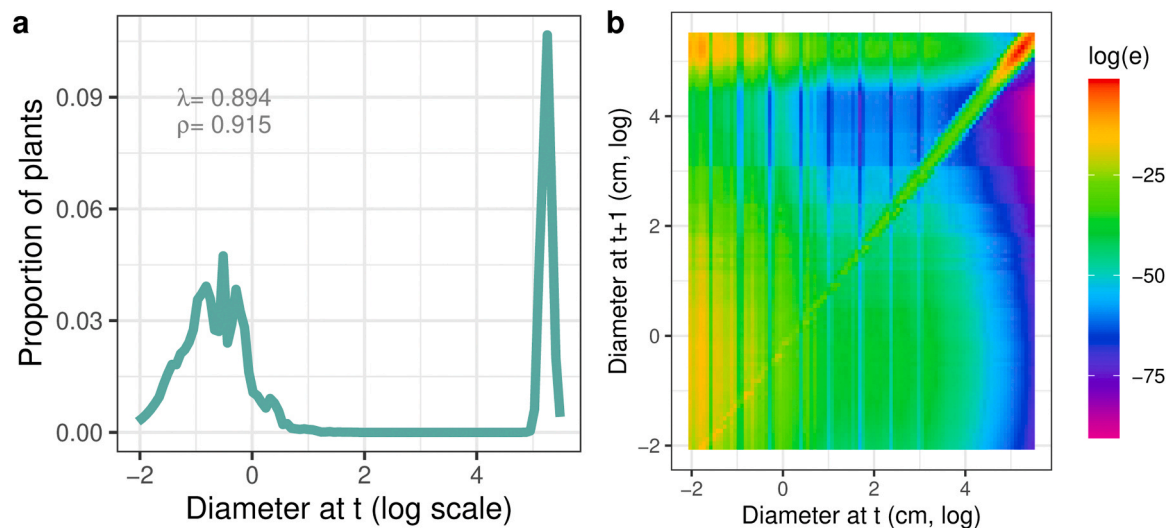


Fig. 4. (a) Stable size distribution for *Vitellaria paradoxa* representing the structure of the populations over the long-term with an asymptotic population growth rate, $\lambda=0.894$, and a damping ratio of $\rho = 0.915$, observed distance values. (b) Elasticity of the asymptotic population growth rate to perturbation of *Vitellaria paradoxa* vital rates indicating that λ is only elastic to changes in the survival of very large individuals (>5 cm, log, see small light green area at the bottom). The elasticity values are small and have been log-transformed $\log(e)$ to improve contrast in the figure.

common due to firewood shortage in the study region. Most local people are trapped between the Atacora chain of mountains and the Pendjari Biosphere reserve where collection of firewood is limited and most firewood species on agroforestry parklands are overexploited. Thus, local people increasingly target species that were previously considered non-firewood for harvest (Gaoue, 2000; M'Woueni et al., 2019). In addition, *V. paradoxa* is often infested by mistletoes which can cause water stress and ultimately affect growth and survival rates (Lamien et al., 2006). The demographic effect of agroforests proximity to natural habitats translated into direct effects on population dynamics. We found decreasing population growth rates with distance from nearest natural habitats highlighting the importance of these nearby forests for the sustainability of agroforestry systems. However, the positive effect of proximity to natural habitats still failed in this case to rescue *V. paradoxa* populations from decline. Previous studies demonstrated similar

negative effects of distance to forest and population size, such as it is found in agroforestry systems, on pollination services, seed production, dispersal, and gene flow (Agren, 1996; Kery et al., 2001). However, because we did not directly test the effect of distance on reproductive performance, our study cannot corroborate these results. From a different perspective, it is also possible that given the proximity to natural forests, *V. paradoxa* plants suffer more herbivory from arthropods which might migrate easily from these natural habitats. For example, proximity to natural forest increase wheat aphids attack rate in croplands in northern China (Yang et al., 2019). However, existing evidence also point to the contrary. For example, in soybean farms in Argentina, natural enemies (biocontrol) were more common and arthropods pests of soybean pods were less common closer to natural forests than not (González et al., 2017). The possibility of both positive and negative agroecological effects of crop or tree crop proximity to

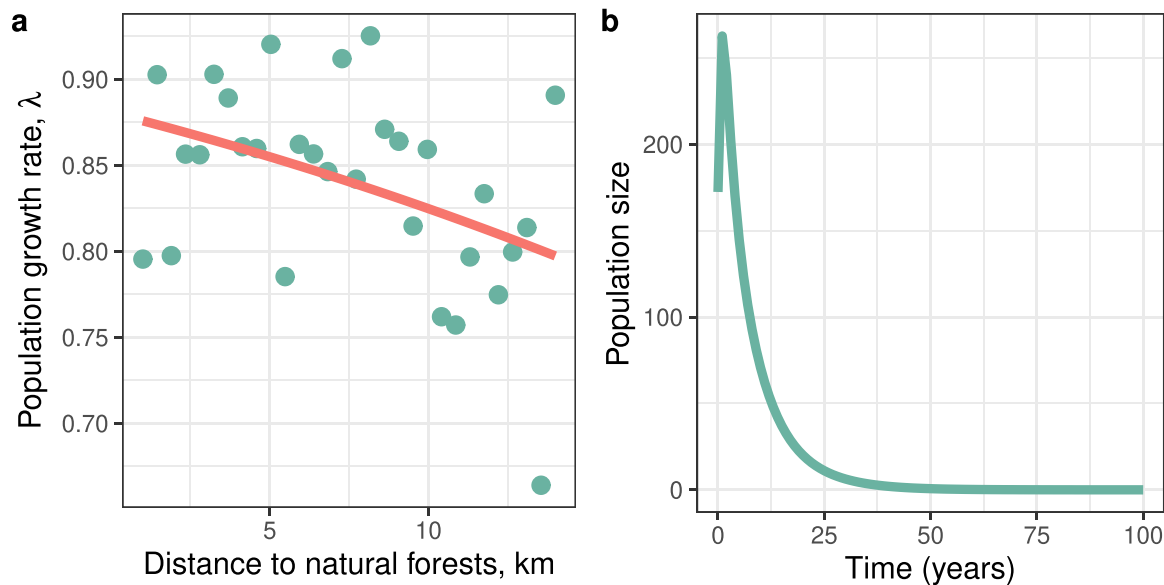


Fig. 5. (a) Effect of mean distance of agroforestry systems from nearby natural habitat on the long-term population growth rate λ of *Vitellaria paradoxa*. The red line was obtained from a linear regression with a significant negative slope ($\beta = -0.009$, $p = 0.003$). (b) Short-term projections of the size of *Vitellaria paradoxa* populations over time showing that within 20 years the number of individuals will decline to near zero. Kernel used for this simulation was based on observed distances of *V. paradoxa* populations to nearby natural habitats for a mean distance of 5.03 km with a standard deviation of 4.50 km.

natural habitat raises the potential for non-linear demographic responses in such systems. With increasing distance from natural forests, the positive influence (benefit) of beneficial species interactions (e.g., pollinators, defense mutualist) will decline while the negative effects (cost) of antagonistic species (e.g., herbivores, parasites) will also decline leading to a threshold distance at which the benefit of proximity will outweigh its cost which will coincide to a maximum demographic performance. However, such nonlinear demographic response was not observed in our system.

The stable size distribution projects that *V. paradoxa* populations would be dominated by old individuals with limited number of seedlings but without juveniles. Previous work on the same system, more than a decade ago, showed similar trend, indicating that years of management had limited success. Djossa et al. (2008) found that agroforestry systems at the Pendjari were dominated by large *V. paradoxa* trees while juveniles, seedlings and saplings dominated new fallow land and shrubs savannas. The lack of juvenile and the dominance of old adult trees in the long-term population structure of *V. paradoxa* is most likely a result of the intensification of land clearing coupled with the reduction of the fallow cycle which is observed in most of west Africa (Kelly et al., 2004; Laris and Wardell, 2006). Additionally, the high cost of fruit production due to recurrent fruit harvesting can suppress seedling recruitment (Doust and Doust, 1988). Our study showed that most seedlings found in the agroforestry parklands were very small with basal diameter less than 0.5 cm making them more vulnerable to fire and thereby limiting recruitment into larger size classes.

Our understanding of the population dynamics of tree species in human-modified landscapes and particularly in traditional agroforestry systems is limited but necessary to better plan the sustainable use of these systems (but see Somarriba, 2012; Sousa et al., 2017). In our study, we projected the short- and long-term dynamics of the most important tree component of agroforestry systems in West Africa. *Vitellaria paradoxa* is a tree that is overexploited for multiple purposes. This recurrent exploitation is gradually leading to its demise. Our integral projection model showed that *V. paradoxa* populations are currently declining at the rate of 10.6% per year. Simulating the dynamics over 50 years predicted that within the next 20 years, *V. paradoxa* populations will locally disappear around the Pendjari Biosphere Reserve. This is consistent with the declining trend reported for the species in West

Africa (Choungou Nguenkeng et al., 2021). In agroforestry landscapes, frequent fire, trampling, and farming interact with recurrent fruit harvest which directly reduces the number of fruits available for germination to limit demographic transitions and ultimately alter the population dynamics of trees such as *V. paradoxa*. There is an expectation for a community-based management of these agroforestry systems by the local people who depend on shea butter and fruits for their livelihood. Our elasticity analysis shows that conserving the largest and most reproductive trees is the best strategy to limit the observed decline of *V. paradoxa*. Conservation of adult and reproductive trees allows natural regeneration around adult trees (Djossa et al., 2008; Lovett and Haq, 2000). Local people intentionally preserve fruit and reproductive trees. However, this practice seems insufficient in our study systems given that large shea butter trees are logged for firewood and to make mortars and pestles. It is important to combine public awareness campaign on the threat that such activities pose to *V. paradoxa* with medium scale firewood plantation campaigns. However, limiting tree felling to carve out mortars and pestles is more challenging given that this is the only species used for such purpose in the region. Wood carving activities are widespread in Africa (Belcher et al., 2013) because mortars and pestles are common kitchen utensils which are used to make pounded yam, one of the staple foods in African culture (Agboola, 2004). Introducing and promoting the use of other species such as *Prosopis africana*, which are carved out to make mortars and pestles in neighboring Nigeria (Agboola, 2004), can reduce the harvesting pressure on *V. paradoxa*.

Our study combines data from different sources to build a model that project the population dynamics of an important agroforestry tree species in a context where data are often sparse or lacking. Thus, our study provides a framework for future investigation using similar approach to understand the transient and long-term persistence of trees in agroforestry systems. However, this study presents a few limitations that can be addressed to improve our mechanistic understanding of how agroforests proximity to natural forest can rescue declining tree populations or promote persistence and the sustainability of traditional agroforestry systems. We did not directly include in our model the influence of proximity to natural forest on the abundance of natural enemies including weed and pests and the prevalence of mutualistic interactions. Understanding how distance from agroforest to natural forest influence pollinators species assemblages in agroforests, and how this affect

flower visitation rate and pollination can provide further insights that can refine management strategies. Given that the probability of colonization by natural enemies and mutualists will vary in opposite direction with proximity to natural forests, it is expected that populations dynamics will exhibit a non-linear response to distance. Estimating the optimal distance that maximizes tree population fitness will provide practical recommendations for landscape level planning. This will facilitate the identification of agroforests that are in most need of further restoration.

5. Conclusions

This study suggests that current methods of conserving shea butter tree are inappropriate, with observed population decline projected to lead to its local extinction. In the absence of new management strategies, the decline of *Vitellaria paradoxa* will directly affect the livelihoods of the thousands of communities that depend on this resource, national economy and the food and cosmetic industries. The projected local extinction of our study species within two decades should encourage the local populations in making greater effort to protect the species. Conservation efforts should not only focus on limiting the mortality of the largest trees but also facilitating recruitment in juvenile life stages to shift the population trends from declining to increasing. In this endeavor, support from Non-Governmental Organizations interested in nature conservancy is greatly needed to guide and reinforce local initiatives. Particularly, finding alternatives for firewood via the diffusion of new technologies on efficient cooking stoves, and promoting alternative source of fuelwoods species. This strategy requires the domestication of locally known and preferred fuelwood species such as *Crossopterix febrigruga*, *Anoetissus leiocarpa* and *Prosopis africana* (Jurisch et al., 2012; Mononen and Pitkänen, 2016; Puentes-Rodriguez et al., 2017) and the promotion local plantations via vegetative reproduction.

CRedit authorship contribution statement

Orou G. Gaoue: Writing – original draft, Visualization, Supervision, Software, Methodology, Formal analysis, Conceptualization. **Daniel N' Woueni:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

<https://doi.org/10.6084/m9.figshare.20642826.v1>

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References

Agboola, D.A., 2004. *Prosopis africana* (Mimosaceae): stem, roots, and seeds in the economy of the savanna areas of Nigeria. *Econ. Bot.* 58, S34–S42. [https://doi.org/10.1663/0013-0001\(2004\)58\[S34:PAMSA\]2.0.CO;2](https://doi.org/10.1663/0013-0001(2004)58[S34:PAMSA]2.0.CO;2).

- Agren, J., 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77, 1779–1790. <https://doi.org/10.2307/2265783>.
- Aleza, K., Wala, K., Bayala, J., Villamor, G.B., Dourma, M., Atakpama, W., Akpagana, K., 2015. Population structure and regeneration status of *Vitellaria paradoxa* (C. F. Gaertner) under different land management regimes in Atacora department, Benin. *Agrofor. Syst.* 89, 511–523. <https://doi.org/10.1007/s10457-015-9787-9>.
- Aleza, K., Villamor, G.B., Nyarko, B.K., Wala, K., Akpagana, K., 2018. Shea (*Vitellaria paradoxa* Gaertn. C. F.) fruit yield assessment and management by farm households in the Atacora district of Benin. *PLOS One* 13, e0190234. <https://doi.org/10.1371/journal.pone.0190234>.
- ASECNA, 2010. Données climatiques, station. de Natitingou, Bénin. ASECNA, Cotonou, Benin.
- Bayala, J., Sanou, J., Teklehaimanot, Z., Ouedraogo, S.J., Kalinganire, A., Coe, R., Noordwijk, M. van, 2015. Advances in knowledge of processes in soil–tree–crop interactions in parkland systems in the West African Sahel: a review. *Agric. Ecosyst. Environ.* 205, 25–35. <https://doi.org/10.1016/j.agee.2015.02.018>.
- Baziari, F., Henquinet, K.B., Cavaleri, M.A., 2019. Understanding farmers' perceptions and the effects of shea (*Vitellaria paradoxa*) tree distribution in agroforestry parklands of Upper West Region, Ghana. *Agroforest Syst.* 93, 557–570. <https://doi.org/10.1007/s10457-017-0150-1>.
- Belcher, B., Campbell, B.M., Cunningham, A., 2013. Carving Out a Future: "Forests, Livelihoods and the International Woodcarving Trade. Routledge.
- Boffa, J.M., 2015. Opportunities and challenges in the improvement of the shea (*Vitellaria paradoxa*) resource and its management: report submitted to the Global Shea Alliance. ICRAF Occas. Pap. xii + 46.
- Bondé, L., Ouedraogo, O., Traoré, S., Thiombiano, A., Boussim, J.I., 2019. Impact of environmental conditions on fruit production patterns of shea tree (*Vitellaria paradoxa* C.F.Gaertn) in West Africa. *Afr. J. Ecol.* 57, 353–362. <https://doi.org/10.1111/aje.12621>.
- Bouvet, J.-M., Fontaine, C., Sanou, H., Cardy, C., 2004. An analysis of the pattern of genetic variation in *Vitellaria paradoxa* using RAPD markers. *Agrofor. Syst.* 60, 61–69. <https://doi.org/10.1023/B:AGFO.000009405.74331.74>.
- Brockington, D., Wilkie, D., 2015. Protected areas and poverty. *Philos. Trans. R. Soc. B: Biol. Sci.* 370, 20140271. <https://doi.org/10.1098/rstb.2014.0271>.
- Brooks, M., Kristensen, E., Benthem, K. J., van, K., Magnusson, A., Berg, C., Nielsen, W., Skaug, A., J. H., Mächler, M., Bolker, B., M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378. <https://doi.org/10.32614/RJ-2017-066>.
- Caswell, H., 2001. *Matrix Models: Construction, Analysis and Interpretation*, 2nd ed. Sinauer, Sunderland.
- Choungou Nguekeng, P.B., Hendre, P., Tchoundjeu, Z., Kalousová, M., Tchanou Tchabda, A.V., Kyereh, D., Masters, E., Lojka, B., 2021. The current state of knowledge of shea butter tree (*Vitellaria paradoxa* C.F.Gaertner.) for nutritional value and tree improvement in West and Central Africa. *Forests* 12, 1740. <https://doi.org/10.3390/f12121740>.
- Core Team, R., 2018. *R: A Lang. Environ. Stat. Comput.*
- Dahlgren, J.P., Ehrlich, J., 2011. Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos* 120, 1183–1190. <https://doi.org/10.1111/j.1600-0706.2010.19063.x>.
- Delaney, A., Dembele, A., Nombé, I., Gnane Lirasse, F., Marshall, E., Nana, A., Vickery, J., Tayleur, C., Stout, J.C., 2020. Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands. *J. Appl. Ecol.* 57, 1504–1513. <https://doi.org/10.1111/1365-2664.13640>.
- Dimobe, K., Goetze, D., Ouedraogo, A., Mensah, S., Akpagana, K., Porembski, S., Thiombiano, A., 2019. Aboveground biomass allometric equations and carbon content of the shea butter tree (*Vitellaria paradoxa* C.F. Gaertn., Sapotaceae) components in Sudanian savannas (West Africa). *Agroforest Syst.* 93, 1119–1132. <https://doi.org/10.1007/s10457-018-0213-y>.
- Dimobe, K., Ouedraogo, A., Ouedraogo, K., Goetze, D., Stein, K., Schmidt, M., Ivette Nacoulma, B.M., Gnoumou, A., Traoré, L., Porembski, S., Thiombiano, A., 2020. Climate change reduces the distribution area of the shea tree (*Vitellaria paradoxa* C.F. Gaertn.) in Burkina Faso. *J. Arid Environ.* 181, 104237. <https://doi.org/10.1016/j.jaridenv.2020.104237>.
- Djossa, B., Fahr, J., Wiegand, T., Ayihouénou, B., Kalko, E., Sinsin, B., 2008. Land use impact on *Vitellaria paradoxa* C.F. Gaertn. stand structure and distribution patterns: a comparison of Biosphere Reserve of Pendjari in Atacora district in Benin. *Agrofor. Syst.* 72, 205–220.
- Doust, J.L., Doust, L.L., 1988. Modules of production and reproduction in a dioecious clonal shrub, *Rhus typhina*. *Ecology* 69, 741–750. <https://doi.org/10.2307/1941023>.
- Duffy, C., Toth, G.G., Hagan, R.P.O., McKeown, P.C., Rahman, S.A., Widyaniyansih, Y., Sunderland, T.C.H., Spillane, C., 2021. Agroforestry contributions to smallholder farmer food security in Indonesia. *Agroforest Syst.* 95, 1109–1124. <https://doi.org/10.1007/s10457-021-00632-8>.
- Elias, M., 2013. Influence of agroforestry practices on the structure and spatiality of shea trees (*Vitellaria paradoxa* C.F. Gaertn.) in central-west Burkina Faso. *Agrofor. Syst.* 87, 203–216. <https://doi.org/10.1007/s10457-012-9536-2>.
- Ellner, S.P., Rees, M., 2006. Integral projection models for species with complex demography. *Am. Nat.* 167, 410–428. <https://doi.org/10.1086/499438>.
- Faure, P., Volkoff, B., 1998. Some factors affecting regional differentiation of the soils in the Republic of Benin (West Africa). *Catena* 32, 281–306. [https://doi.org/10.1016/s0341-8162\(98\)00038-1](https://doi.org/10.1016/s0341-8162(98)00038-1).
- Franklin, J.F., Lindenmayer, D.B., 2009. Importance of matrix habitats in maintaining biological diversity. *Proc. Natl. Acad. Sci. USA* 106, 349–350. <https://doi.org/10.1073/pnas.0812016105>.

- Gaoue, O.G., 2000. Facteurs déterminants pour le zonage de la zone cynégétique de la Pendjari comme base de gestion intégrée. Engineer Degree Thesis, University d'Abomey-Calavi, Abomey-Calavi, Benin.
- Gaoue, O.G., 2016. Transient dynamics reveal the importance of early life survival to the response of a tropical tree to harvest. *J. Appl. Ecol.* 53, 112–119. <https://doi.org/10.1111/1365-2664.12553>.
- Gaoue, O.G., 2022. Dataset for Proximity to natural forest failed to rescue a declining agroforestry tree species. Figshare Dataset <https://doi.org/10.6084/m9.figshare.20642826.v1>. <https://doi.org/10.6084/m9.figshare.20642826.v1>.
- Gaoue, O.G., Horvitz, C.C., Ticktin, T., 2011. Non-timber forest product harvest in variable environments: Modeling the effect of harvesting as a stochastic sequence. *Ecol. Appl.* 21, 1604–1616. <https://doi.org/10.1890/10-0422.1>.
- Gardner, C.J., Nicoll, M.E., Mbohoahy, T., Oleson, K.L.L., Ratsifandrihamana, A.N., Ratsirarson, J., René de Roland, L.-A., Virah-Sawmy, M., Zafindrasilivonona, B., Davies, Z.G., 2013. Protected areas for conservation and poverty alleviation: experiences from Madagascar. *J. Appl. Ecol.* 50, 1289–1294. <https://doi.org/10.1111/1365-2664.12164>.
- Glèlè Kakai, R., Akpona, T.J.D., Assogbadjo, A.E., Gaoué, O.G., Chakeredza, S., Gnanglé, P.C., Mensah, G.A., Sinsin, B., 2011. Ecological adaptation of the shea butter tree (*Vitellaria paradoxa* C.F. Gaertn.) along climatic gradient in Bénin, West Africa. *Afr. J. Ecol.* 49, 440–449. <https://doi.org/10.1111/j.1365-2028.2011.01279.x>.
- González, E., Salvo, A., Valladares, G., 2017. Arthropod communities and biological control in soybean fields: Forest cover at landscape scale is more influential than forest proximity. *Agric., Ecosyst. Environ.* 239, 359–367. <https://doi.org/10.1016/j.agee.2017.02.002>.
- Groenendijk, P., Eshete, A., Sterck, F.J., Zuidema, P.A., Bongers, F., 2012. Limitations to sustainable frankincense production: Blocked regeneration, high adult mortality and declining populations. *J. Appl. Ecol.* 49, 164–173. <https://doi.org/10.1111/j.1365-2664.2011.02078.x>.
- Gwali, S., Nakabonge, G., Okullo, J.B.L., Eilu, G., Nyeko, P., Vuzi, P., 2012. Morphological variation among shea tree (*Vitellaria paradoxa* subsp. *nilotica*) 'ethnovarieties' in Uganda. *Genet. Resour. Crop Evol.* 59, 1883–1898. <https://doi.org/10.1007/s10722-012-9905-8>.
- Jemal, O., Callo-Concha, D., Van Noordwijk, M., 2018. Local agroforestry practices for food and nutrition security of smallholder farm households in Southwestern Ethiopia. *Sustainability* 10, 2722. <https://doi.org/10.3390/su10082722>.
- Jose, S., 2009. Agroforestry for ecosystem services and environmental benefits: an overview. *Agroforest Syst.* 76, 1–10. <https://doi.org/10.1007/s10457-009-9229-7>.
- Jurisch, K., Hahn, K., Wittig, R., Bernhardt-Römermann, M., 2012. Population structure of woody plants in relation to land use in a semi-arid savanna, West Africa. *Biotropica* 44, 744–751.
- Kelly, B.A., Bouvet, J.-M., Picard, N., 2004. Size class distribution and spatial pattern of *Vitellaria paradoxa* in relation to farmers' practices in Mali. *Agrofor. Syst.* 60, 3–11. <https://doi.org/10.1023/B:AGFO.0000009400.24606.e3>.
- Kery, M., Matthies, D., Fischer, M., 2001. The effect of plant population size on the interactions between the rare plant *Gentiana cruciata* and its specialized herbivore *Maculinea rebeli*. *J. Ecol.* 89, 418–427. <https://doi.org/10.1046/j.1365-2745.2001.00550.x>.
- Kessler, J.J., 1992. The influence of karité (*Vitellaria paradoxa*) and néré (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. *Agroforest Syst.* 17, 97–118. <https://doi.org/10.1007/BF00053116>.
- Koh, L.P., Gardner, T.A., 2010. Conservation in human-modified landscapes. *Conserv. Biol.* 24, 236–261.
- Kouassi, K.I., Barot, S., Laossi, K.R., Gignoux, J., Zoro Bi, I.A., 2014. Relationships between ramet and genet dynamics in two clonal palms. *For. Ecol. Manag.* 312, 101–107. <https://doi.org/10.1016/j.foreco.2013.10.017>.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599. <https://doi.org/10.1111/1365-2435.12345>.
- Lamien, N., Boussim, J., Nygard, R., Ouedraogo, J., Oden, P., Guinko, S., 2006. Mistletoe impact on Shea tree (C.F. Gaertn.) flowering and fruiting behaviour in savanna area from Burkina Faso. *Environ. Exp. Bot.* 55, 142–148.
- Laris, P., Wardell, D.A., 2006. Good, bad or 'necessary evil'? Reinterpreting the colonial burning experiments in the savanna landscapes of West Africa. *Geogr. J.* 172, 271–290. <https://doi.org/10.1111/j.1475-4959.2006.00215.x>.
- Leroux, L., Faye, N.F., Jahel, C., Falconnier, G.N., Diouf, A.A., Ndao, B., Tiaw, I., Senghor, Y., Kanfany, G., Balde, A., Dieye, M., Sirdey, N., Alogo Loison, S., Corbeels, M., Baudron, F., Bouquet, E., 2022. Exploring the agricultural landscape diversity-food security nexus: an analysis in two contrasted parklands of Central Senegal. *Agric. Syst.* 196, 103312. <https://doi.org/10.1016/j.agsy.2021.103312>.
- Lovett, P., Haq, N., 2000. Evidence for anthropic selection of the Sheanut tree (*Vitellaria paradoxa*). *Agrofor. Syst.* 48, 273–288.
- M'Woueni, D., Gaoue, O.G., Balagueman, R.O., Biao, H.S.S., Natta, A.K., 2019. Road mediated spatio-temporal tree decline in traditional agroforests in an African biosphere reserve. *Glob. Ecol. Conserv.* 20, e00796. <https://doi.org/10.1016/j.gecco.2019.e00796>.
- MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- Mahata, A., Samal, K.T., Palita, S.K., 2019. Butterfly diversity in agroforestry plantations of Eastern Ghats of southern Odisha, India. *Agroforest Syst.* 93, 1423–1438. <https://doi.org/10.1007/s10457-018-0258-y>.
- Maranz, S., 2009. Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change. *J. Biogeogr.* 36, 1181–1193. <https://doi.org/10.1111/j.1365-2699.2008.02081.x>.
- Maranz, S., Wiesman, Z., 2003. Evidence for indigenous selection and distribution of the shea tree, *Vitellaria paradoxa*, and its potential significance to prevailing parkland savanna tree patterns in sub-Saharan Africa north of the equator. *J. Biogeogr.* 30, 1505–1516.
- Mononen, K., Pitkänen, S., 2016. Sustainable Fuelwood Management in West Africa. *Univ. East. Finl., Finl.*
- N'Woueni, D.K., Gaoue, O.G., 2021. Species ethnobotanical values rather than regional ecosystem pool determine plant diversity in agroforestry systems. *Sci. Rep.* 11, 23972. <https://doi.org/10.1038/s41598-021-03408-3>.
- Nair, P.R., 2007. The coming of age of agroforestry. *J. Sci. Food Agric.* 87, 1613–1619. <https://doi.org/10.1002/jsfa.2897>.
- Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Simons, A., 2009. *Agroforestry Database: a tree reference and selection guide. Version 4.*
- Pardon, P., Reheul, D., Mertens, J., Reubens, B., De Frenne, P., De Smedt, P., Proesmans, W., Van Vooren, L., Verheyen, K., 2019. Gradients in abundance and diversity of ground dwelling arthropods as a function of distance to tree rows in temperate arable agroforestry systems. *Agric., Ecosyst. Environ.* 270–271, 114–128. <https://doi.org/10.1016/j.agee.2018.10.017>.
- Pienaaah, C.K.A., Baruah, B., Luginah, I., 2024. Women's perspectives on addressing the decline of Shea trees in Northern Ghana. *GeoJournal* 89, 9. <https://doi.org/10.1007/s10708-024-11023-8>.
- Puentes-Rodriguez, Y., Torssonen, P., Ramcilovic-Suominen, S., Pitkänen, S., 2017. Fuelwood value chain analysis in Cassou and Ouagadougou, Burkina Faso: From production to consumption. *Energy Sustain. Dev.* 41, 14–23. <https://doi.org/10.1016/j.esd.2017.07.008>.
- Ræbild, A., 2012. Improved management of fruit trees in West African parklands. *Agroforest Syst.* 85, 425–430. <https://doi.org/10.1007/s10457-012-9524-6>.
- Ramula, S., Rees, M., Buckley, Y.M., 2009. Integral projection models perform better for small demographic data sets than matrix population models: A case study of two perennial herbs. *J. Appl. Ecol.* 46, 1048–1053. <https://doi.org/10.1111/j.1365-2664.2009.01706.x>.
- Ratto, F., Steward, P., Sait, S.M., Pryke, J.S., Gaigher, R., Samways, M.J., Kunin, W., 2021. Proximity to natural habitat and flower plantings increases insect populations and pollination services in South African apple orchards. *J. Appl. Ecol.* 58, 2540–2551. <https://doi.org/10.1111/1365-2664.13984>.
- Salguero-Gomez, R., de Kroon, H., Salguero-Gomez, R., de Kroon, H., Salguero-Gomez, R., de Kroon, H., 2010. Matrix projection models meet variation in the real world. *J. Ecol.* 98, 250–254. <https://doi.org/10.1111/j.1365-2745.2009.01635.x>.
- Sanou, H., Picard, N., Lovett, P.N., Dembélé, M., Korbo, a, Diariso, D., Bouvet, J.-M., 2006. Phenotypic variation of agromorphological traits of the Shea tree, *Vitellaria paradoxa* C.F. Gaertn., in Mali. *Genet. Resour. Crop Evol.* 53, 145–161. <https://doi.org/10.1007/s10722-004-1809-9>.
- Schreeckenberg, K., 1999. Products of a managed landscape: non-timber forest products in the parklands of the Bassila region, Benin. *Glob. Ecol. Biogeogr.* 8, 279–289.
- Somarrriba, E., 2012. The population dynamics and productivity of *Acacia pennatula* in the pasturelands of the Nature Reserve Mesas de Moropotente, Estelí, Nicaragua. *Agrofor. Syst.* 84, 1–9.
- Sousa, K., de, Detlefsen, G., Tobar, D., Virginio Filho, E., de, M., Casanoves, F., 2017. Population dynamic and management of *Pinus oocarpa* and *Tabebuia rosea* within silvopastoral systems in Central America. *Agrofor. Syst.* 91, 1119–1127.
- Tom-Dery, D., Eller, F., Reisdorff, C., Jensen, K., 2018. Shea (*Vitellaria paradoxa* C. F. Gaertn.) at the crossroads: current knowledge and research gaps. *Agroforest Syst.* 92, 1353–1371. <https://doi.org/10.1007/s10457-017-0080-y>.
- Tougiani, A., Massaoudou, M., Haougui, A., Laouali, A., Weber, J.C., 2021. *Faidherbia albida* (Delile) tree dieback effects on crop production in the parkland agroforests of Southwestern Niger. *Int. J. For. Res.* 2021, e8895829. <https://doi.org/10.1155/2021/8895829>.
- Verbree, C.L., Aitkenhead-Peterson, J.A., Loeppert, R.H., Awika, J.M., Payne, W.A., 2014. Shea (*Vitellaria paradoxa*) tree and soil parent material effects on soil properties and intercropped sorghum grain-Zn in southern Mali, West Africa. *Plant Soil* 386, 21–33. <https://doi.org/10.1007/s11104-014-2244-0>.
- Waldron, A., Garrity, D., Malhi, Y., Girardin, C., Miller, D.C., Seddon, N., 2017. Agroforestry can enhance food security while meeting other sustainable development goals. *Trop. Conserv. Sci.* 10, 1940082917720667. <https://doi.org/10.1177/1940082917720667>.
- Yang, L., Liu, B., Zhang, Q., Zeng, Y., Pan, Y., Li, M., Lu, Y., 2019. Landscape structure alters the abundance and species composition of early-season aphid populations in wheat fields. *Agric. Ecosyst. Environ.* 269, 167–173. <https://doi.org/10.1016/j.agee.2018.07.028>.