


Ecological Models Reveal a Weakened Population Structure, and Distribution Drivers of *Osyris lanceolata* (Santalaceae) in the Karamoja Sub-Region, Uganda

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Abstract

Osyris lanceolata is heavily and illegally exploited in East Africa for its essential oils, yet little is known about its population status and ecological requirements. This study examined its population structure and environmental factors influencing its distribution in the semi-arid Karamoja sub-region, Uganda. We surveyed 388 plots (5 m radius) at different altitudes, recording life stages, stem diameters, and regeneration patterns, and analyzed soil samples. Multivariate analyses, including Canonical Correspondence Analysis (CCA), Detrended Correspondence Analysis (DCA), Non-metric Multidimensional Scaling (NMDS), and Multiple Regression Modeling (MRM), identified key environmental factors affecting its distribution. Findings show that *O. lanceolata* populations in Moroto, Nakapiripirit, and Amudat districts are severely degraded due to overexploitation. The species is primarily regenerating through coppicing rather than seedlings, with an exploitation intensity of 56.6%. Population densities are low, distribution is irregular, and sustainable harvesting is not viable. Soil properties, particularly Ca²⁺, N, P, K⁺, Na⁺, and

organic matter, significantly influence its abundance. Conservation efforts should focus on identifying suitable provenances for genetic preservation and plantation establishment. Areas with at least 9 trees per hectare in Moroto, Nakapiripirit, and Amudat could serve as potential sites for *ex-situ* plantations. Further research should explore how biotic interactions, genetic diversity, and morphology affect oil yield and quality to support restoration, breeding, and domestication initiatives.

Keywords

Plant Ecology, Hemiparasites, Edaphic Drivers, Ecological Modelling, Multivariate Analysis, Essential Oils, “R”

1. Introduction

Osyris lanceolata Hochst. & Steud. (East African sandalwood) is a root hemiparasitic plant that belongs to the family Santalaceae and genus *Osyris* [1] [2]. Members in this family are culturally and commercially useful species providing essential oils used in the perfumery, cosmetics, and pharmaceutical industries [3] [4]. Locally, the bark and root extracts treat candidiasis, malaria, diarrhea, chest pain, and fever in Africa [4]-[6]. Sandalwood oils have chemo-preventive properties used to manage eruptive skin and inflammatory diseases such as dysuria, bronchitis, gonorrhoea, and urinary infections. The bark and roots also provide red dye for skin tanning [4] while its shoot provides antipyretic agents for cattle. The roots have the ability to accumulate heavy metals and are thus useful in phytoremediation [7]. The oil has blending and anti-septic properties suitable for making fixatives in other fragrances [3] [8]. Traditional oil-producing species such as *Santalum alba* and *Santalum spicatum* have been commercially exploited since the 1990s and their populations have significantly dwindled due to over-exploitation [4] [9]-[11]. This trend has increased the demand for *O. lanceolata* as a source of essential oils with ready markets in Europe, China, and the United Arab Emirates [12] [13]. The pressure on *O. lanceolata* populations has led to the over-exploitation of the species in East Africa [4]. Some populations have completely disappeared while others are rapidly declining despite listing the species under Appendix II of CITES to ensure their survival [11] [13]. The species survives in unique arid and semi-arid habitats, particularly on rocky and stony soils [1] [14]-[17]. It also grows naturally in clumped communities along water galleys [16] [18] [19] and is closely associated with *Rhus natalensis* as a suitable host. The *O. lanceolata* hosts occur as shrubs, trees, herbs, and succulents [18]. As *O. lanceolata* is a hemiparasitic plant, its requirements for edaphic conditions must be related to the requirements of its hosts [16]. However, *O. lanceolata* distribution may not be consistent with soil variables in low-altitude areas [19]. Whether it shows similar behavior to edaphic variables in semi-arid savanna habitats, is yet to be investigated.

Elsewhere, the population and distribution drivers of aerial hemi parasites have been better explained than the distribution drivers of root hemiparasites [4] [20]-[27]. It was established by [28] that mistletoes abundance is significantly correlated with average levels of nitrogen for the woody plants and the overall nutrient status of a biome influences the abundance of mistletoes. Secondly, the host choice for mistletoes is significantly correlated to the mean host nitrogen. Away from hemiparasites, soil nutrients also influence the distribution of non-hemiparasites [29]-[35]. For the root hemi parasites, some studies have linked their distribution to host quality and water availability [20] [21] [24]. This implies that host survival requirements strongly influence the survival of root hemiparasites. Thus, it is important to consider the distribution of *O. lanceolata* and its hosts as a function of edaphic variables interacting with biotic and abiotic factors in the species micro-habitat [26] [34]. The micro-habitat of a species is believed to exhibit different conditions from areas further away [36]. Hence, testing soil variables within the micro-habitat of *O. lanceolata* and further away provides insight into specific variables that influence the species' distribution and survival. Therefore, further studies are necessary to identify edaphic variables, if any, that influence the species survival in dry savanna habitats as a key step towards the establishment of *ex-situ* populations for commercial use [4] [37]. This study builds further on a similar approach to identify edaphic variables that influence the distribution of *O. lanceolata* and its hosts and how the species population structure responds to over-exploitation in the semi-arid savanna ecosystem. Two questions are addressed: i) Which population structural patterns characterise *O. lanceolata* in Karamoja? ii) Which edaphic variables influence the distribution of *O. lanceolata* and its hosts? The study assumes that: (i) *O. lanceolata* population structure remains stable despite over-exploitation in the past. (ii) Its distribution and survival do not correlate with edaphic variables in the semi-arid savanna ecosystem across different altitudes. (iii) There are no significant differences in edaphic variables within the microhabitat and further away from the micro-habitat of *O. lanceolata*.

2. Materials and Methods

2.1. Study Area

The study was conducted in the districts of Moroto, Nakapiripirit, and Amudat of the Karamoja sub-region, located between 1°4' - 4.24°N and 33°50' - 35°E. The sub-region covers approximately 27,000 km² and is bordered by the Republic of South Sudan and Kenya to the North and East respectively. The region is characterized by distinct dry and wet seasons (Egeru *et al.* 2014) with an average rainfall of 400 - 1200 mm, and temperatures ranging between 28°C and 33°C [38]-[40]. The largest human population in Karamoja are mainly pastoralists, with few individuals involved in crop production, practicing on a communal land tenure system.

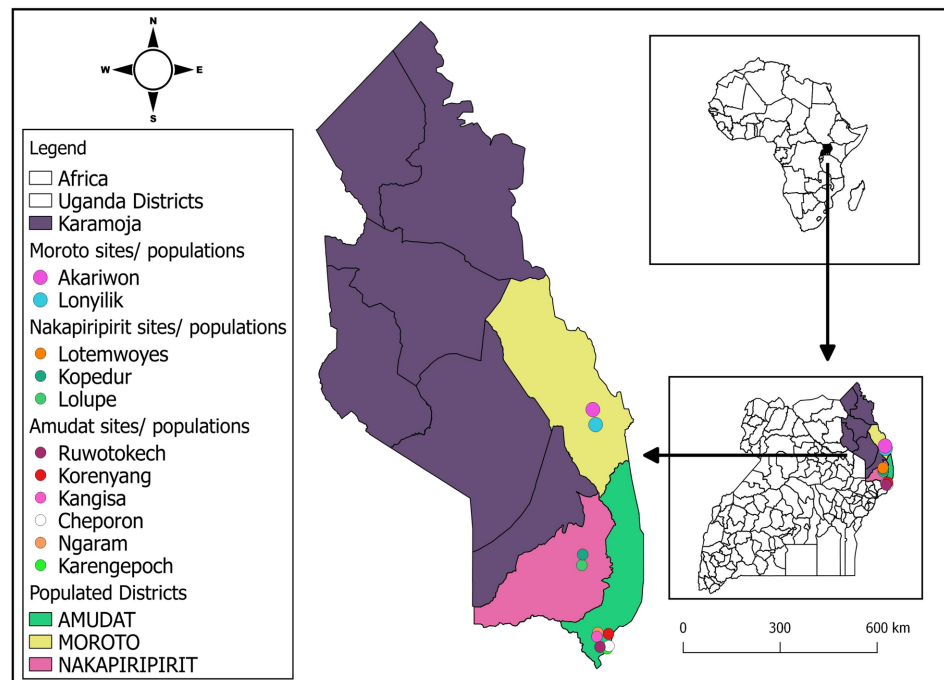


Figure 1. Location of Africa, Uganda, Karamoja sub-region and study populations. Colored dots indicate the selected sites for sampling.

2.2. Data Collection

To characterise the species population structure and distribution drivers, we identified eleven sites representing different altitude zones for sampling. The sites were selected after extensive surveys conducted between 2018 and 2020 in the Karamoja sub-region and these were informed by CITES reports and articles on *Osyris lanceolata*. The selection of target populations was based on species availability and accessibility of the sites. A further criterion was to select populations from a spectrum of altitudes categorised into low and high-altitude zones of Moroto, Nakapiripirit, and Amudat districts. Finally, eleven sites or populations were selected (Figure 1). We considered our sampling plot to be a circle of a 5 m radius with the *O. lanceolata* at the center. The 5 m radius was adequate to cover the whole clump of *O. lanceolata* including its hosts and this was the targeted microhabitat for *O. lanceolata*. The prevailing conditions further away from the micro-habitat were measured beyond 10 m from the *O. lanceolata* clump, and these were areas without *O. lanceolata*, and considered uncondusive for the survival of *O. lanceolata* [36] [41]. In total, we inventoried 388 plots using the nearest neighbor method as described by Mueller-Dombois and Ellenberg (1974). This method enabled us to encounter more species individuals than would be for quadrat sampling [42]. At each site, the initial sampling point was established after encountering the first *O. lanceolata* in a north-south direction. We did not specify sampling intervals due to the patchy distribution of the species, but we moved in a square-like pattern following the nearest-neighbor method. This pattern increased our chances of encountering more individuals of *O. lanceolata* because it offers an opportunity to

spot a target species from all directions. For every sampling point, *O. lanceolata* was recognized by a skilled botanist and categorised into different life stages (seedlings, saplings, and adults) [43]. The seedlings were classified in size class 0.5 - 1.2 cm (diameter), saplings at 1.2 - 5.9 cm, and adults at 6.0 - 19.4 cm diameter [44]. Because *O. lanceolata* is a multi-stemmed plant and its branching starts at lower heights, we measured the stem circumference (circ) for saplings and adults at 55 cm above the ground using a measuring tape and then converted it to diameter using the formula: $D = \text{circ} / \pi$, where; D is the diameter; circ is the circumference, and π is pi or 3.14. For seedlings, the stem circumference was measured at ≤ 20 cm above the ground within the 5 m radius. The altitude for each sampling point was recorded in the field by a GPS (Garmin 64 s). We assessed the species regeneration status by examining the growth mode, the number of coppiced individuals, and the proportion of seedlings and saplings within the sampling point [45]. By exploring the species extent of coppicing, it was possible to estimate the species intensity of destructive illegal harvesting expressed as the proportion of coppiced individuals to the independently growing stems of saplings and adults per site [46].

2.3. Edaphic Variables

A total of 112 soil samples were randomly collected from all sites. Two locations were considered for sampling at each site: one location within the 5 m radius of *O. lanceolata* (*Osyris* samples) and another location at >10 m away from *O. lanceolata* (control samples or non-*Osyris* samples). Using a soil auger, we collected samples at two depths to understand how nutrients vary with depths between *Osyris* and non-*Osyris* samples. Topsoil was collected at 0 - 20 cm while bottom soil at 20 - 40 cm [19]. All samples were packed in tight black polythene bags and labeled using non-erasable ink on a masking tape to indicate the study site, sampling point, and sample category. The labeled samples were temporarily stored under room temperature at NARO-Nabuin Zonal Agricultural Research and Development Institute (ZARDI) in Karamoja and later transferred to Makerere University, for analysis. Before analysis, all samples were air-dried at room temperature, ground, and sieved through a 2 mm sieve. Samples were analyzed for soil pH, measured on a 1:2.5 soil in distilled water suspension using a pH meter. Soil texture was assessed by the bouyoucos or hydrometer method. Exchangeable cations (K^+ , Na^+ and Ca^{2+}) were extracted with neutral ammonium acetate solution and then determined directly from emissions measured by a flame photometer. The nitrogen content (N) was determined by the Kjeldahl method, and phosphorus (P) was measured by Bray 1 method and determined using a spectrophotometer (JENWAR 6405UV/vis) [47]-[49]. Organic matter was determined by the oxidation method [47] [50].

2.4. Data Analysis

We used the species density, and size class distribution and regression analysis to evaluate the strength and stability of the species population structure [42]. A

strong and stable population structure was considered to show an inverse J-shaped curve, a significant number of independently growing saplings and adults, and an adequate number of seedlings with good potential for regeneration through natural seedlings [18] [43] [51] [52]. Poor regeneration potential was considered to indicate a population with only saplings and adults and few seedlings [18] [51]-[53]. The species density (number of individuals per unit area) was calculated per site using two variables: (i) the number of *O. lanceolata* individuals in each site; and (ii) the total area sampled in a site [43]. The sampled area for each site was calculated in Quantum-gis software (*Q-gis*) using *O. lanceolata* coordinates. The area and distance were measured and later used to calculate the species density as follows: $Osd = nol/tas$ where; “*Osd*” = *O. lanceolata* population density; “*nol*” = number of *O. lanceolata* individuals in a sampled population; and “*tas*” = total area sampled in a study site/population. A species density for a stable population structure was considered to be ≥ 45 trees per hectare, while densities ≤ 45 trees per hectare were considered to characterise poor, weak, and unstable population structures with low capacity for recruitment and survival [43] [53]. We calculated descriptive statistics for edaphic variables using the *vegan* package in R version 4.1.2 [54]. To reveal the population structure, stem diameters were arranged into size classes of seedlings (0.1 - 1.2 cm); saplings (1.5 - 6.0 cm), and adults (6.5 cm - 19.4 cm). The frequency of individuals in each size class was graphically represented in a stem diameter curve to characterise the species’ population structure [43]. The disturbed populations were expected to show irregular, reverse J-shaped curves or negative exponential curves while the less disturbed populations usually show sigmoid to bimodal-shaped mound curves [55].

To establish the strength of the population structure, a regression analysis r^2 was computed by a plot between the midpoint of size classes and the transformed values of stem density per size class. The status of population structure in each site was inferred by analysis of the slope of the linear regression of stem diameter classes. The midpoint of each stem size class was used as the independent variable (Midpt), while the density of individuals in each class (D/ha) was used as the dependent variable. D/ha was transformed by $\ln(D/ha + 1)$ to avoid zero individuals in some classes. The regression was made between $\ln(D/ha + 1)$ and Midpt. Steep negative slopes indicate stable and self-replacing populations [18] [51] [52]. The weak negative slopes or flat slopes indicate poor recruitment and declining populations [51] [52].

The non-multidimensional scaling analysis (NMDS) was used to illustrate the difference between soil samples within the species microhabitat and those further away from the microhabitat. A plot of NMDS values of the soil was used to classify the edaphic variables according to their relationship with the distribution of *O. lanceolata* and its hosts. Further, the test for significance in differences between *Osyris* samples and non-*Osyris* samples was done by ANOVA. The canonical correspondence analysis (CCA) was applied to explain the relationships between the species presence and edaphic variables. All edaphic data was condensed and transformed

by detrended correspondence analysis (DCA) before the application of the CCA on species-transformed edaphic variables to explain the relationships between the species distribution, edaphic variables, and altitude [54] [56]. The CCA was implemented by the vegan package in R version.4.1.2 using recommended steps [54].

Multivariate regression modeling (MRM) was used to predict and explain the relationship between *O. lanceolata* distribution and abundance and the influencing edaphic variables. In this model, the response or predictor variable was *O. lanceolata* density (Osd) per site/population against edaphic variables (pH, electroconductivity (EC), Na⁺, Ca²⁺, K⁺, N, P, and organic matter), as independent variables. We hypothesized the abundance of *O. lanceolata* to be a function of specific edaphic variables acting in concert with other biotic and abiotic factors. Further, we expected our model to be significant because the spatial distribution of hemiparasites is influenced by the nutrient status of the soils [18] [28].

3. Results

3.1. Population Structure Patterns in Karamoja

Regression analysis of sampled populations indicated all populations to be undergoing recruitment except one population in Cheporon (CHP), Amudat district (Table 1).

Table 1. Regression analysis slope coefficients and mean quotient of *O. lanceolata* populations.

Population	Slope coefficient	r ² values
Akariwon (AKA)	-0.5608	0.2499
Lonyilik (LON)	-27.126	0.1598
Karengepoche (KAR)	-0.3863	0.2392
Cheporon (CHP)	0.103	0.0021
Kangisa (KAN)	-240.12	0.1688
Korenyang (KOR)	-1.5706	0.0776
Ngaram (NGA)	-1.2702	0.1424
Ruwotokech (RUW)	-127.38	0.0798
Lolupe (LOP)	-2E+08	0.1289
Kopedur (KOP)	-2E+09	0.0832
Lotemwoyes (LOT)	-219.78	0.1336
Low altitude populations(combined)	-7.729	0.0965
High altitude populations (combined)	-3.3483	0.3178
Overall population structure	-4.7058	0.2617

The Lotemwoyes (LOT) population structure was an inverse-J-shaped curve,

having more individuals in the smaller size classes and extremely few individuals in the mature size classes (5 cm - 19 cm) (Figure 2).

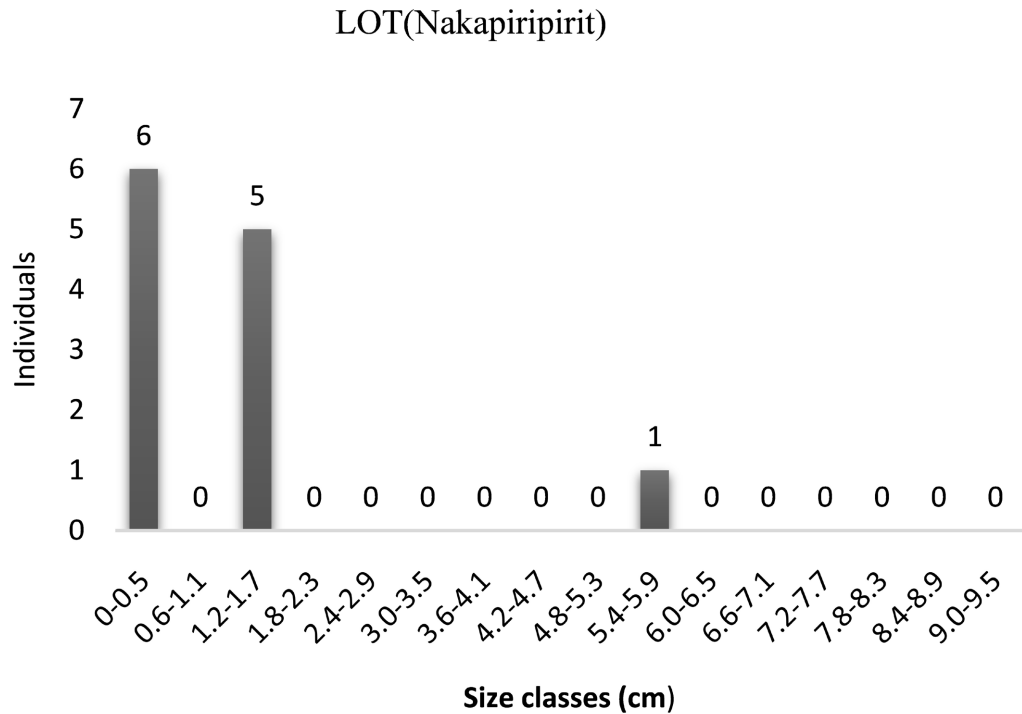


Figure 2. Population structures of Akariwon (AKA) and Lotemwoyes (LOT).

Across the low altitudes, the populations exhibited a general irregular population structure with missing individuals in specific size classes. The populations in high altitudes exhibited a relatively bell-shaped population structure, but with missing individuals in the adult size classes (>10 cm) (Figure 3).

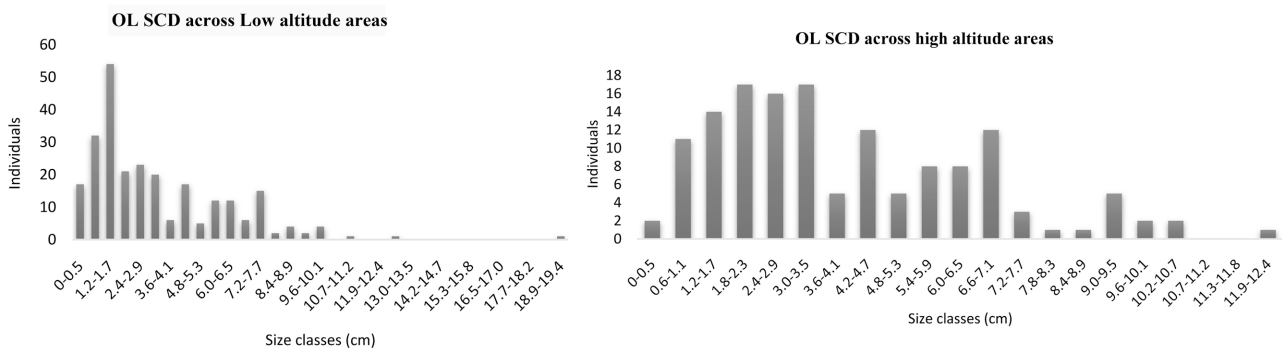
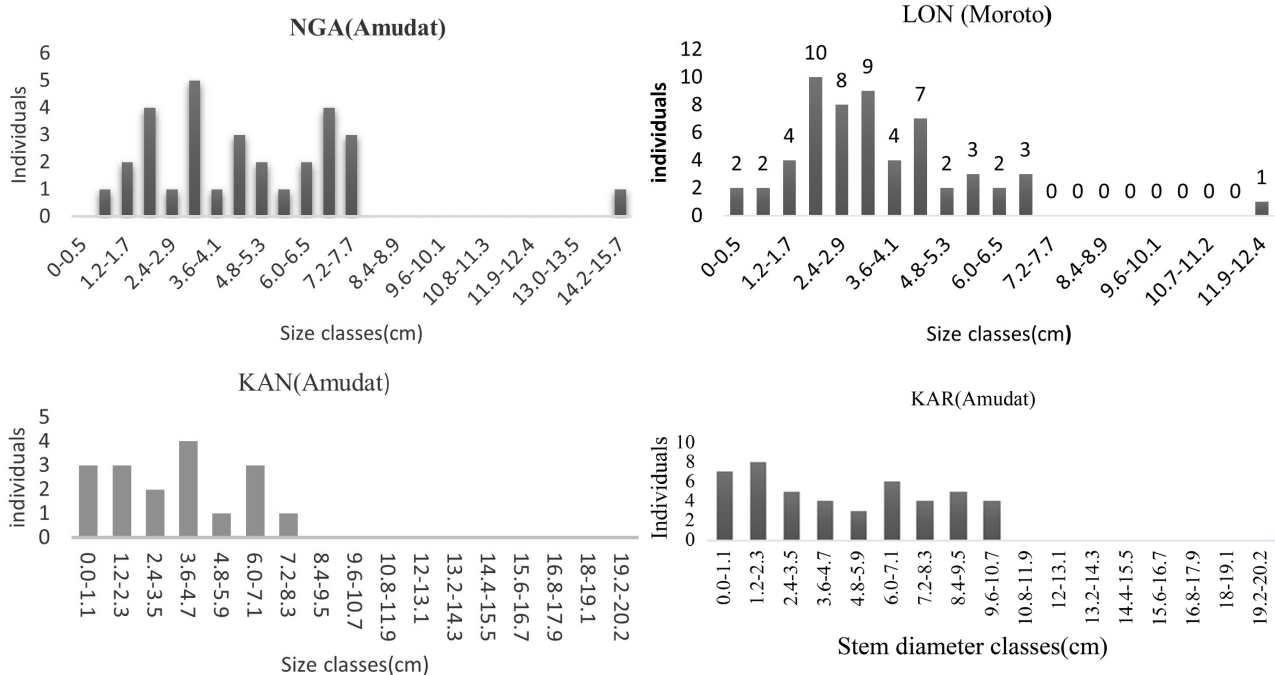


Figure 3. Shows *O. lanceolata* stem diameter classes (SCD) across altitudes.

However, 45.5% of the populations revealed a bell-shaped population structure as observed in Ngaram (NGA), Kangisa (KAN), Karengepoche (KAR), and Lonyilik (LON) exhibiting more individuals in the middle size classes (3 cm - 7 cm) than smaller and larger size classes (Figure 4).



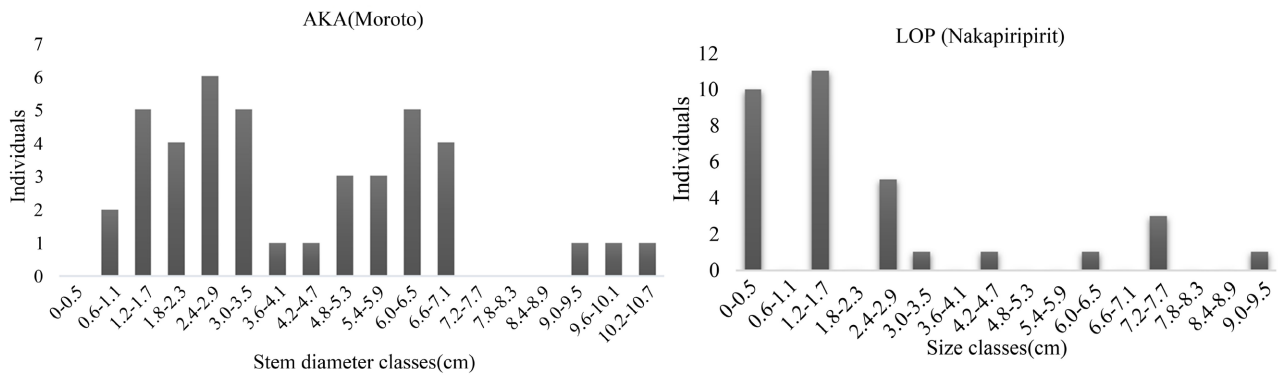


Figure 5. Populations structure of *O. lanceolata* in Lolupe (LOP), Ruwotokech (RUW), Kopedur (KOP), Korenyang (KOR), Akarion (AKA) and Cheporon (CHP).

3.2. General Population Structure

Three hundred ninety-four (394) individuals of *O. lanceolata* were inventoried across all altitudes (low 1275 - 1416 m.a.s.l, and high 1721 - 1800 m.a.s.l). The adults were 196 individuals, 184 saplings, and 14 seedlings. The populations showed an irregular population structure pattern with missing individuals in the higher mature size classes (11 - 19 cm). Out of the 394 individuals, 196 were adults, 184 were saplings, and 14 were seedlings. The population age structure was thus characterised by 50% adults, 46% saplings, and 4% seedlings. Regeneration was more vegetative through coppicing than natural seedlings. The coppiced individuals constituted 56.60%, with 35.02% as saplings and 21.60% as adults. The non-coppiced individuals constituted 43.40%, with a population structure of 4% seedlings, 11.7% saplings, and 28.20% adults. The non-coppiced individuals constituted 43.40%, with a population structure of 4% seedlings, 11.7% saplings, and 28.20% adults. In both low and high-altitude areas, the species population structure showed significantly lower numbers of advanced adult individuals compared to younger individuals. The number of individuals in low and high altitudes declined rapidly between advanced adult size classes (7.2 cm - 18 cm) (Figure 6).

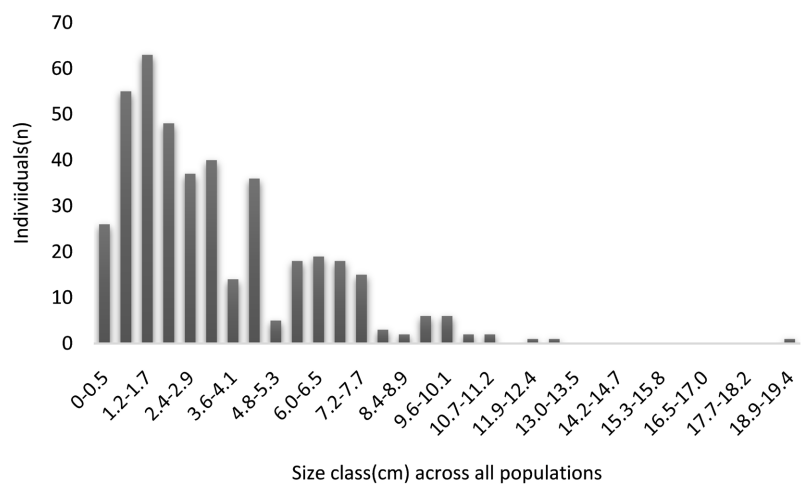


Figure 6. General size class distribution of *O. lanceolata* across populations.

3.3. *Osyris lanceolata* Distribution and Density in Karamoja

The species distribution was patchy and scattered around rocks, deep galleys, streams and even on flat grounds. There was a negligible correlation between *O. lanceolata* density and altitude (cor. coefficient: 0.4174028; $t = 1.378$, $df = 9$, and $p = 0.2015$). ANOVA test indicated no significant differences in the species density across altitudes ($df = 2$, $F\text{-value} = 0.3071$, $p = 0.740$). The Pearson correlation coefficient(r) indicated an insignificant positive linear relationship between the species density and altitude ($R = 0.42$, $p = 0.2$). Within higher altitudes, the density of *O. lanceolata* stood at 1.9399 trees ha^{-1} while in lower altitudes it was lower at 0.0834 trees ha^{-1} (5.1). However, the species densities varied significantly ($F = 174.77$, $p < 0.001$) among populations with the lowest density in Cheporon and the highest in Akariwon (Table 2).

Table 2. *Osyris lanceolata* densities per population.

Population category	Altitude (m)	Area (ha)	Abundance (A)	Density (ha^{-1})
higher altitude (Akariwon)	1787	0.453	42	90.51
higher altitude (Lonyilik)	1721	8.035	57	6.09
higher altitude (Karengepoche)	1794	15.626	46	3.00
Lower altitude (Lolupe)	1407	1.063	33	31.04
Lower altitude (Kopedur)	1416	1.155	51	43.29
Low altitude (Lotemwoyes)	1382	3.292	12	7.59
Low altitude (Cheporon)	1392	16.081	24	1.49
Low altitude (Ngaram)	1345	7.503	30	3.99
Low altitude (Korenyang)	1275	15.435	28	1.81
Low altitude (Kangisa)	1327	1.781	17	9.55
Low altitude (Ruwokech)	1381	4.568	45	10.73

The variation in densities of *O. lanceolata* across altitude zones is represented in Table 3.

Table 3. Variation of *O. lanceolata* densities across altitudes.

Altitude	Area sampled (m)	Abundance (Ha)	Density (h^{-1})
Lower altitude	50.878	216	0.0834
Higher altitude	24.114	145	1.0399
Range	26.764	71	0.9565
Standard Deviation (SD)	18.9250	50,204	0.676348
Variance (Var)	358.1558	2520.5	0.457446

3.4. Edaphic Distribution Drivers

Five soil variables were significantly different between *Osyris* samples and non-*Osyris* samples as follows: (Organic matter (OM) ($r^2 = 0.1687$, $p = 0.001$); N ($r^2 = 0.2123$, $p \leq 0.001$), Na^+ ($r^2 = 0.3282$, $p \leq 0.001$); Ca^{2+} ($r^2 = 0.3719$, $p \leq 0.001$) and P ($r^2 = 0.6534$, $p \leq 0.001$). The ordination analysis of soil variables (NMDS1) against the category of samples (*Osyris* and non-*Osyris* samples) (NMDS2) indicated a significant difference in variables between the two sample categories with edaphic variables in the top *Osyris* samples (close to *O. lanceolata*) being the most distinctly different from non-*Osyris* samples. The *Osyris* samples (1 & 2), had distinct nutrient levels from non-*Osyris* samples. All significant variables (N, Ca^{2+} , OM, Na^+ , and K^+) were clustered towards *Osyris* samples while non-significant variables aggregated towards non-*Osyris* samples as indicated in the NMDS ordination plot (Figure 7).

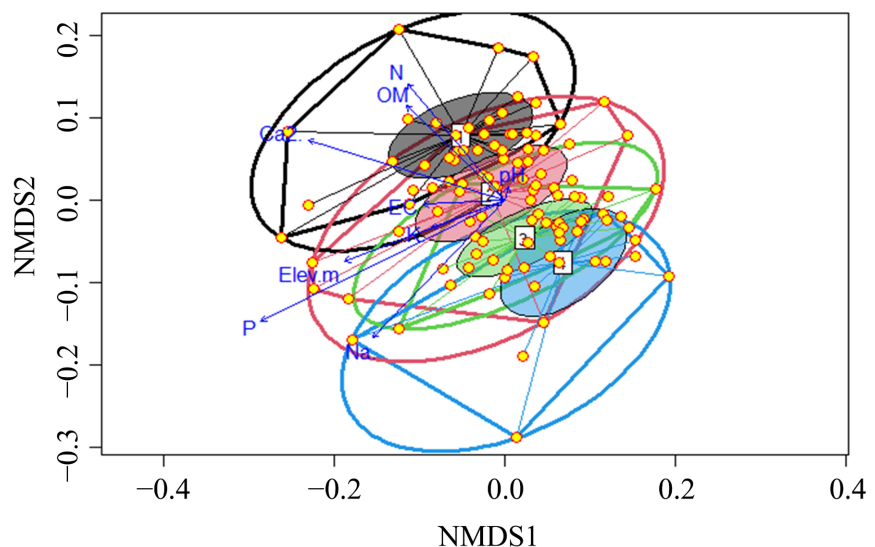


Figure 7. Results of NMDS plot indicating the relationship between *Osyris* samples and non-*Osyris* samples: The sample categories are represented by figures in polygons as follows: 1 = *Osyris*-top sample (close); 2 = *Osyris*-bottom sample-(close); 3 = non-*Osyris* top sample (away); and 4 = non-*Osyris*-bottom sample (away). Colored dots represent the sampled sites.

Also, the constrained ordination undertaken under the reduced model with 999 permutations to test the goodness of fit for the model investigating differences between all edaphic variables was significant ($df = 9$, Chi-square = 0.048717, $F = 35.639$, $p \leq 0.001$). There was a clear indication of a relationship between *O. lanceolata* presence and edaphic variables. The CCA plot also shows all significant variables to be aggregated in Component 1. The non-significant variables were clustered in component 2 which shows variables that contributed more to the presence of *O. lanceolata* (Figure 6). K^+ and OM were closely related together than other variables. The level of significant variables increased with altitude. N increased with salinity and pH levels of the soils (Figure 8).

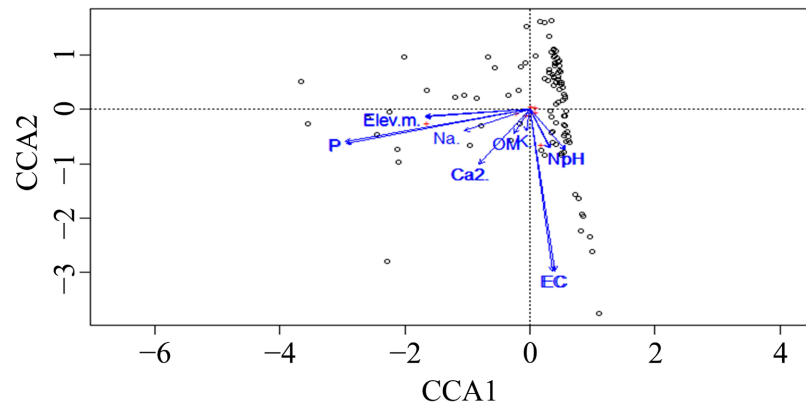


Figure 8. CCA Ordination results indicate a relationship between *O. lanceolata* distribution and edaphic variables. The round dots represent the sampled points.

The multiple regression interaction model (MRIM) revealed that *O. lanceolata* abundance was significantly influenced by nitrogen (N) ($t = 2.083$, $p = 0.04907$), phosphorus ($t = 2.262$, $p = 0.034$), potassium (K^+) ($t = -3.475$, $p = 0.00215$), and sodium (Na^+) ($t = 3.679$, $p = 0.00131$). The applied model was significant ($p \leq 0.001$) across the altitude zones. Regardless of the differences in edaphic variables between samples, nutrient levels indicated a non-uniform pattern in variation with soil depths across sites. Some nutrients increased with soil depths while others decreased. The amount of organic matter, nitrogen, and phosphorus generally deteriorated with the soil depth whereas an opposite trend was observed for potassium (K^+), sodium (Na^+), and calcium (Ca^{2+}). Nutrients that decreased with soil depth include organic matter, nitrogen, phosphorus, and potassium. Nutrient levels for calcium and sodium consistently increased with an increase in soil depth in high-altitude zones but decreased in low altitudes.

4. Discussion

Population structure of *O. lanceolata*

The species population structure was weakened, irregular, and unstable with poor regeneration and recruitment. The 56.60% of coppiced individuals reflects a high intensity of species exploitation. The past illegal harvesting of mature tree individuals explains the rapid decline and persistence absence of adult individuals in all populations. The low number of seedlings could be attributed to grazing and browsing pressure, and the destructive feeding behavior of caterpillars (*Dismegistus sp*) on *O. lanceolata* fruits and seeds hence causing poor seed viability and germination failure. The study results confirm earlier reports of the species being overexploited in the Karamoja sub-region [4] [11] [57] [58]. The species was found to occur within altitudes ranging between 1200 m - 1800 m above sea level. This observation differed from earlier studies that found the species to occur within an altitude range of 1300 - 1760 m.a.s.l [58]. The patchy species distribution may be related to the hemiparasitic nature of *O. lanceolata*, the spatial distribution of edaphic variables, and patterns of gene flow [20] [21] [30] [59].

The inverse-J-shaped population structure represents a weak, dying, and poorly recruiting population as opposed to a healthy, stable, and recruiting population [33] [43] [60]. This is due to the existence of fewer seedlings and even the majority of individuals in lower size classes were coppiced as opposed to regenerating seedlings and independent trees from natural germination. The low number of seedlings might be a result of intensive harvesting, seed germination failure due to poor seed viability, seedling mortality, and past destruction of the old mature trees capable of producing seeds. We observed field evidence of seed damage for *O. lanceolata* by insects and this potentially contributes to seedling mortality and thus germination failure leading to a low abundance of the species seedlings. The scarcity of seedlings is an indicator of weak, irregular, and unstable plant populations [51] [52] [61] [62] incapable of sustaining regular commercial harvesting. These characteristics also indicate poor regeneration potential of a species attributed to germination failure, mortality of seedlings, and habitat fragmentation [33] [60]-[62]. The coppiced individuals indicate past damages to mature trees due to over-exploitation through illegal harvesting of mature trees for extracting essential oils, construction poles (manyattas), and charcoal burning or firewood. Because most juvenile individuals were coppiced as opposed to growing independently from seedlings, and since the scarcity of seedlings was consistent in all populations, the species population is over-exploited across altitudes in Karamoja hence emphasizing the need for responsible management strategies to save the species from further damages. Although most mature individuals were non-coppiced, a large proportion of saplings (SP) were coppiced which points to a gradual shift to a predominantly coppicing population in the future. The 56.60% of coppiced individuals also suggests a high intensity of species exploitation [46] over the years which has weakened the population structure. Thus, this observation raises some questions regarding the uncertainty of the species population structure in habitats with more coppiced individuals given the lower number of seedlings, secondly, the existing level of regeneration through coppicing has dire effects on the species' level of genetic diversity to sustain the species against genetic erosion in the future [61] [62]. Given our findings, we can then predict that the current population structure of *O. lanceolata* is unstable and thus has compromised genetic potential. Since most individuals regenerate through coppicing, the subsequent populations will be exposed to a high risk of reduced genetic diversity due to continued inbreeding [61] [62]. Although regeneration through coppicing is believed to enhance the species continuity through regular regrowth of new individuals and thus mitigating species loss, it leads to further degeneration in genetic diversity levels, especially in subsequent populations. The low species densities, fewer seedlings, and higher number of coppiced individuals are a bottleneck to the species' genetic stability [63] [64] in Karamoja. Further, the absence of individuals in certain size classes in most populations reflects an occurrence of destructive harvesting such as (whole plant uprooting) [11] [13] [57] which leads to lower species densities. The low species density leads to an alteration in the mating

patterns of the species and increases inbreeding which in turn reduces the genetic diversity of the species [63].

The effect of environmental gradients on plant distribution was not significant, despite its emphasis in earlier studies [31] [65] [66]. The absence of a significant correlation between the species density and altitude implies that the abundance of *O. lanceolata* is profoundly influenced by edaphic factors in addition to other environmental factors. For instance, the fragmentation of species habitats may accelerate inbreeding with negative impacts on the species distribution which impacts their genetic diversity [63] [64]. The anthropogenic and environmental factors significantly contribute to alteration in the species population structure, usually manifested in irregular patterns in the species densities. In addition to environmental factors, the patterns of gene flow across altitudes are also limit the species range and density and hence contributing to the alteration in the overall species genetic structure [59]. Thus, assessment of the levels of genetic diversity in line with the current population structures can also provide further insights on the impact of the species exploitation on genetic structure as well. This helps to develop meaningful programs for responsible management in terms of breeding, propagation, domestication, and long-term conservation programs [64] [67].

Edaphic distribution drivers of *O. lanceolata*

Our study revealed that calcium, sodium, phosphorus, and potassium were significantly different between *Osyris* and non-*Osyris* microhabitats. The multivariate regression modeling predicted similar edaphic variables to significantly influence and contribute to the species abundance and density. Thus, these results suggest that the distribution and abundance of *O. lanceolata* are potentially driven by a combination of edaphic variables. The earlier studies [25] [28] across different altitudes and thus, similar nutrients provide ideal conditions for the survival of *O. lanceolata* in natural habitats. The establishment of *O. lanceolata* to host species near hard rocky habitats suggests the need for Ca^{2+} to enhance the species' survival through the acquisition of desired nutrients [25] [27] [28] in line with our study findings because calcium was significantly different between *Osyris* and non-*Osyris* sites hence validating its influence in driving the species distribution. Also, sodium (Na^+); potassium (K^+); phosphorus; and nitrogen were indicated to play an important role in influencing the species density as explained by the CCA ordination results. Our results rhyme with other studies that found soil nitrogen, and phosphorus to be critical variables in determining spatial floral composition [32] [68]-[70]. However, these variables act in concert with environmental gradients, climate, gene flow, and host quality to influence the distribution of root hemiparasites [20] [21].

5. Conclusion

The study revealed an irregular population structure of *O. lanceolata* in Karimoja. This suggests a severely exploited, altered, and weakened population. The

presence of more coppiced individuals, few seedlings, and adults, irregular distribution, and low densities indicate a negative impact of exploitation on the species' population structure. However, a combination of Ca²⁺, N, P, K⁺, and OM significantly influenced the species distribution. These variables showed significant differences between the species microhabitat and away from the microhabitat hence emphasizing their influence on the species distribution and survival. To avert the rapid decline in the *O. lanceolata* population, *in-situ* and *ex-situ* conservation strategies should be intensified to secure the species' germplasm and enhance large-scale commercial harvesting. Thus, the identification of suitable provenances for *ex-situ* populations is urgently needed to save the species from total depletion. Further exploration of biotic drivers for the distribution and survival of *O. lanceolata* clumps is necessary to enhance conservation. The assessment of the species genetic diversity, oil quality, yield, and rapid propagation techniques, should be undertaken to guide the identification of superior provenances with good traits for commercial propagation. The study provides the first empirical evidence on the population structure and distribution drivers of *O. lanceolata* in Uganda.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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