African Sandalwood (Osyris lanceolata Hochst.)

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The increasing demand for ornamental, cosmetic and pharmaceutical products is driving exploitation of plant species globally. Sub-Saharan Africa harbours unique and valuable plant resources and is now a target of plant resource depletion. African Sandalwood (Osyris lanceolata), a multi-purpose and drought-tolerant species, has seen increased exploitation for the last thirty years and is now declared endangered.

Keywords: hemiparasites ; molecular ecology ; population genetics ; conservation strategies

1. Introduction

The high global demand for ornamental, cosmetic and pharmaceutical products is driving exploitation of plant species all over the world [1]. Sub-Saharan Africa harbours an important stock of unique and valuable plant resources, and therefore is a target of expanding plant resource exploitation [2]. African sandalwood (Osyris lanceolata Hochst. & Steud.) is a multipurpose, drought-tolerant and hemiparasitic tree, well known for its essential oils used in perfumery industries [1]. It emerged as a potential commercial species in Africa due to significant decline in original sources of sandalwood oil, e.g., Santalum album L. (Indian subcontinent) and Santalum spicatum (R.Br.) A. DC. (Australia) in the 1990s, and the increasing demand for sandalwood oil over the years [3][4][5]. Dwindling of the species populations in Africa is attributed to overexploitation and lack of robust management strategies [5][6][7][8]. Some populations in Uganda, Kenya, Tanzania and South Sudan have completely disappeared due to illegal harvesting and smuggling of tree logs despite the species being protected under Appendix II of the Convention on International Trade in Endangered Species (CITES) [8][9][10][11]. O. lanceolata is assigned an automated status of least concern (LC) [12] with an unknown population trend but acknowledging decline in east Africa due to over exploitation [8][12].

Apparently, the lack of adequate information to reliably manage a sound resource base for O. lanceolata makes it very difficult to implement informed strategies for in situ and ex situ conservation in Africa [5]. Previous emphasis on plantations (ex situ strategy) and in situ measures for conservation have not succeeded due to information gaps on the species ecology, population dynamics and genetics [13][14][15]. Additionally, identification of suitable sources for genetic resource improvement is difficult without adequate scientific information on the species [15][16]. Knowledge of non-random distribution of genes from these studies may be even more important for conservation of the species [17][18]. Information on species population structure and demographic data help to predict the future stability of a species population amidst environmental and anthropogenic disturbances [19][20].

Whereas the ecology, population genetics and phylo-geography of other economically important species like Prunus africana. (Hook.f.) Kalkman. are documented in Africa [21][22], similar information is lacking for Osyris lanceolata [23]. There are peculiar ecological and genetic aspects of O. lanceolata which need to be understood and aligned with strategies for responsible management, in particular hemiparasitism, complex distribution patterns and low survival rate [24][25]. These broad attributes raise the following questions which require critical analysis: (i) What is the distribution, taxonomy and ethnobotany of O. lanceolata ? (ii) Which environmental factors influence the species distribution and hemiparasitic relationships across habitats? and (iii) How do such factors impact on characteristics of the species population structure, genetic diversity and conservation status in Africa? Understanding these questions contributes to informed conservation strategies.

This review analyses the missing links in population dynamics, ecology, taxonomy and genetic diversity of Osyris lanceolata using the available literature with a special interest in populations in Sub-Saharan Africa. We present the species taxonomy and ethnobotanical uses and discuss the role of hemiparasitism, while identifying emerging questions for further research. A global scope of the species distribution is provided and factors influencing its spatial distribution are explored. Further, we discuss the role of population structure assessment and general trends in the species population in Africa. Finally, the relevance of genetic diversity assessment, the extent of genetic studies on the species and implications for further research and conservation of O. lanceolata in Africa are proposed.

2. Taxonomy of Osyris sp.

Parasitic plants have been the most difficult plant groups to classify due to their specific adaptations in biology and morphology [26]. Most members of the genus *Osyris* are hemiparasitic plants, with complex physiognomy, physiology and morphology [24]. The genus belongs to the angiosperm order Santalales, family Santalaceae. Family Santalaceae has over forty genera and 400 species distributed in the tropics and temperate ecosystems [27]. The three African genera in family Santalaceae include *Thesium, Osyridicarpus* and *Osyris* [8]. Genus *Thesium* is the largest with over 200 species native to Africa and regions with a Mediterranean climate [8].

According to the webpage of the International Plant Names Index (www.ipni.org (accessed on 25 June 2021)) five species of the genus *Osyris* are accepted: *O. alba* L. with Mediterranean distribution in south Europe and north Africa, *O. daruma* Parsa with a range in southern Iran and *O. compressa* (P. J. Bergius) A. DC. and *O. speciosa* (A.W. Hill) J.C. Manning & Goldblatt, both with a main distribution in the Cap provinces. All remaining described species are not accepted to date and treated as one taxon, *Osyris lanceolata* Hochst. & Steud. (see Appendix A), resulting in a very large and inhomogeneous range for the species, with areas in south and east Africa, in parts of southern Europe and Asia. In the Catalogue of life (COL, www.catalogueoflife.org (accessed on 25 June 2021) the taxonomy that forms the base for the Global Biodiversity Information Facility (GBIF), and World Flora Online (WFO), which is a global online compendium of the world's plant species, *O. lanceolata* is subdivided in *O. quadripartita* Salzm. ex Decne with the European and south and east African populations and *O. wightiana* Wall. ex Wight with the Asian populations (Appendix A). In this study, we use the name "*Osyris lanceolata*" in accordance with previous treatments of African sandalwood [28].

In consequence, the species *Osyris lanceolata* Hochst. & Steud. (1832) is represented by various synonyms [28][26] and multiple independent classifications [27]. The species (**Figure 1**) is commonly known as African sandalwood, east African sandalwood, Nepalese sandalwood, or false sandalwood. *O. lanceolata* is highly variable in morphology, especially leaf size [26] and shape depending on climate, altitude, edaphic variables and sex type [26], which may account for the occurrence of various synonyms. For instance, in some field work activities in Uganda, specimens of *Osyris lanceolata* were identified as *Osyris compressa* (Berg.) A. DC due to variations in leaf size and thickness leaves [29] as shown in **Figure 1**b,e.

Figure 1. (**a**) Adult tree of *O. lanceolata* in Uganda; (**b**) "*O. compressa*" (adult tree); (**c**) *O. lanceolata* (sapling) [29]; (**d**) specimen of *O. lanceolata* from Karamoja; (**e**) "*O. compressa*" (Karamoja); (**f**) *O. lanceolata* (Karamoja) [29].

3. Ecology: Habitats and Drivers for Distribution of African Sandalwood

O. lanceolata occurs in a diverse range of habitats including upland dry evergreen forests and mist forests characterised by bushland and grassland that usually extend downwards to rivers and slightly into deciduous woodlands at 900–2700 m above sea level [30]. Other suitable habitats for *O. lanceolata* include: dry savanna forests and woodlands, moist woodlands, thicket edges and dry submontane *Hyparrhenia* grasslands at an elevation range of 1000 m to 1730 m above sea level [31]. However, the species also occurs in rocky and non-rocky habitats [32][33] at even higher altitudes ranging from 900 m to 2250 m and with mean annual rainfall of 600 to 1600 mm with well-drained soils, but it cannot tolerate frost conditions [33].

Despite the reported habitats for the species, little is known about suitable survival conditions, and factors that would influence the species distribution in natural habitats. Understanding plant species distribution drivers helps to analyse the species survival conditions and strategies in habitats which is important in conservation planning. Although scientific evidence suggests *Osyris lanceolata* exhibits a clumped or patchy distribution [34], little is known about drivers of the species distribution. *O. lanceolata* is typically rare throughout its distribution range and also has a non-uniform pattern of distribution even in areas with abundant suitable hosts [34]. The highly patchy nature of distribution clearly suggests the influence of specific factors in determining the species distribution. A recent study by Fox [30] proposes the presence of hosts and habitat attributes as key determinants for the distribution of parasitic plants.

In other studies, the importance of habitat quality [31][32] is stressed, while seed dispersal capability could also influence species distribution [33][35]. Host quality includes water availability, edaphic variables and nutrients [34]. According to the host quality hypothesis (HQH) *O. lanceolata* can only establish and grow if they parasitise a host with sufficient quality such as one with low water stress [34]. In areas where water is limited, parasitic plants are likely to establish on hosts with greater access to water [34]. Proper illustration of this hypothesis requires a detailed field assessment of habitat quality for *O. lanceolata* populations and their hosts in natural populations. In addition, the abundant center hypothesis (ACH) suggests that a species will be more abundant where conditions for reproduction and population growth are most suitable [31]. A further implication of this hypothesis is that population density of a species declines towards areas with less suitable environments [31]. Therefore, if the spatial distribution of a species is correlated with corresponding environmental variables, an insight into drivers of species distribution and survival can be obtained as an indication of desirable survival conditions of a species in natural environments. Although we found studies suggesting specific germination requirements, seed vectors and site–microsite preference [34][31][35][36][37] as key drivers for species distribution, these conditions cannot account for the highly patchy spatial structure of *O. lanceolata* [34]. Thus, empirical data are required to understand key drivers of the distribution of *O. lanceolata* in natural habitats.

4. Implications for Conservation of Osyris lanceolata in Sub-Saharan Africa

This paper highlights four major issues with significant implications for conservation of *O. lanceolata* in Africa. First, the taxonomy of *O. lanceolata* is still complex (see **Table A1**) due to over synonymisation, country range distribution and ambiguity in species ranking. Second, the population dynamics of *O. lanceolata* across its range of distribution are anecdotal, though CITES reports indicate significant population declines, particularly in east Africa due to overexploitation. Third, the drivers of the spatial distribution of *O. lanceolata* in natural habitats are not understood. The species is highly patchy and exhibits an irregularly clustered pattern of spatial distribution which requires further analysis. Fourth, the species genetic diversity and ethnobotany are barely studied and hence not understood. These issues affect conservation of *O. lanceolata* as follows: the confusion in the taxonomy of *O. lanceolata* leads to continuous treatment of different species of *Osyris* as one taxon which may lead to loss of unnoticed populations with diverse morphological and genetic attributes. Secondly, continuous harvesting and utilisation of *O. lanceolata* with unknown population dynamics puts the species at a greater risk of depletion since the absence of population data complicates species monitoring and management. In addition, poor understanding of drivers of the distribution of *O. lanceolata* is a hindrance to conservation in Africa. Drivers of spatial distribution correlate strongly to suitable conditions for survival and fitness of a species in natural habitats and hence such information is necessary in planning for conservation approaches. Additionally, limited understanding of the genetic diversity of the species and structure hinders conservation efforts. For instance, suitable provenances cannot be identified easily to boost conservation programs. Equally, limited documentation of the ethnobotanical uses of the species also hinders conservation initiatives. Local communities may be reluctant to appreciate conservation of a species whose value and benefits are not understood.

The three approaches needed for continued survival of *O. lanceolata* populations include: conservation, restoration and sustainable commercial use. In particular, conservation of threatened habitats for the species population is necessary [38]. As different populations exhibit different population dynamics, conservation planning ought to be undertaken at the population level and reinforced by local investigations which are more informative than global studies [39]. Additionally, locally adapted monitoring protocols that consider different stakeholders at local and regional levels are key in tracking populations of threatened species [40]. However, these actions cannot be realised without adequate scientific information as a basis for informed policy actions. Finally, we emphasise that the risk of extinction of a species without adequate scientific data is high and impacts are extreme if resource extraction continues without planned strategies. Thus, our findings will stimulate constructive debate and more focused research towards responsible management of *Osyris lanceolata* in the long run, to avert the looming threat of extinction of the species in Sub-Saharan Africa.

5. Conclusions

The purpose of this study was to survey relevant research on the taxonomy, ecology, population dynamics, ethnobotany and genetic diversity of *Osyris lanceolata*, and highlight knowledge gaps for further research. We established that *O. lanceolata* is distributed in Africa, Asia, Europe and the Socotra Islands with no identified center of origin. The species has a relatively confusing taxonomy, with unresolved issues in nomenclature, country range distribution, oversynonymisation and uncertainty in biological form (shrub or tree), which calls for a deliberate global revision and harmonisation to resolve anomalies in taxonomy. Information on the species population dynamics across its entire range of distribution is anecdotal. Secondly, several use categories are reported for *O. lanceolata*. There are a handful of studies on the genetics and ecology of *O. lanceolata* in Africa. The available studies help little to understand the underlying factors for the species distribution and its survival in natural habitats. There are no scientific data to explain how the species genetic diversity varies across life stages and between modes of propagation (seed and asexual). Our review suggests that, currently, (i) species distribution drivers which are possible factors for survival of *O. lanceolata* in natural populations are invariably barely studied and (ii) despite the vital role of genetic diversity assessment in the conservation of plant genetic resources, and the availability of molecular techniques for its investigation, it is the least studied area for *O. lanceolata*, which partly underpins the slow progress in improvement in the species and its conservation in Africa. Therefore, a deliberate focus to understand detailed ethnobotanical uses and the ecological, population dynamics and genetic characteristics of *O. lanceolata* is urgently needed in present and future studies to enhance informed strategies for sustainable management of the species in Africa.

References

1. da Silva, J.A.T.; Kher, M.M.; Soner, D.; Nataraj, M.; Dobránszki, J.; Millar, M.A. Santalum molecular biology: Molecular markers for genetic diversity, phylogenetics and taxonomy, and genetic transformation. Agrofor. Syst. 2018, 92, 1301–1315.
2. Ola, O.; Benjamin, E. Preserving Biodiversity and Ecosystem Services in West African Forest, Watersheds, and Wetlands: A Review of Incentives. Forests 2019, 10, 479.
3. Mbuya, L.P.; Msanga, H.P.; Ruffo, C.K.; Birnie, A.; Tengnas, B.O. Useful Trees and Shrubs for Tanzania; SIDA (Swedish International Development Authority): Nairobi, Kenya, 1994; 542p.
4. Page, T.; Hannington, T.; Bunt, C.; Potrawiak, A.; Berry, A. Opportunities for the Smallholder Sandalwood Industry in Vanuatu; ACIAR Technical Reports No. 79; Australian Centre for International Agricultural Research: Canberra, Australia, 2012.
5. Thomson, L.A.J. Looking ahead—Global sandalwood production and markets in 2040, and implications for Pacific Island producers. Aust. For. 2020, 83, 245–254.
6. Rao, M.N.; Ganeshaiah, K.N.; Shaanker, R.U. Assessing Threats and Mapping Sandal Resources to Identify Genetic ‘Hot-Spot’for In-Situ Conservation in Peninsular India. Conserv. Genet. 2007, 8, 925–935.
7. Mwang’Ingo, P.L.; Teklehaimanot, Z.; Lulandala, L.L.; Mwihomeke, S.T. Host plants of Osyris lanceolata (African Sandalwood) and their influence on its early growth performance in Tanzania. S. Afr. For. J. 2005, 203, 55–65.
8. CITES. Consideration of Proposals for Amendment of Appendices I and II; CITES: Geneva, Switzerland, 2013; pp. 1–10.
9. Muhoozi, J. Encroachers Target Kabaruka in Akagera. The East African. Available online: http://www.theeastafrican.co.ke/rwanda/News/Encroachers-target-Kabaruka-in-Akagera/1433218-2093116-sy2phc/index.html (accessed on 23 March 2018).
10. Tajuba, P. How Oil Firm Is Burning Up Karamoja Valuable Trees. Available online: http://www.monitor.co.ug/artsculture/Reviews/oil-firm-burning-up-Karamoja-valuable-trees/691232-2996318-r5xq40/index.html (accessed on 6 August 2021).
11. Bunei, E.K. The Hunt for the Precious Wood: Illegal Trade of Sandalwood as an International Criminal Enterprise in Kenya. Soc. Bus. Rev. 2017, 12, 63–76.

12. Wilson, B. Osyris lanceolata. The IUCN Red List of Threatened Species 2018: e.T200642A2675362. Available online: https://www.iucnredlist.org/species/200642/2675362 (accessed on 2 July 2021).

13. USAID. Uganda Environmental Threats and Opportunities Assessment (Etoa) Final Etoa; USAID: Washington, DC, USA, 2015.

14. Uganda Investment Authority (UIA). Karamoja Investment Profile; Uganda Investment Authority: Kampala, Uganda, 2016.

15. Neuhauser, C.; Andow, D.A.; Heimpel, G.E.; May, G.; Shaw, R.G.; Wagenius, S. Community Genetics: Expanding the Synthesis of Ecology and Genetics. Ecology 2003, 84, 545–558.

16. Mwang'ingo, P.L.; Teklehaimanot, Z.; Hall, J.B.; Zilihona, J.E. Sex Distribution, Reproductive Biology and Regeneration in the Dioecious Species Osyris lanceolata (African Sandalwood) in Tanzania. Tanzan. J. For. Nat. Conserv. 2007, 76, 118–133.

17. Kalisz, S.; Nason, J.D.; Hanzawa, F.M.; Tonsor, S.J. Spatial Population Genetic Structure in Trillium Grandiflorum: The Roles of Dispersal, Mating, History, and Selection. Evolution 2001, 55, 1560–1568.

18. Curto, M.; Nogueira, M.; Beja, P.; Amorim, F.; Schümann, M.; Meimberg, H. Influence of past agricultural fragmentation to the genetic structure of Juniperus oxycedrus in a Mediterranean landscape. Tree Genet. Genomes 2015, 11, 11.

19. Tabuti, J.R.S.; Mugula, B.B. The ethnobotany and ecological status of Albizia coriaria Welw. Ex Oliv. In Budondo Sub-county, eastern Uganda. Afr. J. Ecol. 2007, 45, 126–129.

20. Virillo, C.B.; Martins, F.R.; Tamashiro, J.Y.; Dos Santos, F.A.M. Is size structure a good measure of future trends of plant populations? An empirical approach using five woody species from the Cerrado (Brazilian savanna). Acta Bot. Bras. 2011, 25, 593–600.

21. Muchugi, A.; Lengkeek, A.G.; Kadu, C.A.C.; Muluvi, G.M.; Njagi, E.N.M.; Dawson, I.K. Genetic variation in the threatened medicinal tree Prunus africana in Cameroon and Kenya: Implications for current management and evolutionary history. S. Afr. J. Bot. 2006, 72, 498–506.

22. Kadu, C.A.C.; Parich, A.; Schueler, S.; Konrad, H.; Muluvi, G.M.; Eyog-Matig, O.; Muchugi, A.; Williams, V.; Ramamonjisoa, L.; Kapinga, C.; et al. Bioactive constituents in Prunus africana: Geographical variation throughout Africa and associations with environmental and genetic parameters. Phytochemistry 2012, 83, 70–78.

23. Qasem, J.R. Host range of the parasitic weed Osyris alba L. in Jordan. Weed Biol. Manag. 2006, 6, 74–78.

24. Nurochman, D.; Matangaran, J.R.; Santosa, G.; Suharjito, D.; Sari, R.K. Autecology and morphological properties of sandalwood (Santalum album) in Pidie District, Aceh, Indonesia. Biodivers. J. Biol. Divers. 2018, 19, 406–412.

25. Gathara, M.; Makenzi, P.; Kimondo, J.; Muturi, G. Prediction of Osyris lanceolata (Hochst. Steud.) Site Suitability Using Indicator Plant Species and Edaphic Factors in Humid Highland and Dry Lowland Forests in Kenya. J. Hortic. For. 2014, 6, 99–106.

26. Fay, M.F.; Bennett, J.R.; Dixon, K.W.; Christenhusz, M.J.M. Parasites, their relationships and the disintegration of Scrophulariaceae sensu lato. Curtis's Bot. Mag. 2010, 26, 286–313.

27. Osyris lanceolata Hochst. Osyris lanceolata Hochst. & Steud. In The Plant List 2016. Available online: http://www.theplantlist.org/tpl1.1/record/kew-2396402 (accessed on 6 August 2021).

28. Polhill, P.M. Flora of Tropical East Africa: Santalaceae; Royal Botanic Gardens Kew: Richmond, UK, 2005.

29. Mugula, B.B. Field Surveys for Mapping Osyris Lanceolata in Karamoja, Sub-Region, Uganda. Field Work; 2020; (Unpublished).

30. Dennenmoser, S.; Vamosi, S.M.; Nolte, A.W.; Rogers, S.M. Adaptive genomic divergence under high gene flow between freshwater and brackish-water ecotypes of prickly sculpin (Cottus asper) revealed by Pool-Seq. Mol. Ecol. 2017, 26, 25–42.

31. Fox, J.E.D. Why is Santalum Spicatum Common Near Granite Rocks? J. R. Soc. West. Aust. 1997, 80, 209.

32. Pfenninger, M.; Salinger, M.; Haun, T.; Feldmeyer, B. Factors and processes shaping the population structure and distribution of genetic variation across the species range of the freshwater snail radix balthica (Pulmonata, Basommatophora). BMC Evol. Biol. 2011, 11, 135.

33. Amundrud, S.L. Abiotic and Biotic Processes Shape Species Distributions and Ecological Communities across Spatial Scales. Ph.D. Thesis, University of British Columbia, Vancouver, BC, Canada, 2020.

34. Kuijt, J. The Biology of Parasitic Flowering Plants; University of California Press: Berkeley, CA, USA, 1969.

35. Kamondo, B.; Giathi, G.; Osore, C.; Machua, J.; Kagunyu, L.; Wafula, A.; Bala, P.; Njuguna, J.; Wakori, S.; Maingi, F.; et al. Growing of East African Sandalwood: Guidelines for Tree Growers; Kenya Forestry Research Institute (KEFRI):

Nairobi, Kenya, 2014.

36. Mortelliti, A.; Amori, G.; Boitani, L. The role of habitat quality in fragmented landscapes: A conceptual overview and prospectus for future research. Oecologia 2010, 163, 535–547.
37. Laurance, W.F. Habitat destruction: Death by a thousand cuts. Conserv. Biol. All 2010, 1, 73–87.
38. Cogoni, D.; Fenu, G.; Dessì, C.; Deidda, A.; Giotta, C.; Piccitto, M.; Bacchetta, G. Importance of Plants with Extremely Small Populations (PSESPs) in Endemic-Rich Areas, Elements Often Forgotten in Conservation Strategies. Plants 2021, 10, 1504.
39. Sulis, E.; Bacchetta, G.; Cogoni, D.; Fenu, G. From Global to Local Scale: Where is the Best for Conservation Purpose? Biodivers. Conserv. 2021, 30, 183–200.
40. Fenu, G.; Bacchetta, G.; Christodoulou, C.S.; Cogoni, D.; Fournaraki, C.; Gian Pietro, G.D.G.; Gotsiou, P.; Kyratzis, A.; Piazza, C.; Vicens, M.; et al. A Common Approach to the Conservation of Threatened Island Vascular Plants: First Results in the Mediterranean Basin. Diversity 2020, 12, 157.
