REVIEW

The Ecology, Distribution, and Anthropogenic Threats of Multipurpose Hemi-Parasitic Plant *Osyris lanceolata.*

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Abstract

Osyris lanceolata Hochst. & Steud. ex A. DC. is a multipurpose plant with high socioeconomic and cultural values. It is endangered in the biogeographical region of eastern Africa, but of less concern in other regions where it occurs. The few natural populations remaining in the endangered sites continue to encounter many threats, and this has raised concerns about its long-term sustainability. Yet, existing knowledge about the ecology and distribution of the plant is scarce to inform strategies for the conservation and sustainable management of the species. In this study, we conducted a scoping review of the available literature on current knowledge about the plant. We recapitulated existing knowledge about the abiotic and biotic factors influencing the contemporary distribution of the plant, the anthropogenic threats, and existing conservation efforts. Based on the limited studies we reviewed, we identified that the plant prefers specific habitats (hilly areas and rocky outcrops), frequently parasitizes Fabaceae but can parasitize plants from a wide range of countries, have inadequate ex-situ propagation protocols which present issues for the survival of the species. Overharvesting from the wild driven by demand from regional and global markets poses further threats to the existing natural populations, especially in eastern Africa. A combination of ecological, social, and trade-related conservation measures can be envisioned to help improve the plant's persistence. These include, but are not limited to, a better understanding of the species ecology to inform conservation planning, monitoring of trade flow and improve transnational environmental laws and cooperation among countries to prevent species smuggling.

1. Introduction

Osyris lanceolata Hochst. & Steud. ex A. DC. is an evergreen tree or shrub and a phanerophyte belonging to family *Santalaceae* (Adamson, 1939; Herrera, 1988c; Kuijt, 1969). The species is commonly known by different names, including African sandalwood, East african sandalwood, Nepalese sandalwood, or False sandalwood (Teixeira da Silva *et al.*, 2016). The plant is widespread in tropical and subtropical regions and occurs over much of southern and eastern Africa, northern Africa and southern Europe, and southern Asia (Herrera, 1988c; Mwangingo *et al.*, 2008; Andiego, 2016; Strohbach, 2017; Mugula *et al.*, 2021). It belongs to the same genus with *O. compressa* (P.J.Bergius) A.DC.and *O. speciosa* (A.W.Hill) J.C.Manning & Goldblatt, both with their main occurrence in the Cape province of South Africa, *O. alba* L. (Syn. *O. mediterranea* Bubani) with distribution in northern Africa and the Mediterranean, and *O. daruma* Parsa in southern Iran.

The species scientific synonyms are *O. quadripartita* Salzm. ex Decne. for the Mediterranean and African populations and *O. wightiana* Wall. exWight for the Asian populations. The Mediterranean and African populations of *O. guadripartita* has synonyms *O. abyssinica* Hochst. ex A. Rich., *O. densifolia* Peter, *O. laeta* Peter, *O. oblanceolata* Peter, *O. parvifolia* Baker, *O. pendula* Balf.f., *O. quadrifida* Salzm. ex A.DC., *O. quadripartita* var. *canariensis* K¨ammer, *O. rigidissima* Engl., *O. tenuifolia* Engl. and *O. urundiensis* De Wild. The Asian populations of *O. wightiana* Wall. ex Wight has synonyms as *O. divaricata* Pilg, *O. arborea* Wall., *O. nepalensis* Griff, *O. wightiana* var. *puberula* (Hook. fil.), *O. wightiana* Wall., *O. wightiana* var. *rotundifolia* (P.C. Tam), *O. arborea* var, *spitata* Lecomte, *O. abyssinica* var. *speciosa* A.W. Hill, *O. wightiana* var. *spitata* (Lecomte) P.C. Tam (GBIF, 2023a; GBIF, 2023b; World Flora Online (WFO); Catalogue of life (COL, www.catalogueoflife.org (accessed on 29 September, 2022)). The plant is hemi-parasitic which could parasitize other species but has own photosynthetic activity. It is dioecious with unisexual flowers. Male flowers have slightly longer stamens and ovary is rudimentary. Female flowers have more prominent bracteoles with shorter perianth tube. The fruit is a small drupe of up to 1 cm in size with rudimentary disk, exocarp fleshy, endocarp crustaceous and globose seeds (Shu, 2003). They have unique phenological characteristics of being evergreen and with all year pro- duction of ripe fruits in Mediterranean climates (Herrera, 1988c) and intermittent flowering and fruiting pattern in tropical and sub-tropical habitats depending on variations in rainy seasons (Andiego, 2016; Mwangingo *et al.,* 2008). This enables it to cope with the broad range of the bio-climatical conditions of its occurrences (Herrera, 1988c).

O. lanceolata has high socioeconomic, ecological, and cultural values, and is used globally for various purposes (Tesitel *et al.,* 2021). The plant is used for medicine (Shrestha *et al.,* 2003; Bhattarai , 2010; Gautam, 2011; Hilonga *et al.*, 2019; Semenya and Maroyi, 2019; Ambu *et al., 2020; Kathambi et al.,* 2020; Kunwar, 2022), essential oils (Ashenafi, 2015; EBI Report., 2017; Bapat Vishwas *et al.,* 2021), erosion control and soil conservation (Mutisya *et al.,* 2019; Orwa *et al.,* 2009), and as an agent to help extract and remove elements of pollutants in soil (known as soil phytoremediation) (Weiersbye, 2006; Navarro-Cano *et al.,* 2018; Navarro-Cano *et al.,* 2019). The plant is also used in ethnoveterinary medicine (Nyahangare *et al.,* 2015; Moichwatense *et al.,* 2020; Mwangi *et al.,* 2021) and provides a resilient food source for local consumption (Joshi *et al.,* 2019; Mutie *et al.,* 2020). The plant is currently classified as endangered ac- cording to the International Union for Conservation of Nature (IUCN) in several countries in eastern Africa, but not elsewhere (CITES 2013a; CITES 2013b; Grooves & Rutherford, 2016; Wilson, 2018; Thomson *et al.,* 2020). The plant's high economic values and demands from the market are driving anthropogenic threats to the endangerment of the species (CITES, 2013b; Grooves & Rutherford, 2016; Wilson, 2018; NMK, 2019). The population in eastern Africa is predicted to be disappearing in the wild by 2040 (CITES, 2013b; Grooves & Rutherford, 2016; Wilson, 2018; Thomson *et al.,* 2020)

Despite increasing threats to the survival of the plant in eastern Africa and potentially elsewhere, there is inadequate systematic information about the ecology and distribution, let alone the various supporting and limiting factors that influence the plant's occurrences in the wild (NMK, 2019; Mugula *et al.,* 2021). Furthermore, data and studies from other parts of the world are scarce, despite the plant's ecological, socioeconomic, and cultural importance in many areas. Limited data and information hamper our ability to judiciously plan for the management, conservation, and propagation efforts to prevent the species' populations from extinction. Understanding the suit of abiotic and biotic factors and anthropogenic threats influencing the plants in eastern Africa and other parts of the world is critical for the conservation and sustainable management of the species.

Here we conducted a scoping review of the ecology and distribution of *O. lanceolata* using the available literature. We aimed to identify existing knowledge about the plant, including the abiotic and biotic factors, anthropogenic threats to the populations, and existing conservation efforts, as well as missing links and emerging questions for further research and inquiry. We paid special interest to the populations from various biogeographical regions globally where the species occur. More specifically, we aimed to answer from the literature the following questions: (1) where have studies related to *O. lanceolata* been conducted? (2) what abiotic factors potentially affecting the distribution of the plants did these studies find and assess, i.e., paleobiogeography (past species range shift), terrestrial conditions (soils, altitude, slope, land cover), and climate (temperature, rainfall, and humidity)? (3) what biotic factors did these studies examine, i.e., host plants, dispersal, and interaction with other species (either supporting or limiting growth)? (4) what anthropogenic threats to the survival of the species did these studies assess? (5) what conservation practices and programs have been conducted and reported to reduce threats to the population? By answering these questions, we hope to gain insights into the plant's ecology and existing conservation efforts to inform future strategies for the long-term survival and sustainability of the plant in the wild.

1. Materials and methods

1.1. *Taxa and known distribution of the study species*

The distribution of *O. lanceolata* spreads across four biogeographical regions: (1) eastern Africa; (2) southern Africa, (3) northern Africa and the Iberian Peninsula (southern Europe), and (4) southern Asia (Fig. 1), based on the known occurrence reported in the Global Biodiversity Information Facility (GBIF, 2023).

1.2. *Review methodology*

We synthesized available published scientific work in relation to the geographical distribution of *O. lanceolata* and the abiotic, biotic, and anthropogenic factors influencing the distribution of the plant, as well as existing conservation actions. Because existing research on the species has not been extensively conducted, a scoping approach was sought to map the available literature conducted in different countries and continents (Arksey & O'Malley, 2007; Munn *et al.,* 2018;

Lauwers *et al.,* 2020).

Relevant studies were identified by searching for evidence in elec- tronic databases. These include academic literature databases such as SCOPUS, Web of Science, ProQuest, SciELO., and Google Scholar, and grey literature databases such as CITES (Convention on International Trade in Endangered Species), donor agency websites, and websites of government agencies in countries where the plant occurs. In the literature search, we entered either a single syntax of the species' known synonyms, such as '*Osyris lanceolata*', '*Osyris quadripartita*', '*Osyris wightiana*', '*Osyris* species', or 'African sandalwood' (see Section 2.1 on taxa), or a combination of each of these syntaxes with keywords relevant to the scope of our study, such as 'threats', 'distribution', 'trade', 'cultivation', 'conservation', 'invasive species', 'biological invasions', 'abiotic', 'hemi-parasitism', 'host', 'climate', 'topography', 'elevation', 'slope', and 'preservation'.

From all studies found using the search criteria above, we further selected those that were highly relevant and met either one of the following criteria: (1) studies that targeted *O. lanceolata* or the synonyms; (2) studies of many plant species including *O. lanceolata* or the synonyms being one of them; or (3) studies that were carried out on the habitats or natural environment containing *O. lanceolata* or the synonyms. We investigated studies that are either based on empirical field-based data or indigenous knowledge (ethnobotany or ethnoecology). To avoid duplication of reporting, we excluded past literature reviews and meta-analyses from our evaluation. These were only included for discussion purposes.

For each study, we recorded information on the geographical location, abiotic factors (bioclimatic, temperature, rainfall, topography, slope, and soils), biotic factors (interaction with other vegetations and host plants, and dispersal mechanism), anthropogenic threats, and conservation management (in-situ and ex-situ regeneration and threat mitigation activities). For the host species, we classified them according to the genus and used the taxize package in R (Chamberlain & Szocs, 2013; R Core Team, 2016) to extract the family classification of these host plants. The number of the papers reviewed for every family were converted into proportions of reviewed papers per family per region by dividing for example the number of papers in Fabaceae by the total numbers of papers in eastern Africa multiplied by 100. And this was repeated for all biogeographic regions. As shown in Fig. 2 and demonstrated in equation below

$$Proportion\ of\ Papers = \frac{the\ number\ of\ the\ papers\ reviewed\ per\ host\ family}{Total\ number\ of\ papers\ reviewed\ per\ Biogeographical\ Region}*100$$

Similarly, the number of the papers reviewed for every threat were converted into proportions of reviewed papers per threat per region by dividing for example the number of papers in overharvesting or illegal trade by the numbers of papers in eastern Africa multiplied by 100. As shown in Fig. 3 and demonstrated in equation below.

$$Proportion\ of\ Papers = \frac{the\ number\ of\ the\ papers\ reviewed\ per\ anthropogenic\ threat}{Total\ number\ of\ papers\ reviewed\ per\ Biogeographical\ Region}*100$$

2. Results and discussion

Our search based on entering the relevant syntaxes into the academic and grey literature databases yielded 352 articles. From these articles, we found 186 that were relevant and of sufficient quality, and therefore included in the review (Tables S1-S5 in the Supporting Information). It is worth noting that it is difficult to find studies done on *O. lanceolata* alone. Most relevant studies are conducted on habitats of *O. lanceolata* and other plants, either based on empirical field surveys or indigenous knowledge. Field surveys are usually conducted within the local administrative unit with a limited number of sites.

The geographical distribution of the reviewed studies spanned 21 countries and four biogeographical regions: eastern Africa, northern Africa and the Mediterranean region, and southern and southwest Asia. We found a total of 103 studies evaluating the abiotic factors (Table S1), 30 studies on the biotic factors (including 21 studies on hosts in Table S2 and 9 studies on pollination processes in Table S3), 40 studies on the anthropogenic threats (Table S4), and 15 studies on the conservation management of the species (Table S5).

We outline below our findings related to each of the research questions that we aimed to answer, including the abiotic and biotic factors reported to be influencing the ecology and distribution of the plant, anthropogenic threats to the plant, and conservation actions that are currently undertaken. We will then summarize the knowledge gap about the species and draw some potential actions that may be required to enhance the continuing existence of the plant in the natural environment.

2.1. *Abiotic factors*

2.1.1. *Paleobiogeography*

The current global distributions of *O. lanceolata* is best be explained not only in the context of the present occurrence of large water and land masses, but also the past geographical conditions and tectonic movements of lands and the associated changes in the ecology and climate. Currently, the species is spread across three main continents (Fig. 1), including Africa (eastern, northern, and southern), Europe (the southern part, in the Iberian Peninsula and Arabian Peninsula), and Asia (southern and southwest). The discontinuous continental global range of the plant in Africa, Asia and Europe is indicative of an earlier shared dispersal range. There is a continuous distribution only from southern to eastern Africa and disjunct populations in northern Africa, the Iberian Peninsula, Balearic Islands, Canary Islands (Macaronesia Region).

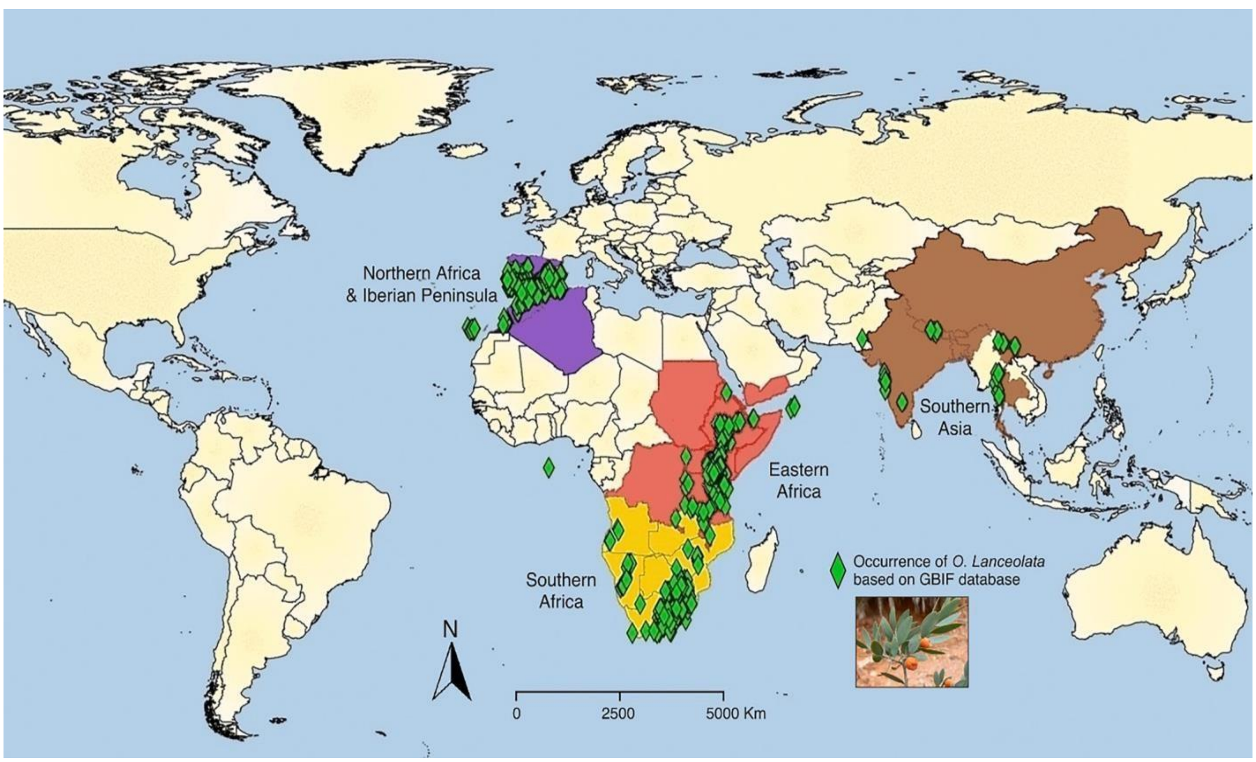

Fig. 1. Countries where *O. lanceolata* are reported to occur according to the Global Biodiversity Information Facility (GBIF) database and the associated biogeographical regions.

and Mediterranean region, Socotra (Yemen), Arabian Peninsula, and southern and southwest Asia. This indicates that there are spatial-related factors driving the distribution.

The characteristic *O. lanceolata* distribution is not different from other flora and fauna documented in these biogeographic regions. A phytogeographic link exist between the flora in the horn of Africa, Mediterranean, southwest Asia and the Sudano-Zambezian (Balfour, 1898; Gillett, 1941) with some flora with disjunct populations/distributions like *O. lanceolata* (Thulin & Warfa, 1989; Affenzeller *et al.,* 2018). Similarly, there is a biogeographical conformity of the southwest Arabian and African Coasts of the Gulf of Aden/horn of Africa which are separated by a distance of less than 30 km at the Bab El Mandeb Strait (Lavranos, 1978). These are considered as a single phytogeographical unit with strong Mediterranean and European Affinities of some plant species (Newton, 1980; White & Leonard, 1991) and with zoogeo-graphical relationships (Cassola & Miskell, 1990).

The migrations into the two opposite directions (southern and southwest Asia, southern Europe and the Middle East) may have occurred during several periods since the late tertiary allowing the contact of elements of different historic sources (Fici, 1991). Europe and Africa were separated by the Tethys Sea during much of the Cretaceous and Early Tertiary periods, although land bridges existed. Between 148 and 80 million years B.P., Africa rotated towards Europe; its northern parts were in contact with emerged lands in current Sardinia, Italy, and probably Spain. During the early Paleocene, Africa, and Europe again began to drift apart, although connections through the Iberian and Italian Peninsulas were maintained. During the Miocene, Africa shifted northward again by about 10 degrees reaching its current position. About 17 million years ago, remarkable floristic and faunistic exchanges with Europe took place probably through the Balkans.

The Arabian Peninsula became separated from eastern Africa 10 million years ago as a consequence of the rifting process, which during the Pliocene gave origin to the Red Sea. The African and the Arabian coasts of the Red Sea are considered by several authors as an important Quaternary irradiation route of Holarctic taxa, particularly during the glaciation periods when eastern Africa experienced a pluvial phase. Wickens (1975), stipulates that the Red Sea was characterized by a dry Mediterranean-type climate, in which periods of increased rainfall or cooler temperatures allowed the penetration of temperate taxa from the Mediterranean southwards to the uplands of eastern Africa through the coastal Ethio-Sudanian hills. With regards to the Horn of Africa, Gillet (1941), explains the scattered distribution of several Xerophilous woody plants in north-western Somalia by a hypothetical pluvial phase in recent geological times. During this period, the sub-desert formations and the *Commiphora*-bush-Acacia open deciduous scrubs were replaced by more mesophytic vegetation, such as the evergreen bushland, where the *O. lanceolata* occurs (Fici, 1991).

O. lanceolata is considered to be a survivor of a richer, tropical- margin vegetation that developed through the Tertiary period (Raven, 1973; Herrera, 1984). Changes taking place in this habitat were greatly influenced by the displacement of continents during the last 100 million years. The plant's dispersal was aided by continental drift (Raven & Axelrod, 1974). The circum-Mediterranean (plus the Canary Island), the warmest portions of the Mediterranean, Madagascar, the Cape Region of South Africa, and other places in eastern and southern Africa, are the current refugia for *O. lanceolata* (Thonner, 1915; Thorne, 1972; Bramwell & Bramwell, 1974; Raven & Axelrod, 1974; Jalas & Suominen, 1976).

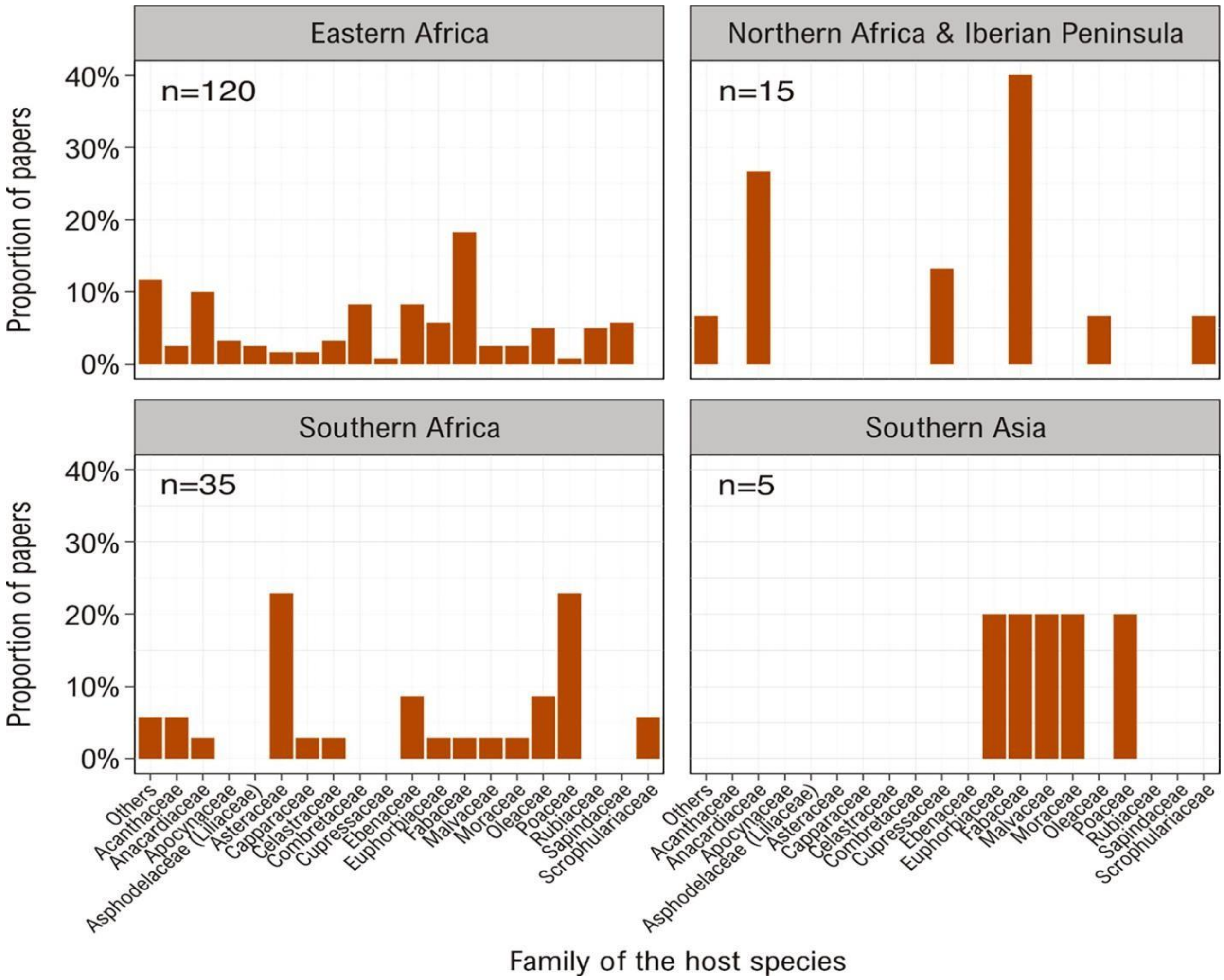

Fig. 2. Families of the host species co-occurring with the *O. lanceolata* across different biogeographical regions. n represents the total number of papers reviewed for the family of the hosts per biogeographical region.

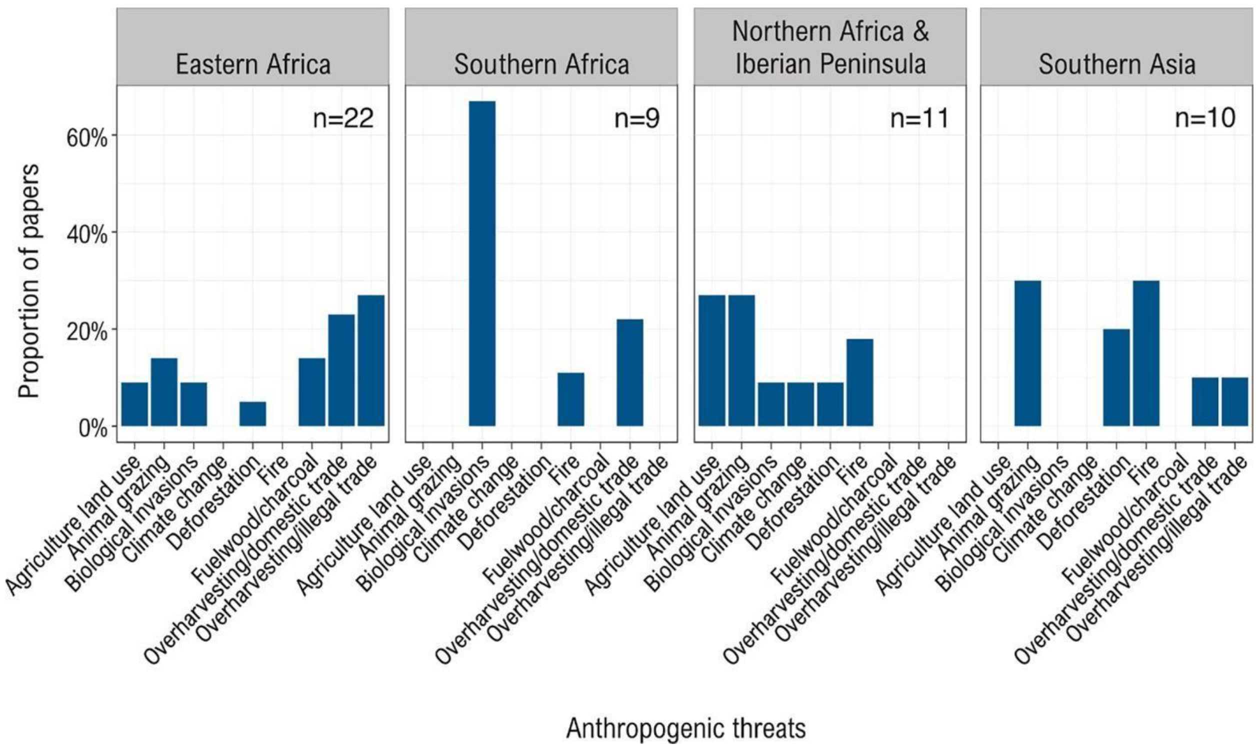

Fig. 3. Anthropogenic threats to *O. lanceolata* across the four biogeographical regions. n represents the total number of papers reviewed for anthropogenic threats per biogeographical region.

2.1.2. *Climate and terrestrial environment*

The influence of precipitation and temperature on the distribution of the plant has not been well studied to enable reliable inference. How- ever, several local studies have revealed that the species' vegetative and reproductive phenological phases follow distinct patterns between the dry (and warm) and wet (and cooler) years (Herrera, 1984; Herrera, 1986; Mwang'ingo *et al.,* 2008; Rodríguez-Gallego & Navarro, 2015; Andiego, 2016). This implies that rainfall and temperature have an important role in the growth and potential distribution of the plant. The plant occurs in the form of a tree in areas with humid and sub-humid climates, but the morphology changes to a shrub in arid and semi-arid conditions (Mwang'ingo, 2003; Gathara, 2015; Gathara *et al.,* 2014).

It reproduces more through coppicing (saplings/shoots emanating from an adventious bud at the base of the rootstocks or coppice that has been cut near the ground or otherwise burnt back) in the wild as compared to the seeds (Herrera, 1987; Mwang'ingo *et al.,* 2008; Mukonyi *et al.,* 2012; FSSD-MWE, 2022). In the Mediterranean-type climate, which is associated with summer droughts and frequent fires, the capacity to sprout is observed in plants like *O. lanceolata* which produces fleshy, vertebrate-ingested fruits, heavy seeds and low fruit production accompanied by a high incidence of dioecy (Herrera, 1987). The sprouting capacity is an ancestral trait akin to the sub-tropical sclerophyllous taxa, allowing the plant to survive the seasonal dryness of the Mediterranean climate (Wells, 1969). The sclerophyllous species that sprouted existed before the Pleistocene and were able to evolve after the occurrence of the true Mediterranean climate conditions (Pons, 1981). The high capacity to sprout may also be due to the resource allocation strategy associated with the reproductive effort and the concept of trade-offs in resource limited environments (Kumari *et al.,* 2020; Liu *et al.,* 2021).

Our reviewed papers across different biogeographical regions indicate that the plant occurs in habitats with an altitude ranging between 30 and 3000 m above sea level (Table S1). For *O. lanceolata* to grow and proliferate, it requires a specific micro-climate niche that consists of rocky outcrops, hilly and very steep areas and habitats in dry upland and riverine forests, forest edge, riverbanks, lowland bush and in arid and semi-arid areas which are extremely vulnerable as they are not protected but in communal and private lands (*FSSD-MWE,2022; Khayota et al.,* 2021; Otieno & Hilonga, 2022; Khayota *et al.*, 2022). It occurs in diverse soil types ranging from nitisols, acrisols (Muriuki *et al.,* 2011; del Ario Anguilar & Rodriguez, 2018; Gathara *et al.,* 2022), abundant in andosols (Ochanda, 2011; Strohbach *et al.,* 2012; Jauro, 2012; Nyaga, 2021), rendzina, poorly developed regosols with lithosols being dominant (Burke & Wittneben, 2008; Dallahi *et al.,* 2017), phaeozems(Gathara, 2015; Meddour & Sahar, 2022), and anthrosols like in mine tailing soils (Moya-Pe´rez *et al.,* 2022; Lemprecht, 2010; Liu *et al.,* 2008; Navarro-Cano, Goberna, & Verdú, 2019; Navarro-Cano, Verdú, & Goberna, 2018; Ona´, Goberna, & Navarro-Cano, 2021; Rosner & van Schalkwyk, 2000; Weiersbye *et al.,* 2006; FSSD- MWE, 2022; Moya-Perez *at al.,* 2022).

Eastern Africa. In this region, *O. lanceolata* occur in Horn of Africa (northern Somalia, Djibouti, Harar), Eritrea, Ethiopia, Kenya, Tanzania, Uganda and Democratic Republic of Congo. The plant occurs in broad geographical vegetation types, including: (i) lowland areas with semi- arid rangelands and shrubby habitats dominated by *Commiphora*, acacia, Somali-Maasai scrub, and bushlands; (ii) dry combretum wooded grassland to miombo woodlands; (iii) lower upland forest dominated by *Podocarpus latifolius (*Thunb.) R. Br. ex Mirb., *Olea* *capensis* Thunb., *Juniperus procera* Hochst. ex Endl., *Warburgia ugandensis* Sprague.; (iv) mid-upland semi-deciduous forest, (v) dry conifer afromontane forest dominated by *J. procera*; and (vi) dry evergreen afromontane forest with *Olea europaea* L. and *J. procera*. The plant also occurs in dry forest edges and margins in arid, semi-arid, and humid conditions (Marshall, 1998; Mwang'ingo *et al.,* 2003; Mwang'ingo *et al.,* 2005; Mwang'ingo *et al.,* 2008; Mwang'ingo *et al.,* 2010; Ochanda, 2009; Muriuki *et al.,* 2011; Mukonyi *et al.,* 2012; Gathara *et al.,* 2014; Kindt *et al.,* 2014; Kariuki, 2018; Andiego, 2016; Bekele *et al.,* 2019; Erbo *et al.,* 2020; Gebrehiwot *et al.,* 2019, Gebrehiwot *et al.,* 2020; Hilonga *et al.,* 2019; Kariuki *et al.,* 2018; Kuma & Shibru, 2015; Medley *et al.,* 2019; Musyoka *et al.,* 2019*;* Schmitt *et al.,* 2019; Seifu *et al.,* 2018; Soromessa, 2015; Warinwa *et al.,* 2016; Koricho *et al.,* 2020; Wekhanya, 2016; Kariuki *et al.,* 2018; Ogendi & Ondieki, 2020; Kayombo *et al.,* 2020; Lusweti *et al.,* 2020; Birhanu *et al.,* 2021; Erbo & Bejigo, 2021; Nyaga, 2021; Kioko, 2021; Masota, 2021; Okumu, 2022).

Southern Africa. The plant occur in South Africa, Zambia, Zimbabwe, Namibia, Angola, Malawi and Botswana in montane grasslands, afro- montane evergreen forests, high rainfall miombo woodland, secondary scrub savanna, caves and subterranean habitats, dry forest margins, evergreen bushland, grasslands composites of bushveld of *O. europaea* and strand veld, temperate and tropical thickets, incipient forests at lower altitudes, riparian vegetations, and Karoo riviere vegetation types (Weiersbye *et al.,* 2006; Burke & Wittneben, 2008; Clark *et al.,* 2009; van Staden & Bredenkamp, 2005; Clark *et al.,* 2011; Strohbach, 2012; Strohbach, 2013; du Toit & Cilliers, 2015; Frisby *et al.,* 2015; Nyahangare *et al.,* 2015; Clark *et al.,* 2017; Strohbach, 2017; Timberlake *et al.,* 2018; Clark *et al.,* 2019; Rasethe *et al.,* 2019; Semenya & Maroyi, 2019; Timberlake *et al.,* 2020; Strohbach, 2021; Jauro, 2022).

Northern Africa and the Iberian Peninsula. In this region, the plant is evergreen, root hemi-parasitic, and dioecious shrub up to 3 m in height, spreading across the Macaronesia (Canary Islands), northwest Africa, Belearic Islands in Spain and the Iberian Peninsula (Spain and Portugal). In Iberia, the plant is almost restricted to the south Coast region, where it mostly occurs on sandy soils. The northern limits of the plant's distributional range closely coincide with the average temperature of 10 ˚C in January and 350 days frost free. In southern Spain, the plant parasitizes evergreen and summer drought-deciduous shrubs of many species (Herrera et al., 1988a; Herrera, 1988b). It occurs in a variety of habitats, mainly in arid, semi-arid, and dry infra to the thermos and supra- Mediterranean climate belts. This includes the dry Mediterranean- Ibero-Atlantic biogeographic territories, Mediterranean-type scrub lands with or without semi-arid Mediterranean forest species *Tetraclinis articulata* (Vahl) Mast., shrublands and brushwood with Ibero-North African species, Mediterranean sclerophyllous shrublands with some planted pine woods, highly Xerophytic scrub vegetation, thermo- sclerophyllous woodlands of *Olea* and *Juniperus*, Canary palm-tree community and in Thermo-Mediterranean kermes oak and forests on deep soils in sub-humid regions of Western Algeria (Herrera, 1984; Herrera, 1987; Herrera 1988c; Carrion *et al.,* 2003; Dallahi *et al.,* 2017; Del Arco Aguilar & Rodríguez Delgado, 2018; Baumel *et al.,* 2018; Lopez-Saez *et al.,* 2018; Siba & Aboura, 2018; Navarro-Cano *et al.,* 2019; Benmechta *et al.,* 2021; Quinto Canas *et al.,* 2021; Ona´ *et al.,* 2021; Moya-Pe´rez *et al.,* 2022; Meddour & Sahar, 2022).

Southern Asia. In this region, the *O. lanceolata* spreads across the Arabian Peninsula especially in Yemen, Socotra (an archipelago in Yemen) and Saudi Arabia (Albaha Region in Sarawat Mountains) as well as Southern Asia (India, Nepal, Bhutan, Central Nepal, India, Bangladesh and China). It is distributed in tropical, subtropical, and temperate regions with a concentration in arid and semi-arid regions (Macklin & Parnell, 2002). The specific habitats includes sub-tropical Alpine forests, chir pine forests, western subtropical broad-leaved hill forests, semi-evergreen to thorny scrub forests, tropical montane evergreen forests, *Schima-Castanopsis* forests, temperate and sub-alpine broad leaved and coniferous forests, and secondary succession shrubs (Davidar *et al.,* 2007; Liu *et al.,* 2008; Arinathan *et al.,* 2011; Gautam, 2013; Rahangdale & Rahangdale, 2014; Rahangdale & Rahangdale, 2017; Tamang *et al.,* 2017; Jamtsho & Sridith, 2017; Joshi *et al.,* 2019; Marpa *et al.,* 2020; Ambu *et al.,* 2020; Tshewang *et al.,* 2021; Jamtsho *et al.,* 2021; Liu *et al.,* 2022).

2.2. *Biotic factors*

2.2.1. *Host plants*

We found 21 studies evaluating the host plants of *O. lanceolata.* These studies indicate that the plant co-occurs with different hosts in different biogeographical regions (Fig. 2). In some regions, certain taxa are more prevalently found as a host than in other regions. The Fabaceae family appears to be the most prevalent host associated with *O. lanceolata* in its natural habitats in eastern Africa, northern Africa and the Iberian Peninsula, and southern Asia. However, in southern Africa, Asteraceae and Poaceae families were found to be the most prevalent hosts.

Although some studies have indicated that hosts play a major role in the distribution of hemi - parasitic plants (Fox, 1997), the quality of hosts may as well be an important component. Host quality could include the capacity to withdraw soil water and other edaphic nutrients, be more attractive to seed dispersers, and be more conducive to seedling establishments (Watson, 2009). The quality of the host may be determined by a range of internal and external factors. Internal factors include the host's physiological traits in managing water and nutrient contents, bark thickness for root parasitism, and root depth. External factors include the position of the host in the landscape and proximity to nutrient sources. Studies have also indicated that hosts can act as a buffer between the *O. lanceolata* and the environment (Herrera *et al.*, 1988a), and sometimes may enable *O. lanceolata* to adapt to enhanced nutrient up- take especially in Mediterranean habitats with nutrient-poor soils (Lamont, 1982; Lamont, 1983). In the Mediterranean climate and dry tropics where there are fluctuations in water and nutrient availability, *O. lanceolata* may need to parasitize a broad range of hosts as a strategy to maximize the survival of the population (Kuijt, 1969; Atsatt, 1970; Atsatt & Strong, 1970). Hosts may modify the expressions of genetic variability in *O. lanceolata* (Atsatt, 1970; Atsatt & Guldberg, 1978) to enhance nutrient uptake in poor soils as part of adaptation strategy in the Mediterranean habitats (Lamont, 1982; Lamont, 1983) and tropical arid and semi-arid lands (Gathara *et al.,* 2014; Gathara, 2015). Additionally, the hosts may enhance continuous physiological activity of *O. lanceolata* throughout the whole year, which is contributed partly by the host in favoring phenotypical canalization (measure of the ability of population to produce the same phenotype regardless of its variability in its environment) of the hemi-parasite (Kuijt, 1969; Atsatt, 1970; Atsatt & Strong, 1970; Herrera, 1984). In some studies, it has been reported that sandalwoods under the same Santalaceae family have a flexible/plastic phenology whereby a single genotype is able to give rise to a wide range of phenotypes if exposed to different environments (Fatima *et al.,* 2017).

1.1.1. *Pollination*

To establish new colonies and extend the existing distributional range, *O. lanceolata* would need a successful pollination process, seed dispersal mechanism, and deposition of seeds in the right microsites in suitable habitats and hosts. The success of pollination rate is influenced by the number of pollen grains produced, the presence of pollinators, and the distance from one tree to the other tree, especially for dioecious plants (Andiego, 2016). Several studies have also indicated that though pollination mechanisms are an important element in large-seeded plants like *O. lanceolata*, it may not play a role on its own in determining the number of seeds produced after fertilization. This is because the number of seeds produced from these plants depends greatly also on the availability of the resource (i.e. water and carbon) used to produce them than the amount of pollen that was produced (Herrera, 1987; Kumari *et al.,* 2020). Furthermore, it's flowers are inconspicuous, and hence rarely visited by pollinators (Herrera *et al.,* 1984). The pollination mechanism of O. lanceolata has certainly not been fully studied. A small number of studies have observed species of Calliphoridae, Tiphiidae, and Sphecidae families, and small and medium-sized flies are the primary pollinators of the plant in the Mediterranean ecosystems (Herrera, 1984; Herrera, 1988d).

In tropical regions, the flowering phase of *O. lanceolata* occurs biannually between January and June and between September and December with each time period taking place about 109 days (Mwang'ingo, 2008; Andiego,2016). This flowering phenology is a conservative trait within the evolutionary lineages (Kochmer & Handel,1986; Wright & Calderon, 1995) and plays an important role in the species' pollination success through the regulation of pollen flow and pollinators' foraging behavior (Sakai, 2001). In the Mediterranean climate, the flowering lasts longer, around 200 days and the timings are different between sexes. The flowering times for females are between March and September, for males nearly the entire year, and for both sexes the peak period is around May and June (Herrera, 1988c). The fruiting phenology in both Mediterranean and tropical climates vary among trees within a given population and between populations (Herrera, 1988c; Mwang'ingo *et al.,* 2008; Andiego, 2016). In the Mediterranean region, the capacity of the plant to vegetatively sprout and produce is associated with the production of fleshy, vertebrate-ingested fruits, heavy seeds, and low fruit production, along with a relatively high incidence of dioecy in Mediterranean climates (Herrera, 1987).

In eastern Africa, *O. lanceolata* has limited reproductive success in the natural environment as compared to its Mediterranean counterparts. Low level of pollen production or limited pollinators' movement, un- synchronized budding, flowering, and pollination periods between males and females, and poor mechanism of pollination of the species have been identified as the primary factors of the low reproductive success and regeneration of the plant in this region (Mwang'ingo *et al.,* 2008; CITES, 2013b; Andiego, 2016). Poor pollination under natural pollination might be a consequence of insufficient/low level pollen production or limited pollinators leading to failure of the pollen to move across trees as observed in some trees such as figs (Wiebes, 1979). The pollen failure to reach the target plant might also be due to distance between male and female plant being farther apart than the effective distance required (Simons, 1996). However, the critical distance between the male and female for effective pollination in this dioecious plant remain unknown. Overharvesting of female trees (CITES 2013a; CITES 2013b) coupled with dioecy can lead to highly skewed sex ratios with larger distances apart between male and female, hence leading to decreased pollination and fertilization rate, increased abortion rate leading to production of low level of seed, with some having low germination capacity and poorly developed embryos (Mwang'ingo *et al.,* 2008).

The fact that *O. lanceolata* flowers are inconspicuous and hence rarely visited by pollinators (Herrera *et al.,* 1984). Yet, in most dioecious species males tend to be visited more frequently than females as they offer more floral reward in terms of pollen and nectar (Baker, 1976), can lead to reduced pollen availability among the females, reduced fertilization rate and increased abortion rate. Additionally, insufficient pollen production might be due to greater reproductive costs of females to produce pollens in environments with limited availability of resources like water and carbon (Kumari *et al.,* 2020; Charnov, 2020), but this is not investigated in this plant.

Assisted pollination has been identified as a potential measure to help increase the pollination rate, fertilization and reproductive success, viability, and amount of *O. lanceolata* seeds/fruits in their natural environment (Mwang'ingo *et al.,* 2008; Andiego, 2016). Knowledge of species phenological phases is important to enabling a timely collection of good quality and quantity of seeds and seed development (e. g. through optimizing fertilization, seed formation, and maturity) to assist the regeneration of the plants (Jackeline & Freitas, 2008).

1.1.1. *Seed dispersal*

O. lanceolata does not have fruit-set without fertilization (agamospermy) but it sometimes produces empty seeds without embryos in eastern Africa which is likely due to poorly developed ovaries (Mwang'ing'o *et al.,* 2008; Andiego, 2016). Most of this species bear few drupe seeded fruits that are consumed and dispersed by vertebrates (Herrera *et al.,* 1988a). Seed dispersers of the plant in the tropical and sub- tropical regions are not well understood. However, in the Mediterranean climates, such as the coastal dunes of southern Spain (with warm and dry conditions), the seeds are dispersed by a frugivorous bird *Sylvia atricapilla* (Linnaeus, 1758) (Herrera, 1984). The plant matches its fruiting season to the autumn and winter periods when abundant avian dispersers are available. Many birds migrate from central and northern Europe and the high mountains of the Mediterranean region at the end of summer to the wintering areas such as the Strait of Gibraltar to take advantage of the fruiting trees and shrubs (Rodríguez-Gallego & Navarro, 2015). The regeneration of seed dispersed by frugivorous birds depends on whether it is seriously damaged during transportation, such as seeds falling to the ground and the pulp being desiccated (Herrera *et al.,* 1988a). Seeds also need to be deposited by dispersing agents on a suitable microsite with a suitable host. Therefore, the role of zoochory for vectors like *S. atricapilla* cannot be overlooked in its great role in connecting and distribution of *O. lanceolata* to distant populations in Mediterranean region (Rodríguez-Gallego & Navarro, 2015).

The dispersal of *O. lanceolata* seeds are confined to particular regions, depending on their dispersal range and their ability to become established in new locations. The effective dispersal range of the species depends on the season in which the seed is shed. This is because the plant has mechanical dormancy which delays immediate germination (Msanga, 1998) and the recalcitrant character of the seed which does not allow long-tern viability in the soil bank and this act together to limit regeneration and recruitment from seeds. Therefore, the coincidence of rainy season and seed dispersal is important in recalcitrant seeds because immediate regeneration is more crucial than seed bank (Bazzar, 1991). The survival of seeds during dispersal will also depend on numerous factors, including herbivore and pathogenic attack on seeds and proximity of regenerating seedlings to mother plants (which may cause high mortality rate due to the presence of host-specific seed predators, herbivores, fungi, and pathogens). Other barriers to the survival of the seeds also include proximity to mother trees, whereby falling branches, shading, drought stress, and competition for resources due to clustering can lead to high seed mortality (Mwang'ingo *et al.,* 2008).

O. lanceolata regenerates more from rootstock/coppice in the wild as compared to the seeds

(Herrera, 1987; Mwang'ingo *et al.,* 2008; Mukonyi *et al.*, 2012: FSSD-MWE, 2022; Khayota, *et al.,* 2021; Khayota *et al.,* 2022). Coppicing/resprouting is also as a response to disturbance events such as herbivory and fire that shape woody plant communities in African Savanna ecosystems (Sebata, 2017). This plant also occurs in this ecosystem as a browse plant and resprouting helps it to continuously regenerate (Khayota, *et al.*, 2021; Mwang'ingo *et al.,* 2010).

1.1. *Anthropogenic threats*

The majority of studies on threats related to *O. lanceolata* and its taxons were conducted in eastern Africa where the plant is endangered (Fig. 3). Different habitats of the plant in different biogeographical regions are posed by different threats. Threats from biological invasions were reported most often in southern Africa, whereas overharvesting was reported most often in eastern Africa (Mukonyi *et al.,* 2012) besides land use-related activities. In northern Africa and the Iberian Peninsula and southern Asia, land use-related activities, such as overgrazing, deforestation, and fire occurrence, which lead to vegetation changes and decreasing hosts are the major threats (Benmechta *et al.,* 2021; Carrion *et al.*, 2003; Moya-Perez *et al.,* 2022; Siba & Aboura, 2018; Moya-Pe´rez *et al.,* 2022).

1.1.1. *Biological invasions*

Invasive species represent a serious ecological effect on native biodiversity. They have the capacity to overtake entire biomes by out- competing native species as they colonize new habitats because of their high reproductive and dispersal abilities and survival rates and are supported by the absence of coevolving predators. Biological invasions can be exacerbated by increased land degradation (through overgrazing and deforestation), overharvesting, and climate change (Tshewang *et al.,* 2021). Invasive species can threaten species diversity, alter soil properties, degrade wildlife forage, alter fire regimes, threaten endangered species, and decrease crop yield (Zhang & Chen, 2011). Invasive species are the second greatest threat to biodiversity after habitat destruction according to the International Union for Conservation of Nature (IUCN) (Zhang & Chen, 2011).

A study by Wekhanya (2016), in the Oldonyo Sabuk National Park, Kenya, showed that the allelopathic properties of the invasive plant *Lantana camara* L. destroys the physicochemical processes of soils and prevent seed germination and seedling growth of native plants like *O. lanceolata.* In the Bvumba mountains of Zimbabwe and Manica highlands of Zimbabwe and

Mozambique where the *O. lanceolata* occurs, there is a high number of invasive species as a result of intense human activities in the area. The area is invaded by *Acacia melanoxylon* R.Br. tree in the grassland and previously cultivated land, and forest herb *Hedychium gardnerianum* Sheppard ex Ker Gawl in cleared forest areas after the fire (Timberlake, 2020). In the afromontane region of Nyanga Massif of Zimbabwe, *Pinus patula* Schiede ex Schltdl. & Cham. occurs as an invasive species in *O. lanceolata* habitats (Clark *et al.,* 2017). Invasive species also occur in other countries in the habitats of *O. lanceolata* (Clark *et al.,* 2009; Clark *et al,* 2017; Schimdt, 2019; Tshewang *et al.,* 2021; Strohback, 2021). Further studies are required to understand the impact of invasive species on *O. lanceolata* habitats.

1.1.2. *Overharvesting*

Overharvesting of *O. lanceolata* appears to be primarily driven by trade and market demand. Trade of the plant is illegal in some countries in eastern Africa, but in some other countries within the same region trade is permitted. In eastern Africa, different forms of illegal trade of the plant are carried out, ranging from domestic and cyber trade involving Illegal Wildlife Trade on the Internet to forest crimes, and these activities appear to extend internationally to other parts of the world.

O. lanceolata was among the plants advertised for sale between March 2018 and June 2021 in online platforms surveyed in Cameroon, Chad, the Central Republic of Congo, Gabon, and Nigeria (Woollof *et al.,* 2022). The Illegal Wildlife Trade on the Internet can be difficult to regulate due to the anonymity the internet creates to the seller and hence making it easier to find potential buyers and sellers online than the physical world (Olmos & Mandujano, 2016). Additionally, legislation relating to wildlife has often been written to prevent wildlife trade in physical markets rather than the online markets (Lavorgna *et al.,* 2020). Forest Crime is illegal extraction and logging of *O. lanceolata* from the natural populations like forests and related trade or forest illegality (illegal logging and related trade) which relates to illegal use of forest land and forest resources (Blaser & Zabel, 2016; Kioko, 2022). The uncontrollable nature of illegal cyber trade of endangered plants and forest crimes can lead to unsustainable harvesting, which may further lead to wicked problems in the environment like biodiversity loss and extinction of endangered plants like *O. lanceolata*. This situation can even become more complicated for this plant as it not widely domesticated and is mostly sourced from the wild especially in eastern Africa (Mwangi *et al.*, 2021).

There are industries for essential oil extraction and processing re- ported in the eastern African countries of Tanzania, Uganda, and Ethiopia. Uganda started its commercial trade of sandalwood around 2011 with the establishment of Sky Beam Africa Limited (SBAL) in Tororo district, after government bans on *O. lanceolata* in Kenya and Tanzania. However, SBAL closed its operations in Uganda in 2019, after failing to adhere to Environmental Impact Assessment agreements on *O. lanceolata* regeneration in the areas they harvested it. The Uganda Wood Impex Limited (UWIL) which is still operating get its raw Sandalwood materials from the Democratic Republic of Congo (DRC) (FSSD-MWE,2022; Kioko, forthcoming). There were four operating factories in Tanzania in 2012, but a limited supply of *O. lanceolata* led to their closure *(Mukonyi et al.,* 2012). In Tanzania commercial harvesting of raw materials in the country by Siera Limited located in Babati- Manyara, Afro-Aromatics in Mombo-Tanga and Natural Aromatics LTD in Dar es Salaam was common before government restrictions in 2006 and this might have caused massive decline of the plant. For now, the Siera Limited factory source its raw materials mostly from Australia (Australian sandalwood) and to the little extent from India (Indian Sandalwood) and from Uganda, South Sudan (African sandalwood) as well as Dubai and China and exports sandalwood oils and spent dust mainly to India, United Arab Emirates, Taiwan, China, Australia, Singapore and Sudan as well as Dubai through Kilimanjaro International Airport, Julius Nyerere international Airport and Dar es Salaam Port. Afro-Aromatics Factory in Mombo-Tanga Imports sandalwood raw materials from eastern Africa (African sandalwood) in (Congo, Uganda and South Sudan) and exports Sandalwood oil to Dubai, USA and India through Port of Tanga and sometimes through Julius Nyerere international Airport while Natural Aromatics LTD Factory in Dar es Salaam imports sandalwood raw materials from Uganda, Congo and South Sudan (African sandalwood) and exports the sandalwood oil and spent dust to India, Saudi Arabia and China through Julius Nyerere international Airport and Dar es Salaam Port (Otieno & Hilonga, 2022). Ethiopia has an ongoing industry based on a signed agreement between the Ethiopian Biodiversity Institute (EBI) and DOCOMO Plc., a USA- based company to harvest *O. quadripartita* from the wild and extract essential oils from the heartwood (Ashenafi Ayenew, 2015); however, there is overexploitation of this plant and the reduction of the abundance and distribution in Ethiopia (Kuma *et al.,* 2015; Gebrehiwot *et al.,* 2020; Bekele *et al.,* 2019).

O. lanceolata distributed in native range sites in Kenya, Tanzania, Uganda, South Sudan, Rwanda, and Burundi is listed as endangered in Appendix 11 of CITES (CITES 2013a; CITES 2013b; Grooves & Rutherford, 2016; Wilson, 2018; NMK, 2019). However, the threat of illegal trade continues until now in these eastern African countries. This threat facing *O. lanceolata* was first known by scientists during the second workshop on "Setting Forestry Research Need and Priorities" held in Moshi, Tanzania (Mwang'ingo & Mwihomeke, 1997). It was highlighted as one of the biodiversity issues during the "Eastern Arc Biodiversity Conference" held in Morogoro, Tanzania (Burgess *et al.,* 1998). The intensive and uncontrolled harvesting of the plant began in the early 1900s after a decline in Indian and Australian sandalwood as major sources of the perfume and fragrance industry (Walker, 1966; Ruffo *et al.,* 2002; Mwangingo *et al.,* 2003). Such consumption demands with the existence of global supply chains interconnecting human societies and environment across distant places have been known to lead to local anthropogenic pressure on biodiversity (Rudel, 2007; Meyfroidt *et al.,* 2013; Verburg *et al.,* 2015; Chaudhary & Kastner, 2016; Marques *et al.,* 2019). This factor, coupled with the inherent vulnerabilities of *O. lanceolata* and intrinsic biological risks such as mechanical dormancy, recalcitrant seeds, slow growth and its habitat specific requirements will likely lead to population decline and regional extirpation if conservation measures are not put in place.

While numerous legal frameworks are used to protect the endangered species from overexploitation, some laws involving government bans and CITES have proven ineffective to control the illegal trade of *O. lanceolata* in eastern Africa. Despite the ban on export of logs and tree harvesting in protected areas by the Tanzania government in natural forests to address illegal logging (ICTSD, 2006), Kenyan Presidential decree ban under the Kenya Forest Act 2005 (Gazette Notice No. 3176) (GoK, 2007) on harvesting and trade of Kenyan sandalwood species and its derivative, the Uganda ban on trade of raw sandalwood following the listing of the species in Appendix II of the CITES and the irregularities associated with smuggling the raw sandalwood from neighboring countries (FSSD-MWE, 2022), massive overharvesting of the plant from their natural areas continued to occur. The ban has proven harder to enforce as the illegal trade is conducted through dynamic and increasingly resilient transnationally organized criminal groups (Bunei, 2017; Kioko, 2021). According to the UNODC (2009), these organized criminal groups are in the form of shifting alliances of loose, flexible networks of key individuals operating at national, regional, and international levels. In eastern Africa, for instance, the criminal groups include individuals from west Africa, Asia, and Europe. This is being heightened by the ongoing cyber-enabled wildlife trade in central Africa and Nigeria where *O. lanceolata* is one of the plants advertised for sale (Woollof *et al.*, 2022). Although CITES has been at forefront of fighting forest crimes and wildlife trade of *O. lanceolata*. In eastern African states (CITES, 2013b; Laina, 2016; NMK, 2019), the larger domestic and international demand for the plant might render the plant protection measures from the illegal trade ineffective (Corlett, 2020).

1.1. *Conservation management*

Conservation actions have been taken primarily in the eastern Africa biogeographical region where *O. lanceolata* is endangered. The species is listed in CITES (2013), as a measure to mitigate overharvesting and high levels of international trade. The listing of any species in CITES mandates legal and sustainable trade regulation, promotes international cooperation, and encourages multi-sector collaboration and access to capacity-building programs. A project is currently underway for the sustainable harvesting and trade of the plant in the eastern African states of Kenya, Uganda, and Tanzania with the support of the CITES (CoP-17 Secretariat). The project aims to deliver a locally appropriate market model for sustainable and legal trade for the conservation and sustain- able management of the plant, considering the economic development in eastern Africa. The project involves developing a data tracking mechanism that assesses and verifies whether or not a proposed export is detrimental to the survival of the species. This data will then be used to inform the setting of harvesting regimes and trade quotas, and licensing and concession areas for the *O. lanceolata* management units (Laina, 2016; NMK, 2019). Another important work supported by CITES also includes a preliminary survey on the exploitation to inform the development of guidelines on the sustainable utilization of the plant. How- ever, this effort has been hampered by inadequate scientific data on the current status of the species in terms of biology, ecology, population distribution, population densities, levels of off-take, and trade to appropriately guide the decision-making process. There is therefore a need to generate data on these aspects to inform the process of developing appropriate policy legislative and administrative structures for the plant’s sustainable use (NMK, 2019).

The natural mode of regeneration of *O. lanceolata* is through coppicing and seed (Herrera, 1987; Mwang’ingo *et al.*, 2008). Propagation by seeds in the wild is often difficult due to the dioecy of the plant and the spatial arrangement of the male and female trees in the landscape. These features affect the plant's reproductive outcome and the supply of seed at the right time (Mwang'ingo *et al.,* 2008). In addition, the seeds have mechanical dormancy and storing the seeds is challenging as the seeds are recalcitrant or can only be viable within a limited time (one year) and must be stored in ambient temperatures (Kamondo *et al.,* 2021). There are several ex-situ conservation interventions which have been attempted to address this issue. This includes the introduction of contemporary vegetation propagation methods such as marcotting (air layering) (Teklehaimanot *et al.,* 2004; Mwang'ingo, 2006; Machua *et al.,* 2009; Giathi *et al.,* 2011; Kamondo *et al.,* 2014) and other biotechnological approaches (Kalabamu & Feyissa, 2015). However, these methods have not been implemented more extensively, especially in the endangered sites of eastern Africa, due to inadequate data and understanding of the ecology, distribution, and genetics of the plant to guide suitable assisted propagation activities (Laina, 2016; NMK, 2019; Mugula *et al.,* 2021).

1.1. Knowledge gaps and recommended actions

Large demands and slow population increase require the application of both in-situ and ex-situ conservation measures to support the continuing existence of the *O. lanceolata* species, especially in eastern Africa where it is endangered. To do so, understanding the species' ecology and spatial variations are critical, and this includes knowledge of the habitat preference in terms of both abiotic and biotic factors and barriers to survival due to anthropogenic threats. The species distribution modeling (SDM) approach can be used to identify areas where the plant may occur (in relation to abiotic and biotic proxies) and the vulnerability of these habitats to anthropogenic threats (associated with socio-economic parameters) to help guide the design of judicious conservation strategies (Fig. 4). Although a shift in climate patterns has been observed in many parts of the world, only one study that we reviewed considers climate change as a potential threat to the species. The impact of climate change on the future distribution of the plant remains uncertain. As such, SDM can help predict the potential distribution of the plant under various future scenarios in climate and landscape conditions.

Some biotic factors influencing the plant's persistence have been studied, although to a limited extent. This mainly pertains to the characteristics of the host species and the plant's pollination and seedling strategies. *O. lanceolata* parasitizes a broad range of species and may partly share the phenological patterns of its host species which enable it to maintain sustained physiological activity for a period equivalent to the phenological cycles of its hosts. There is a limited understanding of the variability of this interaction mechanism between *O. lanceolata* and the hosts across different biogeographical areas globally. The pollination mechanism (both the pollination process and the pollinators) of *O. lanceolata* has not been fully studied beyond reporting the role of insects and flies in assisting the pollination (Herrera 1988d; Mwang'ingo *et al.*, 2008). The seed dispersal mechanism of the plant and the role of seed dispersers have not been fully understood and only a few studies exist. More knowledge of species phenology and reproductive biology could help solve the potential reproductive problems of the plants and improve the quality of seeds to support better conservation management (Fig. 4).

Overharvesting of *O. lanceolata* linked to illegal trade activities is a major issue in eastern African countries (Bunei, 2017; Okumu, 2022; Lusweti *et al.*, 2020). Despite numerous pieces of evidence on this issue, there is very limited information and studies investigating the market linkages, routes, and drivers of these illegal trade activities. The plant has multiple end uses and demands, especially from the oil and herbal industries, yet data on consumption patterns are scarce. A mechanism that allows tracking and monitoring the regional and international demand and supply, market linkages, and value chain of the species is required to inform conservation measures. To tackle the illegal smuggling of the *O. lanceolata* several regulatory measures may be required (Fig. 4), and these could potentially include:

- Harmonization of transnational environmental laws among countries to prevent illegal smuggling of *O. lanceolata* especially in the region where it is endangered. Currently, trade of the plant is not prohibited in some countries in eastern Africa, such as Ethiopia and Democratic Republic of Congo.
- The adoption of national and regional policies, such as the African Union Strategy on Combating Illegal Exploitation and Illegal Trade in Wild Flora and Fauna to ensure online trade is mentioned explicitly in the objectives relating to any wildlife trade.
- The adoption of a regional legal framework based on harmonized environmental laws in line with CITES' specific measures can be included in future regional policies. For example, CITES recommends developing a list of CITES Appendix II species most found for sale online in Update to Resolution Conf. 11.3 (Rev. CoP18).
- The eastern African countries where the plant is endangered could consider ratifying the Council of Europe Convention on Cybercrime to facilitate a regionally harmonized response

to wildlife trade online and enable more effective access to data required to investigate offenders.

- The eastern African biogeographical region should ensure that they have bio-prospecting policies, as well as bioprospecting policy frameworks to govern the exploitation and commercialization of medicinal plants (Kiraithe *et al.,* 2019). This can help deter any form of commercial over-exploitation targeting medicinal plants with identified direct medicinal uses such as O. lanceolata (Wildlife Direct, 2009).
- The Forest Conservation and Management Acts of the endangered range sites should be strengthened by ensuring that there are no conflicts in the mandates of prosecuting sandalwood trafficking cases.
- Reform in national laws regarding the rights of local communities to participate in the sustainable harvesting and propagation programs and sharing of the benefits accrued from these programs.

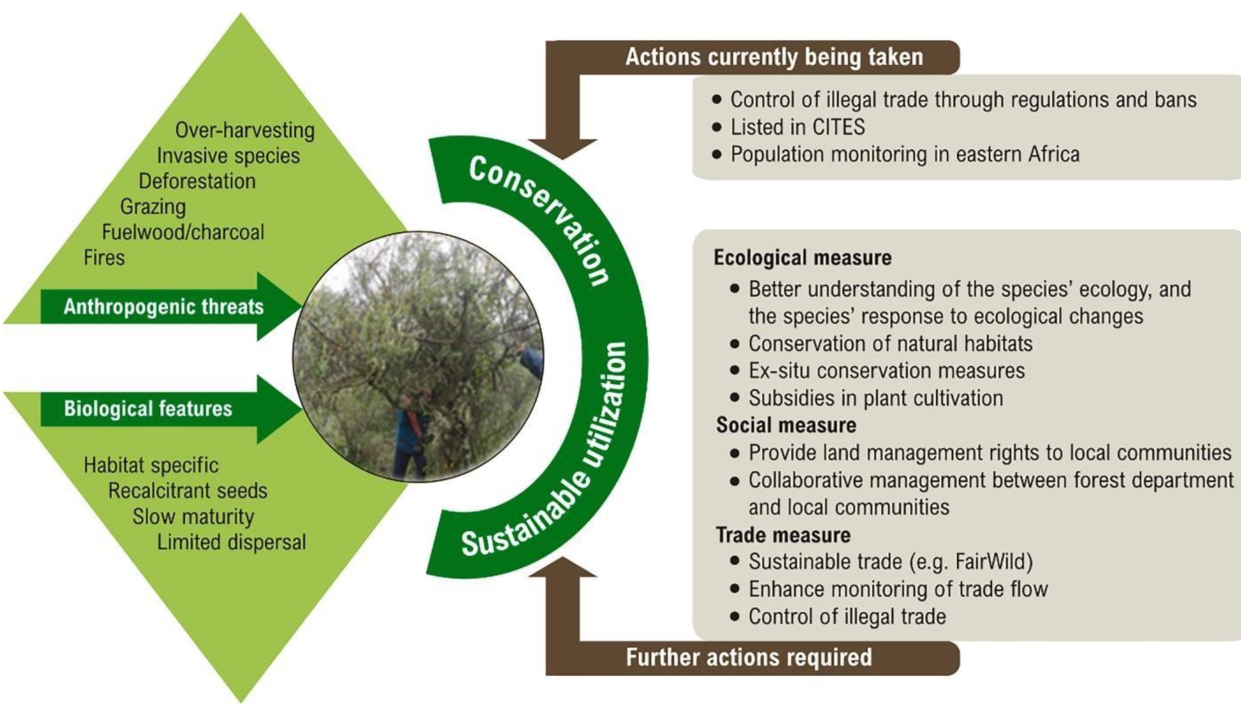

Fig. 4. Schematic diagram outlining the biological features and anthropogenic threats affecting the population of *O. lanceolata*, and the set of actions being taken and needed for the sustainable utilization and conservation of the species.

3. Conclusion

The distribution of *O. lanceolata* is influenced by abiotic factors (such as climate and landscape conditions) and biotic factors (such as hosts, pollination, and dispersal). Anthropogenic pressure, such as over harvesting due to demand from the regional and global market, biological invasions, and other agricultural land use activities were identified as major threats to the species. To date, there has been limited research on the biological and ecological requirements of the plant to inform in-situ and ex-situ conservation measures. It is not known how the plant's distribution and abundance have changed through time. Furthermore, the future distribution and potential adaptability of the plant in response to climate change and continuing anthropogenic threats are unknown. Further research on these areas would be required to help inform the conservation and sustainable management of the plant.

A combination of approaches to conservation can be envisioned to help improve the plant's persistence. These could include enhancing the ability of the plant to regenerate and reducing the anthropogenic pressure. In areas where the plant occurs, coppice management (tending the existing rootstocks or coppices) may be a sensible solution to assist regeneration, as *O. lanceolata* is more of a sprouter than a seeder plant. Various measures can potentially be required to reduce anthropogenic pressures, and these could include tackling the ecological, social, and trade aspects related to the plant. Ecological measures could include a better understanding of the plant's ecology, protection of the natural habitats, and consideration of potential ex-situ conservation activities. Social measures could include the establishment of community-based natural resource management programs whereby local communities can take part as integral players in conservation and monitoring. The occurrence of the plant on public and community lands necessitates participatory management by local communities to assure sustainable utilization and conservation of the species. Trade measures could include enhanced monitoring of trade flow, control of illegal trade, and harmonization of transnational environmental laws among countries, especially in the region where the plant is endangered, to prevent smuggling.

Author Contributions

Literature search, drafting of the manuscript, material preparation, study conceptualization, design, formal analysis and writing the first review draft were performed by Jane Gachambi Mwangi, formal analysis and review editing-Truly Santika. Jeremy Haggar, Salisu Mohammed, Truly Santika and Kabir Mustapha Umar commented on previous versions of the

manuscript, approved the final manuscript and supervised the work.

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CRediT authorship contribution statement

Jane Gachambi Mwangi: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Jeremy Haggar:** Writing – review & editing, Supervision. **Salisu Mohammed:** Writing – review & editing, Supervision. **Truly Santika:** Writing-review & editing, Supervision. **Kabir Mustapha Umar:** Writing – review & editing, Supervision.

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

Data will be made available on request.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2023.126478.

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