Journal of Arid Environments 229 (2025) 105368

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Rapid conservation assessment of *Boswellia sacra* in Oman reveals complex threat and population patterns

Stephen Johnson [a], Ali Bait Said [b], Petr Vahalík [c], Lukáš Karas [d], Maïa Sarrouf Willson [e], Frans Bongers [f,*]

[a] FairSource Botanicals, LLC, 560 Fox Drive #643, Fox Island, WA, 98333, USA
[b] Environment Authority, Ministries Street, Al Khuwair, Sultanate of Oman
[c] Department of Forest Management and Applied Geoinformatics, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 1, 613 00, Brno, Czech Republic
[d] Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 1, 613 00, Brno, Czech Republic
[e] Environment Society of Oman, Ajit Khimji Building No. 1197, Ruwi Street No. 2519, Darsait, Muscat, Sultanate of Oman
[f] Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, the Netherlands

ARTICLE INFO

Keywords:
Frankincense
Burseraceae
Population structure
Non-timber forest products
Arabia

ABSTRACT

Boswellia sacra is an iconic dryland tree in southern Arabia and Somalia. A cultural keystone species, it produces frankincense resin long used for its medicinal and aromatic qualities. Recent research has indicated population declines and unsustainable exploitation of multiple species of *Boswellia*, including the Somalian *B. sacra* populations. However, information on the Arabian populations is minimal and contradictory. Therefore, we conducted a broad-scale rapid assessment of the *B. sacra* populations in the Dhofar mountains of Oman to map the species' range, identify major threats, and predict if the same pattern of population collapse seen in other species is occurring in Oman.

Based on field surveys and distribution mapping, *B. sacra* likely occupies a range of at least 3465 km^2 in Oman. We observed regeneration across almost all populations, with 97 % of transects including at least 10 % small trees or saplings. However, population patterns were variable; both reverse-J shaped and bell-shaped population structures were observed in different locations. Threats identified varied geographically, and included overgrazing, resin overharvesting, mining, insect/pest attacks, and wind/flooding. Grazing pressure was prevalent across many populations, while harvesting pressure was concentrated in specific areas.

We conclude that the data do not currently indicate significant or widespread declines in *B. sacra* in Oman, as seen in other species. Still, given the burgeoning threats, improved socio-ecological management systems are needed to maintain this status. Key priorities include research to elucidate drivers of population patterns, improved rangeland management, enhanced monitoring and management of resin tapping, and identification of potential additional reserves.

1. Introduction

Boswellia sacra Flück. is a small to medium sized deciduous tree that grows in southern Arabia (Oman and Yemen) and Somalia. It is one of approximately 24 species in the genus *Boswellia* Colebr. (Burseraceae: Sapindales), the botanical source of the aromatic terpenoid oleo-gum resin frankincense (Thulin, 2020). Frankincense has been internationally traded as incense and medicine for millennia, and today is used in the modern perfume, cosmetics, and aromatherapy industries, in addition to retaining its role as incense and natural medicine (Hull, 2008; Pickenhagen, 2017; Thulin, 2020; Canney Davison et al., 2022). *Boswellia sacra* is the second most widely traded frankincense species, after *Boswellia papyrifera* Hochst., and is by far the most valuable in financial terms, with a market value potentially up to $1 billion USD annually; global annual international trade in all species of frankincense resin appears to exceed 15 000 tonnes annually and is increasing (Cunningham and DeCarlo, 2022).

Harvesting frankincense inherently entails costs to the tree: resin

* Corresponding author.
E-mail address: frans.bongers@wur.nl (F. Bongers).

https://doi.org/10.1016/j.jaridenv.2025.105368
Received 25 September 2024; Received in revised form 14 February 2025; Accepted 9 March 2025
Available online 12 March 2025

harvesting can act as a significant carbohydrate sink, reduce seed set and annual growth, and can allow greater opportunities for pest attacks (Rijkers et al., 2006; Silpi et al., 2006, 2007; Mengistu et al., 2012, 2013; Negussie et al., 2018). Although produced for millennia, the sustainability of frankincense today is in question. Extensive studies from Ethiopia, Eritrea, and Sudan have indicated a widespread population collapse of *B. papyrifera* due to adult mortality (caused by inappropriate harvesting, insect attacks, and land clearance for agriculture) and blocked regeneration (caused by grazing animals and fire) (Bongers et al., 2019). A similar pattern of blocked regeneration and population collapse has been seen in multiple *Boswellia* species in Socotra, likewise due to grazing and stochastic events such as cyclones (Attore et al., 2011; Lvončík et al., 2020; Maděra et al., 2024). Sustainability concerns have also been noted in *Boswellia serrata* Roxb. ex Colebr. in India due to harvesting and *Lantana camara* Linn. invasion (Soumya et al., 2019).

Despite the significant economic value of *B. sacra*, it has received relatively little attention. Research on the supply chains of *B. sacra* and *B. frereana* Birdw. in Somaliland found widespread concerns about sustainability and inequality from harvesting communities and harvesting practices that frequently exceeded guidelines in traditional knowledge. Furthermore, it found an intensification of harvesting of *B. sacra*, while harvesting of *B. frereana* declined (DeCarlo et al., 2020). However, while the Somalian and Arabian populations of *B. sacra* are considered a single species botanically, the socio-ecological dynamics surrounding frankincense production are distinct, with different regimes of land tenure, governance, legal structures, ecology, and harvesting systems (Farah, 1994, 2008; Ibrahim, 2023). The chemistry of the resins is also somewhat different between the two populations, leading to them being widely considered as separate products by industries using frankincense, and thus experiencing different market pressures (Woolley et al., 2012; Cunningham and DeCarlo, 2022). Consequently, results from studies of one population or one region cannot be readily extrapolated to another, with consequences for diversity of species and region-specific guidelines for sustainability of use and management (Canney Davison et al., 2022; Johnson et al., 2023, 2024).

There is little published information about the status of the Arabian populations of *B. sacra*. In Oman, a study in 2014 estimating tree densities in the Jebel Samhan Nature Reserve indicated potential population declines, believed by locals to be primarily related to incorrect resin tapping and over-tapping (Bait Said et al., 2014); additionally, a tapping study found increased adult mortality at higher tapping intensities (Al-Aamri, 2014), and the latest IUCN Red List assessment (Thulin, 1998) noted high levels of grazing leading to reduced reproduction, a problem also noted by Raffaelli et al. (2003, 2006). The presence of boring beetles that attack the trees (Strumia et al., 2007) and periodic cyclones have been identified as well, which can cause significant mortality in other species of *Boswellia* (DeCarlo et al., 2020; Lvončík et al., 2020; Negussie et al., 2018; Maděra et al., 2024). The species was globally assessed as Near Threatened in 1998 (Thulin, 1998) and nationally assessed in Oman as Near Threatened in 2014 (Patzelt, 2014), although in both cases on the basis of limited field data. There are no studies, to our knowledge, covering the populations in Yemen. *Boswellia sacra* in southern Arabia thus appears to be facing many of the same threats that are driving population declines in other species, although the magnitude and impact of these threats remains unknown.

In order to address this gap and determine if there is evidence for population decline requiring immediate intervention, we conducted a rapid assessment of the conservation status of *B. sacra* in the Dhofar mountains of southern Oman. While *B. sacra* is also known to have an even larger range in Yemen, southern Oman is the center of the frankincense harvesting industry in the Arabian Peninsula and likely the best-preserved population. During this assessment, we aimed to: 1) Map the distribution of *B. sacra* in Oman; 2) Estimate population structure and regeneration in several key populations to assess whether there is evidence for population collapse as seen in other species; and 3) Examine the presence of threats and estimate their prevalence in Oman. Based on these results, we discuss potential management considerations and the need for follow-up studies to further elucidate key dynamics.

2. Methods

2.1. Study site

This study was conducted in the Dhofar mountains in southern Oman, located at approximately 16.7–17.4N, 52.9–55.3E (Fig. S1). The Dhofar mountains consist of three limestone mountain groups, being from the western border of the country, Jebel Qamar (~1500m), Jebel Qara (~900m), and Jebel Samhan (~1850m). Much of Jebel Samhan is protected in the 4500 km^2 Jebel Samhan Nature Reserve (JSNR). The mountains are heavily influenced by the annual Khareef monsoon, from mid-June to mid-September, and receive more than 200 mm of precipitation annually compared to less than 100 mm in the surrounding deserts, although precipitation is highly variable between microsites, may be higher in some areas of the mountains, and can be significantly higher during years with cyclones (Ghazanfar, 1992; Friesen et al., 2018). Precipitation data show high spatial and inter-annual variability, but there may be a general trend of reducing rainfall in Dhofar (Al-Sarmi et al., 2017). Much of this precipitation comes in the form of thick fogs, supporting a seasonal desert cloud forest. The remaining months of the year are largely devoid of precipitation, with temperatures that exceed 30 °C.

2.2. Distribution and threat mapping

Prior to fieldwork, we constructed an initial expected distribution map by collating known locations of *B. sacra* in southern Oman from herbarium records, GBIF (https://www.gbif.org/), expedition reports, scientific papers (e.g., Raffaeli et al., 2006; Farah, 2008; Coppi et al., 2010), and local observations by the team during extensive prior field visits.

We then analyzed the geo- and hydro-morphological characteristics associated with each observation point and used this to predict likely occurrence of *B. sacra* across the Dhofar region as a whole. With a rare few exceptions, the observation points were all located exclusively within wadis in the Dhofar mountains. All spatial analyses were processed using the ArcGIS Pro Ver. 3.1.0. (ESRI) software. Morphological and hydrological characteristics of the Dhofar region were analyzed based on the digital elevation model (DEM) clipped from the ALOS - AW3D model created by Japan Aerospace Exploration Institute (JAXA). The DEM was used for slope steepness determination and hydrological analyses (flow directions, accumulated surface runoff, and stream ordering) to distinguish the location of all wadis in and around the Dhofar mountains. Hydrological analysis identified accumulative surface runoff, and thus the position of all wadis for which the stream ordering was applied to describe the width of canyons. Streams ordered 1 were surrounded with a buffer zone of 100 m, orders 2–5 150 m, stream orders 5–10 250 m, stream orders 10–50 300 m, and stream orders higher than 300 were surrounded with a buffer zone of 400 m. Based on the above-mentioned criterion for confirming the presence of the species, the selected wadis were marked as an area with a predicted occurrence of *B. sacra*. The predicted area of occurrence of *B. sacra* thus includes the unvisited area inside the wadi whose occurrence has been confirmed at their beginning in the upper parts of the Dhofar Mountains, or in their end parts near the northern border of the mentioned mountain range. This generated a predicted distribution map, which we used to identify survey locations and refined using our field data of confirmed species locations.

In February–March 2022, we conducted a field survey of the locations where *B. sacra* was predicted or reported to occur based on our predicted distribution map, previous records, and discussions with locals once in the field. Due to the large predicted area of occurrence and the lack of existing data, we did not have pre-determined transect locations or sample numbers. Instead, we conducted an exploratory assessment with transect locations determined after initial visits to each area. This survey thus does not systematically quantify the population dynamics of the target species, but rather is designed to provide initial detection of significant population collapse or threats as seen in other *Boswellia* species.

We visited locations primarily by 4 × 4 Landcruiser using off-road tracks to access as many locations as possible. During visits we periodically stopped to examine trees up close, and used binoculars, laser rangefinders, and a high-resolution camera to examine trees further away. We also used a boat to examine coastal cliffs around Hasik and the Royal Air Force of Oman kindly provided a helicopter to allow us to access remote areas within the Jebel Samhan Nature Reserve. We conducted two low altitude transect overflights of the entire Jebel Samhan mountain range and landed at three sites within the mountains to assess the trees at ground level. Due to helicopter-based time constraints, we were not able to assess individual trees in the details we needed (see below), leading to exclusion of individual tree evaluations of these three mountain top locations. The Hojary population pressure evaluations were thus mostly based on other locations than the three mountain top locations in the Jebel Samhan Nature Reserve.

We used the ArcGIS Collector app (ESRI) to document locations and tree status data in the field. Data collected were categorized into individual tree points (detailed data on selected individual trees), and group points (data about a broader set of trees in the immediate area to record population structure, harvesting intensity, etc.). Data collected included: (1) number of trees, (2) grazing pressure, (3) resin harvesting pressure, (4) cutting of branches, (5) pest attacks, (6) landslides, (7) wounds to the tree.

Points 2–5 were subjectively scored on a scale of 1–4 (1 = none, 2 = low, 3 = intermediate, 4 = high): Grazing pressure (2): 1 = none (no signs of grazing), 2 = low (only a few branch tips grazed, <25 %), 3 = intermediate (25–75 % of branch tips grazed), 4 = high (>75 % branch tips grazed, some branches and bark ripped-off).

Resin harvesting pressure (3): 1 = none (no signs of tapping), 2 = low (only a few tapping signs on a few stems and branches, <25 %), 3 = intermediate (25–75 % of branches with tapping spots), 4 = high (>75 % branches and stems with tapping spots, severe wounding over large bark areas, clearly exposed wood as a result of deep tapping).

Cutting of branches (4): 1 = none, 2 = low (<25 % of branches cut off), 3 = intermediate (25 %–75 % of branches cut off), 4 = high (>75 % of branches cut off).

Pest attacks (5): 1 = none (no signs of insect pests), 2 = low (only a few insect bore holes, <25 % of the branches/stems affected), 3 = intermediate (25 %–75 % of branches/stems with insect bore holes), 4 = high (>75 % branches/stems with bore holes, several dead branches/stems with bore holes). Wounds to the tree (6): 1 = none (no old tapping wounds), 2 = low (only a few old tapping wounds, <25 % of stems/branches with tapping wounds, sometimes clearly recovering from part tapping), 3 = intermediate (25–75 % of branches/stems with old wounds), 4 = high (>75 % branches/stems with old wounds, wounds large and deep).

Additional data collected at the individual tree level included (8) tree height, (9) number of basal branches, (10) diameter at 30 cm above ground level, and (11) crown surface diameter.

Both the above-mentioned layers (tree points and group points) were shared using the cloud service of ArcGIS Online (ESRI) and uploaded to the mobile app to be ready to use in offline mode. Data were synchronized with the online layer after every single field measurement. Thus, all newly recorded trees were shared with all data collectors continuously. Records of specific trees together with group points were used to evaluate population conditions, threats, and area of occurrence description.

Additionally, we analyzed the data in light of the traditional frankincense resin grading system. In Oman, frankincense resin has traditionally been harvested throughout the Dhofar mountains, and the resin is categorized into four distinct grades, depending on the geographic provenance (Farah, 2008). Thus, the grades relate not just to perceived product quality, but mainly to geographic and ecological criteria. In the traditional system, the "Hojary" frankincense type comes from the plateaus and slopes of the high altitude (>1200m) areas in Jebel Samhan and from mid-level plateaus and sea-oriented wadis at the east part of the Jebel Samhan mountains. Much of the Hojary area is protected by the Jebel Samhan Nature Reserve. The "Nejdi" frankincense type comes from the mid-level plateaus and desert-oriented wadis in the northern part of the Dhofar mountains (Jebel Qara, Qamar and Samhan). The "Shazri" frankincense type comes from the high-altitude plateaus and sea-oriented wadis at the west part of the Dhofar mountains, called Jebel Qara. The "Sha'abi" frankincense type comes from low altitude plains and sea-facing cliffs and wadis around Salalah, more western Mughsail and Fazayah and more eastern Sadah in the southern foothills of the Dhofar Mountains. This traditional classification has significant conservation implications due to the ecological differences in the grade regions, the pressure of resin harvesting (due to the different prices and demand for different grades), and the prominence of this system in local traditional land management (Farah, 2008). Hojary is considered to be the highest quality grade, traditionally, followed by Nejdi, Shazri, and Sha'abi, although evidence for systematic chemical differences is limited (Al-Saidi et al., 2012; Schmiech et al., 2019).

2.3. Regeneration and population structure transects

To assess regeneration, we established 58 transects opportunistically during our survey, in selected locations throughout the distribution of *B. sacra* in Dhofar. Most transects were 10 × 100m, although some were larger or smaller depending on the constraints of the field site (total survey effort: 6.59 ha). All the *B. sacra* trees within these transects were counted and grouped into two classes: large and small. Small trees were defined as less than 1m in height and having branches no larger than 5–6 cm in diameter. Large trees were defined as greater than 1m in height and/or having branches larger than 5–6 cm in diameter.

From these transects, 26 were selected for more detailed data collection and analysis of population structure. The exact locations of the transects were documented using GPS coordinates and photographs to allow re-survey of the transect in the future. For each tree in the detailed transects, we measured tree height, diameter at base (30 cm above the ground), crown diameter, number of basal branches, phenology (presence of seeds, flowers, leaves, etc.), grazing pressure, resin harvesting pressure, presence of branch cutting, presence of pest attacks, condition of the leaves, and presence of any wounds. This allowed us to evaluate the population structure of the trees within these transects, and to more precisely quantify the threats being faced by the population. We conducted 3–6 detailed transects per location/population and averaged the height and basal diameter data across transects at each location.

We constructed population frequency-diameter size graphs in order to visualize population structure. We also conducted Kruskal-Wallis tests to examine whether there were significant differences in harvesting and grazing pressure between locations, with Dunn's test and Holm-Bonferroni corrections for post-hoc comparisons. Pearson's Chi-Squared test was used to test whether insect attack frequency differed between locations. All analyses were conducted in JASP Version 0.19 (JASP Team, 2024).

3. Results

3.1. Distribution of *B. sacra* in Oman

The location of 1987 individual trees were recorded of which 1022 trees were measured and evaluated in terms of their condition and potential threats. The occurrence and quantification of trees were mapped and counted at 710 spots (group points creation).

Boswellia sacra was predicted based on the geo- and hydro-morphological characteristic modeling to occupy a range of at least 3465 km^2 in southern Oman (Fig. 1A). Surveys found the species to be widely distributed in the Jebel Qara, Jebel Qamar, and Jebel Samhan mountains, from sea level up to a maximum recorded elevation of 1,774m ASL. Many areas of predicted occurrence were impossible to visit due to their remoteness, suggesting that the total range of *B. sacra* in Oman is likely substantially larger than directly confirmed.

Based on the traditional descriptions of the grade areas, the Hojary frankincense type is predicted to cover an area of 1142 km^2 in the eastern and southern part of Jebel Samhan, while the Nejdi frankincense type is predicted to cover 2086 km^2 in the northern part of the Dhofar Mountains. The Shazri frankincense type territory is predicted to cover 449 km^2 and the Sha'abi frankincense type is predicted to cover an area of 148 km^2 in the southern foothills of the Dhofar Mountains (Fig. 1B).

3.2. Tree characteristics

Wide variation in all characteristics was observed, with relatively few differences between resin types. Trees in the Sha'abi and Shazri resin type areas were generally shorter, with smaller crowns than those in the Nejdi and Hojary areas. Fewer single-stemmed trees were observed in the Hojary area than in the other three resin types (Fig. S2).

3.3. Major threats

Multiple pressures on *B. sacra* were observed across Dhofar. The most commonly observed threats were intense grazing by ungulates, particularly camels, resin over-harvesting, insect/pest attacks, mining, and floods/wind damage to trees in exposed positions (Table 1). Cutting of branches for livestock was not observed.

Camel grazing was prevalent across much of Dhofar, with the exception of the interior of Jebel Samhan. Two-thirds (66.63%) of trees surveyed were moderately or severely grazed, with the prevalence of intense grazing highest in the Shazri and Sha'abi regions (Fig. 2). Grazing pressure was highest in flat areas and gentle slopes closer to villages and camps, while trees towards the top of steep slopes, on cliffs, and in very remote wadis were more protected. However, camels were observed grazing high on steep slopes when few other browsing opportunities existed in the immediate area. Small seedlings and large mature individual trees were often present on wadi bottoms, with few intermediate stages, indicating hampered regeneration. Some areas, such as Wadi Dowkah and around Raysut and Rabkoot, were heavily browsed with no apparent regeneration.

Resin harvesting was spatially variable, with some populations showing no apparent harvesting and others experiencing significant commercial harvesting. High intensity harvesting was prevalent in the interior of Jebel Samhan (Hojary), although this was not reflected in Fig. 2 as time constraints prevented collecting data on individual trees. High intensity harvesting was also seen around Ayoon and Titam (Nejdi), with modest levels of harvesting observed in other areas such as Fazayah, Wadi Adownib, and Wadi Aful (Sha'abi). In these harvested locations, many trees showed evidence of excessive tapping, with harvesters cutting past the cambium into the wood of the tree. This practice induces scarring and opens the trees to insect attacks. Interestingly, trees in many other areas, such as Sadah, showed old tap marks (indicating harvesting had taken place 2–10 years ago), but no recent harvesting. In most cases, the old harvesting wounds were closed and healing, indicating the ability of the trees to regenerate well if given a chance to rest. However, in many cases only the outer bark had closed the wound, demonstrating that healing completely is a long-term process requiring multiple years of undisturbed regeneration.

Evidence of attacks by boring insects, most likely cerambycid and/or buprestid beetles, was present on trees in most areas, although they most often infested a single branch or trunk rather than the entire tree. No obvious geographic pattern in pest attack intensity was observed, although intensively harvested trees seemed to suffer greater pest attacks.

Mining, primarily for limestone, takes place around Mudam and Titam, heavily affecting the local populations of *B. sacra*. Although the overall percentage of the trees' total range and population affected by mining is small, there is significant negative local impact. Mining activity kills trees in the immediate vicinity and hampers photosynthesis, negatively impacting tree vitality.

Flooding and wind cause tree mortality by uprooting or undermining trees. Trees on exposed cliffs and at the bottoms of wadis are particularly vulnerable to this pressure, which can kill both adult trees and seedlings. Periodic cyclones bring both heavy rains and high winds and are likely to increase in strength and frequency with ongoing climate change (Fig. 3).

Within the detailed transects, the prevalence of insect attacks varied significantly amongst locations (X^2 (5, N = 912) = 36.519, $p < .001$), with the number of affected trees in each location ranging from 2 % to 27 % (Table S1). Resin harvesting (H(5) = 218.436, $p < .001$) and

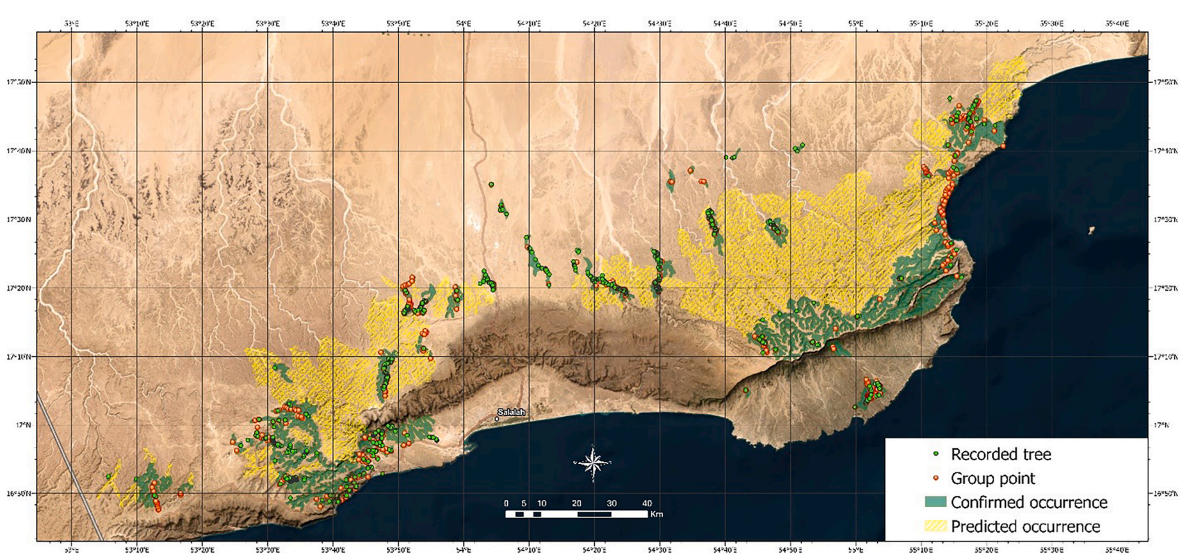

Fig. 1A. Areas predicted by geo- and hydro-morphological characteristic modeling (yellow) and confirmed by observation (green) to contain *B. sacra* in the Dhofar Mountains, southern Oman. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

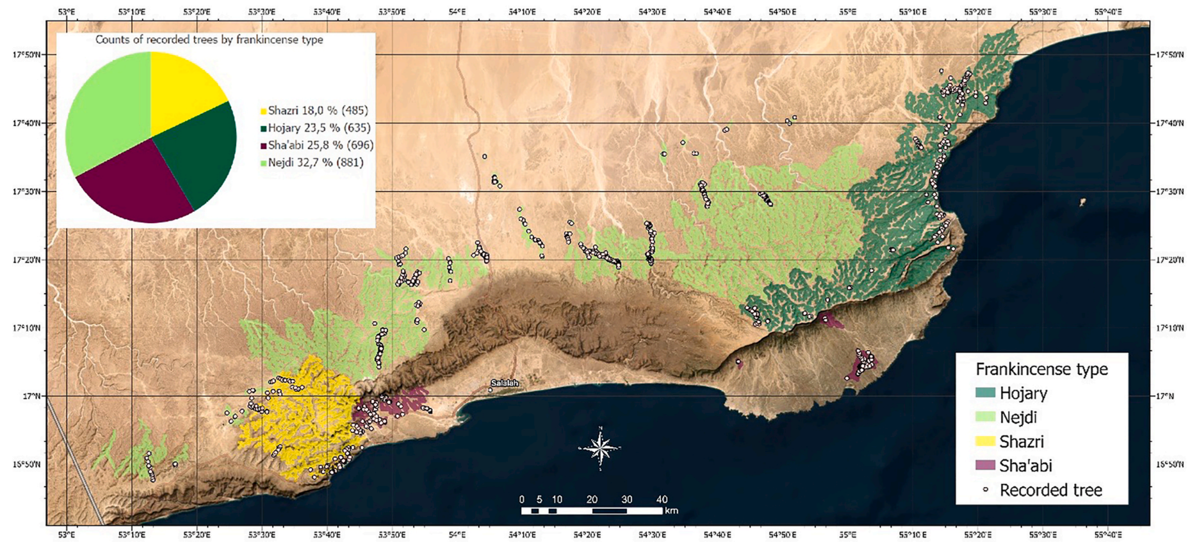

Fig. 1B. Predicted occurrence of the four main commercial resin types: Hojary, Nejdi, Shazri, and Sha'abi.

Table 1
Summary of major threats facing *B. sacra* in southern Oman.

Threat	Key Observed Areas	Risk Factor
Ungulate grazing	Almost all locations except the interior of Jebel Samhan	High intensity grazing damages adults, increasing their vulnerability to pests and environmental stress, and suppresses regeneration
Resin Harvesting	High levels in Jebel Samhan and in wadis around Ayoon and Titam. Reported from Wadi Adownib and Wadi Aful	High intensity harvesting drains carbon reserves, reduces reproduction, increases vulnerability to pests, and can kill the tree over time
Insect/Pest Attacks	Almost all locations, but at low levels	Insect attacks kill branches or individual trunks. High intensity attacks can kill adult trees
Mining	Mudam and Titam	Mining kills adult trees in the mining area and spreads dust which inhibits photosynthesis in the general vicinity
Floods/Wind Damage to Trees	Wadi bottoms and exposed areas across Dhofar	Trees in wadi bottoms are vulnerable to being uprooted by floods; trees in exposed areas can be blown down by high winds like cyclones

grazing ($H(5) = 445.137$, $p < .001$) pressure likewise varied significant across transect locations. Resin harvesting intensity was significantly different across all three transect locations (Sadah, Titam, and Amdat) where it was observed (all $p < .001$). Grazing intensity also varied, with levels relatively high in Sadah, Fazayah, and Adownib; moderate to low in Titam and Amdat; and absent in Hojar. All transect locations were significantly different from each other ($p \leq .03$), with the exception of Sadah and Adownib ($p = .847$), Titam and Amdat ($p = .739$), and Titam and Hojar ($p = .100$).

3.4. Regeneration and population structure

A total of 1924 trees were counted in 58 transects (26 detailed transects and 32 rapid regeneration transects). Of these, 818 (42.5 %) were small trees (Fig. 4A), while 1106 (57.5 %) were larger trees (Fig. 4B). Height consistently increased with greater basal diameter (Fig. 4C). There was a wide variation in the percentage of small trees in each transect (mean = 37.5 %, SD = 20.4 %), indicating a significant degree of variation in regeneration rates between sites (Fig. 4D). All but two transects contained at least one small tree, with almost all transects (97 %) containing at least 10 % small trees. Very few transects (12 %) contained more than 60 % small trees, indicating general predominance of large individuals (Fig. 4D).

Of the six populations studied in greater detail (Table S1, Fig. S3), two (Fazayah and Adownib) revealed reverse-J shaped population curves, with a predominance (57 % and 48 %, respectively) of individuals less than 5 cm basal diameter and fewer than 10 % of individuals exceeding 20 cm in basal diameter. The remaining four populations (Sadah, Amdat, Titam, and Hojar) indicated bell-shaped population curves, with few (<20 % in all cases) individuals smaller than 5 cm basal diameter and a predominance of medium (5–30 cm) individuals. Individuals larger than 30 cm basal diameter were uncommon in all populations, never representing more than 20 % of all individuals (Fig. 5).

4. Discussion

In this study, we used a rapid assessment methodology to map the distribution of *B. sacra* in southern Oman and assess whether significant population decline is likely to be occurring. We documented populations throughout the Dhofar mountains, examined population structure and regeneration across multiple sites, and used field observations to identify key threats. We found that *B. sacra* remains extant and often abundant throughout the Dhofar mountains, although it experiences pressure from multiple threats, including livestock overgrazing, resin overharvesting, land conversion/mining, insects and natural threats like cyclones. Different population structures and regeneration rates were observed across different sites, likely a result of the diversity of environments in which the trees can be found combined with the spatial and temporal dynamism of the threats.

4.1. Distribution and tree characteristics

We found *B. sacra* to be widely distributed in southern Dhofar, with an estimated range of at least 3465 km^2 from sea level up to almost 1800 m. Four major areas are recognized traditionally, which produce the four grades of frankincense resin: Hojary, Nejdi, Shazri, and Sha'abi. These classifications are largely ecologically based, defined by altitude and the orientation of the wadis (sea-facing or desert-facing), which in turn affects levels of precipitation. Using these classifications, both Hojary and Nejdi have wide predicted ranges, over 1000 km^2 and 2000 km^2, respectively, while both Shazri and in particular Sha'abi have

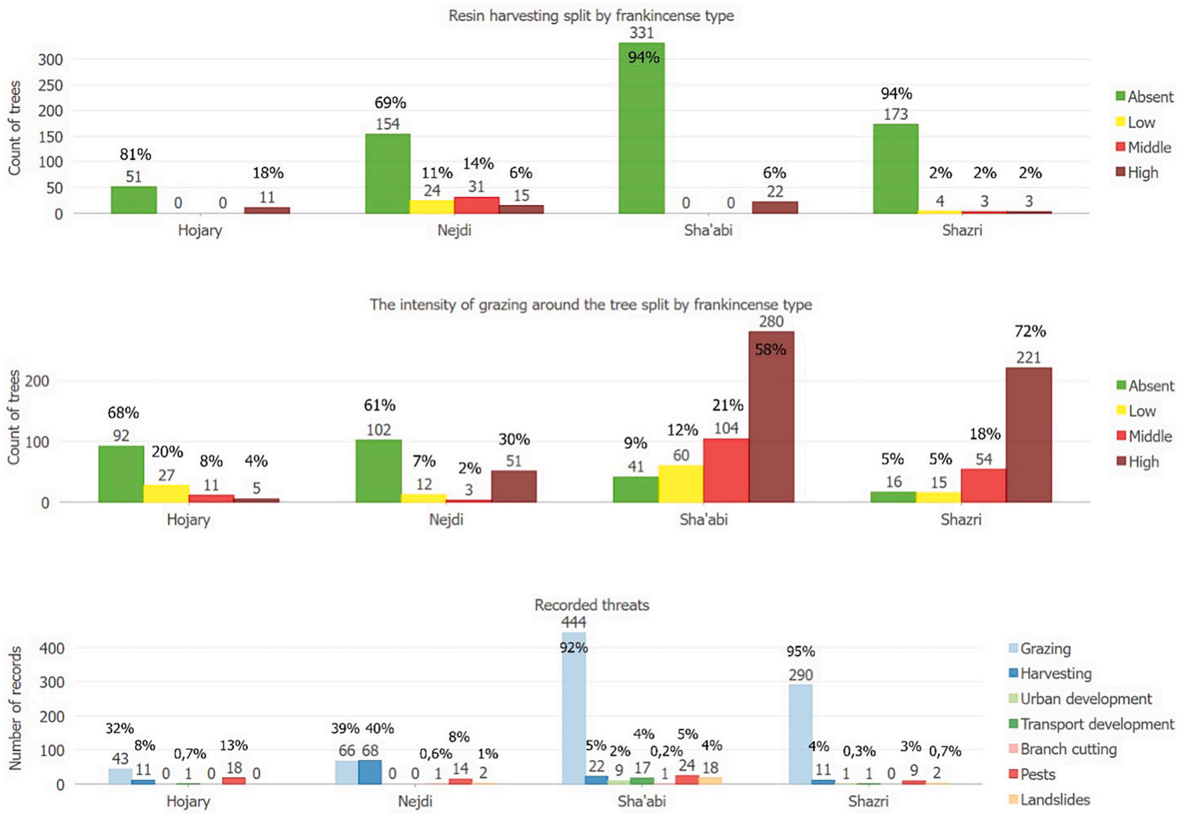

Fig. 2. Pressures on populations of *B. sacra* in major resin regions. A. Resin harvesting B. Grazing, C. All pressures together. The Hojary results are based only on trees in the northern and lower valleys and not on the populations on top of the mountain range, which were heavily tapped, but could not be evaluated in detail due to time constraints (see section 2.2.).

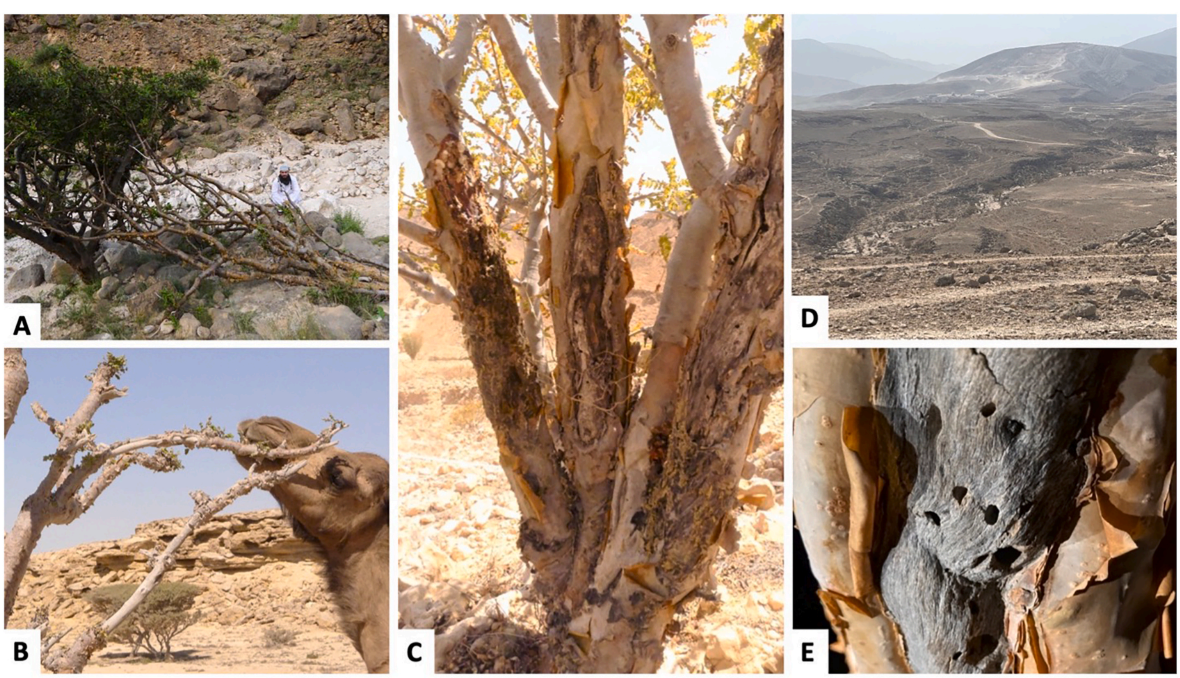

Fig. 3. Major threats to *B. sacra* in southern Oman include mechanical damage from wind and flooding (A); grazing by ungulates, particularly camels (B); improper or intensive resin harvesting (C); mining (D); and attacks by insects (E).

relatively small ranges, less than 450 km^2 and 150 km^2, respectively. Relatively few differences in tree morphology were observed between these areas, although trees in the Shazri and Sha'abi areas tended to be smaller. There are still large areas of predicted occurrence of *B. sacra,* for which we were not able to confirm the species' presence in the current study. A large proportion of this area is extremely remote, with no road

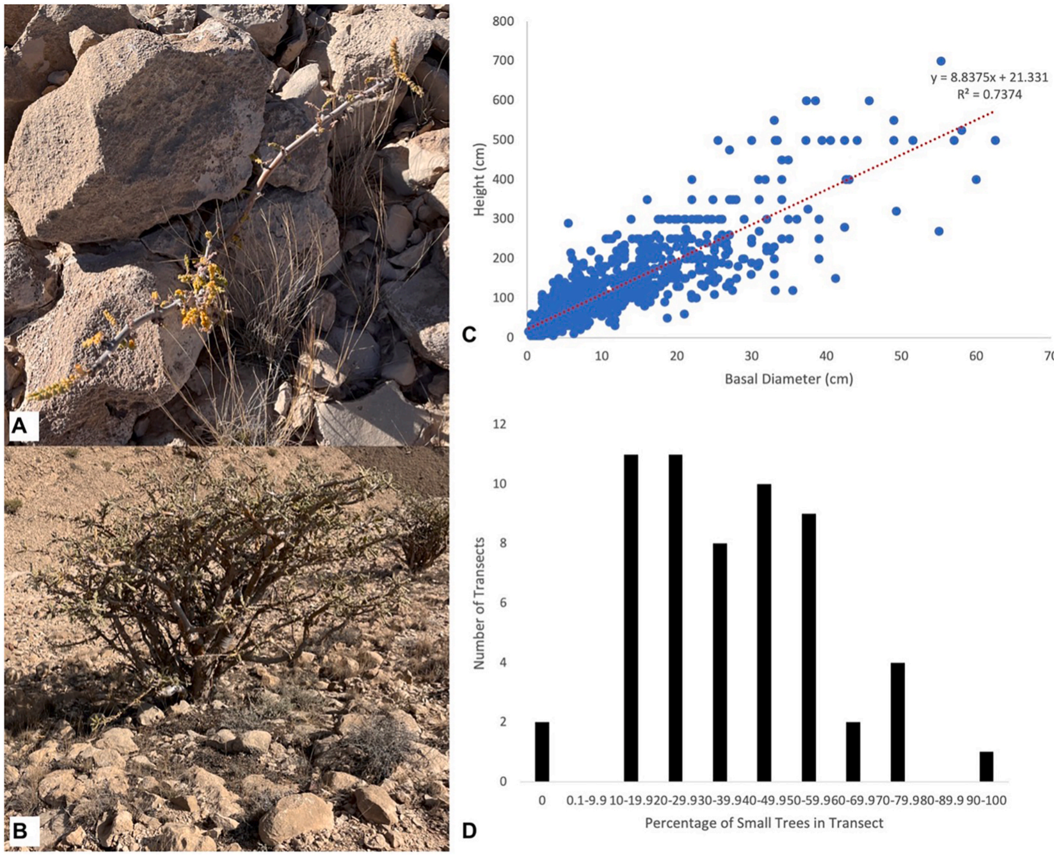

Fig. 4. *Boswellia sacra* tree sizes in the recorded transects. Small trees (A) and large trees (B); height and diameter of *B. sacra* trees (n = 904) (C), and proportion of small vs. large *B. sacra* individuals within transects (mean = 37.5 %, SD = 20.4 %, n = 58 transects) (D).

and thus requiring either extensive multi-day expeditions on foot or use of aircraft to confirm occurrence. While this was beyond the scope of the current study, further investigation should be carried out in order to refine the occurrence map of *B. sacra* in Oman.

4.2. Population status of B. sacra in Oman

Two of the populations measured in detail showed a reverse-J population curve, while four show bell-shaped distributions. Reverse-J curves are generally regarded as indicative of healthy populations (where regeneration is high and there is steady adult mortality over time), while bell-shaped distributions can indicate hampered regeneration as they demonstrate a low proportion of young/small individuals and a predominance of medium size adults (Condit et al., 1998). Bell-shaped distributions are seen in other *Boswellia* species with blocked regeneration (Attorre et al., 2011; Bongers et al., 2019). Reduced regeneration may be possible in *B. sacra*, as many populations experience grazing pressure from camels. Still, bell-shaped populations may still be healthy and expected in long-lived species with an adult persistence strategy; in this case, there is low regeneration year to year, but also low adult mortality, leading to a population composed primarily of medium to large adults, but which is nonetheless stable (Cousins et al., 2014). The observed population structures did not map clearly onto grazing pressure, with both reverse-J populations (Fazayah and Adownib) experiencing significantly higher grazing pressure than in some bell-shaped populations (Titam and Hojar) which experienced very little grazing. This suggests that population structure is being driven by multiple factors, not just grazing, and that *B. sacra* in Oman may not be following the same pattern observed in other *Boswellia* species.

Indeed, regeneration rates varied widely between different sites, with the vast majority of transects containing between 10 and 60 % small (generally young) trees, and transitional saplings present in almost all populations. This contrasts with the pattern seen in *B. papyrifera* and Socotran *Boswellia*, where new seedlings may be abundant, but are prevented from transitioning into saplings and young adult trees by intensive ungulate grazing pressure (Attorre et al., 2011; Bongers et al., 2019; Madĕra et al., 2024). *Boswellia sacra* in Oman is clearly subject to grazing pressure, but it does not appear to be completely blocking populations from regenerating except in some areas near to settlements and on flat, easily accessible terrain. Likewise, although resin harvesting is known to reduce flower and seed production and seed viability (Rijkers et al., 2006), regeneration was nonetheless present even in populations experiencing resin harvesting. Flowering was variable between sites, with coastal areas appearing to have more flowering trees than areas in the interior. Still, most areas visited had at least one flowering tree, suggesting that water availability plays a critical role in promoting reproduction (Hulshof et al., 2012). The 1998 IUCN Red Listing suggested that *B. sacra* rarely flowers or sets seed in Oman due to heavy grazing (Thulin, 1998), but our results indicate that the areas for which this is true are limited.

4.3. Variability of threats

Threats including grazing by camels and other ungulates, harvesting of frankincense resin, mining activity, and insect attacks, were commonly observed across most populations surveyed, in line with previous observations in Oman (Raffaeli et al., 2003; Strumia et al., 2007; Farah, 2008; Al-Aamri, 2014), and threats observed in other species (Attorre et al., 2011; Bongers et al., 2019; DeCarlo et al., 2020). Community informants supported our field observations with the same threat identifications and identified the impact of cyclones as a

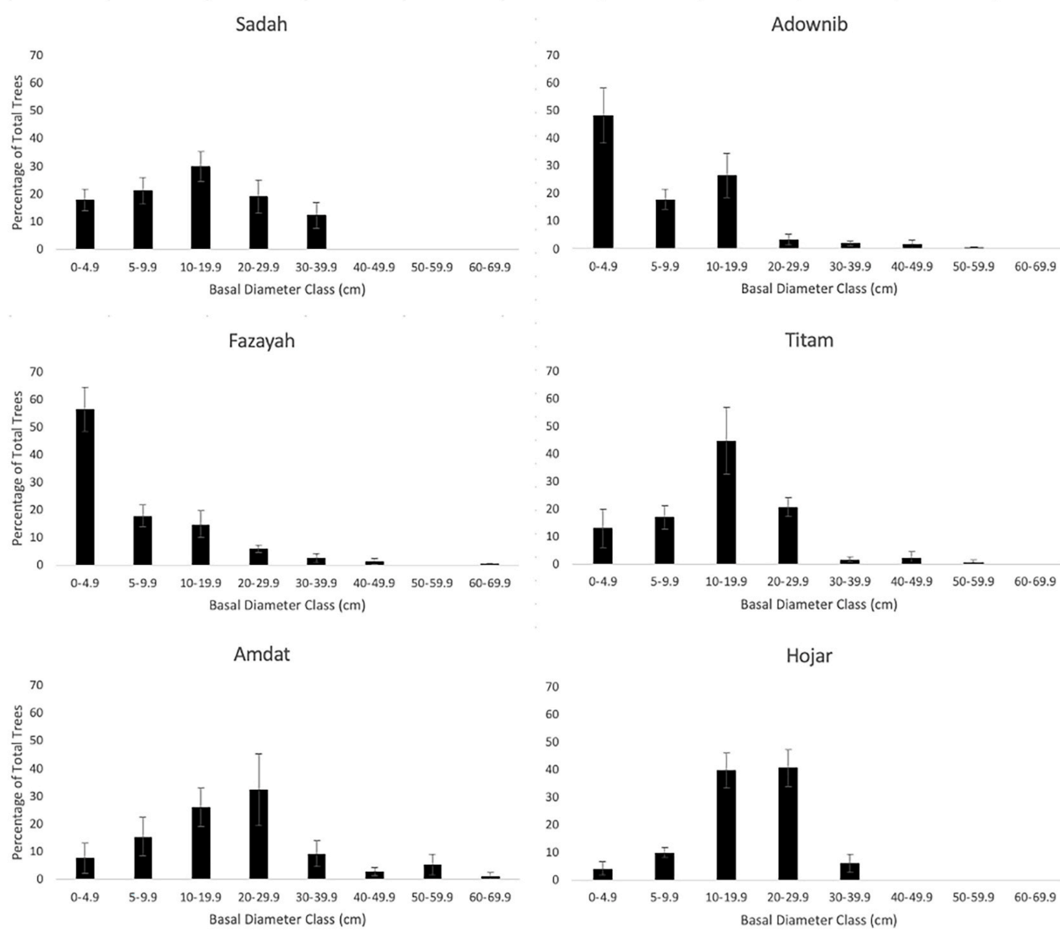

Fig. 5. Population structure of *B. sacra* across six populations in Dhofar (mean ± SE, n = 3–6 transects per location; total number of transects is 26, total number of trees is 912).

significant factor as well.

A key finding was the multi-scale spatial variability in the impact of these threats. Frankincense resin harvesting was concentrated in specific populations, particularly in Jebel Samhan, where harvesting intensities were relatively high. We observed little to no harvesting pressure in many populations, even populations close to human settlements or roads, suggesting that resin harvesting is not a pervasive pressure on the trees in Oman like it is in Somalia (DeCarlo et al., 2020). However, these observations are biased by the legal pressure on harvesters. Most resin harvesters are undocumented workers from Somalia who as a result prefer to select remote and difficult access sites (Farah, 2008), potentially leading to an under-estimate of the extent of harvesting in this survey. Although many people interviewed claimed that sustainable tapping methods were commonly used, we observed a significant proportion of aggressively tapped trees, often with wounds cutting too deeply. The undocumented status of most harvesters likely contributes to this pattern of harvesting, as the uncertainty of potential deportation degrades harvester land tenure security and may encourage shorter-term, more aggressive exploitation strategies (Kusters et al., 2006; Varghese and Ticktin, 2008; Ostrom, 2009; Hernández-Barrios et al., 2015). While there is not sufficient evidence currently to indicate that improper harvesting is driving a population decline, it is certainly a stress factor and can cause increased mortality long-term (Torquebiau, 1984; Varghese and Ticktin, 2008; Al-Aamri, 2014; Cherenet et al., 2020; Daracan et al., 2020). Several sites also contained trees with no evidence of current harvesting, but with old healing harvesting taps that indicated significant harvesting activity in the last few years. This highlights both the dynamic nature of harvesting pressure as a threat, and the potential for heavily harvested populations to recover if allowed to rest.

Likewise, grazing pressure largely follows a seasonal gradient as grazing livestock are moved throughout the year. During the post-Khareef season of relative vegetative abundance (September–January), livestock are moved around the escarpments and largely sustained on natural vegetation (Ball and Tzanopoulos, 2020). During the dry season and during the Khareef itself, however, livestock are kept closer to camps and villages and are often sustained on purchased feed, as well as more intensive grazing of the available natural vegetation in these areas. On a finer scale, grazing pressure concentrates on easier to access trees, such as those on flat areas, on gentle slopes, or towards the bottom of slopes. Trees higher up on steep slopes and in cliff areas experienced lower grazing pressure; as a result, these areas can act as a natural refuge. The topography of the Dhofar mountains creates steep slopes virtually throughout the range of *B. sacra*, so these refugia are largely continuously available throughout its range. Livestock populations have increased significantly in Dhofar over the recent past, with populations of goats, camels, and cattle increasing by 96 %, 170 %, and 257 %, respectively, from 1982 to 2012, and this greatly intensified grazing pressure has had broad scale impacts on native ecosystems (Ball and Tzanopoulos, 2020; Spalton, 2020). Pastoralists are well aware of the ecologically detrimental impacts of overgrazing, particularly by camels, but there is strong sociocultural pressure to maintain herds. Livestock herds also act as a reserve source of value, if families experience unexpected expenses and need to raise capital quickly. This is a common pattern seen in other multi-use ecosystems, such as frankincense-producing areas of Ethiopia, with the economic and cultural value making change difficult (Lemenih et al., 2007; Woldeamanuel, 2011). As a result, while increasing production costs and changing values have put some pressure on this pastoral system, significant decline in stocking rates is unlikely in the near future (Ball et al., 2020). This persistent and likely increasing grazing pressure will have predictable consequences for the *B. sacra* populations in Oman, driving a reduction in the total population and possible extirpation of the species from flat/accessible areas near settlements and migration routes.

4.4. Overall conservation status

While the study revealed key threats affected wild *B. sacra* populations in Dhofar, and in some cases threatening local extirpation of specific populations, we do not see evidence for the same pattern of broad-scale population decline as described in other species (Bongers et al., 2019). While there is not sufficient data to assess the global status of *B. sacra*, a regional classification of Near Threatened may be appropriate considering the total extent of occurrence and the likely declines seen in areas heavily impacted by humans, together with the widespread broader impacts of grazing, cyclones, and resin harvesting. The Oman government, together with the NGO Environment Society of Oman, is currently updating the Red List status assessment for *B. sacra*. Still, the areas experiencing likely declines appear to represent only a small percentage of the overall population in Dhofar, and even populations with moderate to high levels of grazing appeared to be regenerating. Consequently, we don't see a threat of significant population declines in the near future. However, it is important to note that these findings only apply to Oman, an area that is well-known for frankincense but represents only part of the overall range of *B. sacra*. The species is also known from a large area of eastern Yemen, where it may be experiencing different pressures and population patterns; further research on the Yemeni populations is needed. Oman has the distinction of being the only range state of *B. sacra* with strong central governance and no ongoing violence conflicts, and thus represents a critical opportunity to implement effective conservation programs that may be stymied in other range states.

4.5. Conclusions and management implications

The lack of broad-scale decline and relative population health seen in this study is a welcome contrast to the findings in several other congeners. However, it is important to note that this study represents an initial evaluation of the ecological status of *B. sacra* in southern Oman, rather than a comprehensive population viability analysis. The data suggest considerable heterogeneity in the pressures and drivers of regeneration rates and population structures, necessitating further research to elucidate the drivers of these population patterns. Major threats identified, such as intense grazing and resin over-harvesting, are likely to accelerate and broaden in impact, as both grazing animal populations and the international market for frankincense products continue to expand (Ball et al., 2020; Cunningham and DeCarlo, 2022). Tackling these challenges will require both further investigation into the socio-economic drivers of pastoralism and harvesting management, as well as developing more sophisticated management systems for multi-use rangelands, likely with government support. Enhanced government monitoring and permitting of resin harvests, along with temporary work permits for skilled migrant harvesters, could help reinforce appropriate harvesting practices and limit collection to sustainable levels. This would also allow certification of genuine Omani frankincense resin to enhance the value of production, as the mixture of Omani-origin, Yemeni-origin, and Somali-origin frankincense resins has been frequently noted as a concern by informants. Given the range size and remoteness of much of the *B. sacra* total population in southern Oman, it may be most efficient to concentrate enhanced management efforts on specific, high-value populations in new and existing reserves. Most of Jebel Samhan is already a protected reserve, but additional populations in Jebel Qara or Jebel Qamar could be protected through new reserves; this would also help preserve the full range of genetic diversity identified in *B. sacra* in Oman (Coppi et al., 2010; Akbar et al., 2019). Additionally, we observed a relatively high level of resin harvesting within the Jebel Samhan Nature Reserve, along with grazing pressure in more accessible populations within the reserve. This highlights the importance of developing a management plan for the reserve, and of sharpening enforcement of reserve boundaries to ensure that the trees within these boundaries are protected from human threats. While we do not see evidence of broad-scale decline at this time, the burgeoning pressures observed, particularly grazing and resin harvesting, along with the impacts of climate change-intensified extreme weather events, emphasize the importance of developing enhanced socio-ecological management systems to protect this iconic species into the future. Long-term monitoring plots should be established to better understand the diverse regeneration patterns observed and to detect any population declines in the future. Well-developed guidelines for resin harvesting and sustainable tree and rangeland management are already available. However, effective implementation of these guidelines, with incentives for sustainable behavior and strong monitoring to ensure compliance, will need to be a priority going forward.

CRediT authorship contribution statement

Stephen Johnson: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Ali Bait Said:** Writing – review & editing, Methodology, Investigation. **Petr Vahalík:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Lukáš Karas:** Visualization, Validation, Formal analysis. **Maïa Sarrouf Willson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Frans Bongers:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Funding

Funding was provided by a grant agreement from the British Foreign, Commonwealth & Development Office, signed in January 2022 between HE Ambassador Bill Murray (former ambassador to Oman) and HH Sayyida Tania Al Said (former ESO president).

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Stephen Johnson reports a relationship with FairSource Botanicals that includes: equity or stocks. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This project was carried out by the Environment Society of Oman, with funding from the British Foreign, Commonwealth & Development Office (FCDO). The team would like to thank Ms. Anushka Weragama and Ms. Samia Younis from the FCDO for their continuous support and follow-up on project updates. From the Environment Society of Oman, the team would like to thank Mr. Bashar Zeitoon for his involvement in overall project coordination, and Ms. Rabab Al Lawati and Mr. Ali Al Rasbi for support in engaging local community members and understanding their perceptions. The team would also like thank all ESO board members, and all staff from the Environment Authority in both Muscat and Dhofar for their overall project support. All surveys were conducted under permits from the Environment Authority No. 6210/11/23 and No. M202280 (Jabal Samhan Nature Reserve). Field surveys were carried out with the support of rangers from the Environment Authority and the Jebel Samhan Nature Reserve. Approval for ESO to receive external funding was obtained by the Ministry of Social Development (Letter No. 222404224, January 17, 2022).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2025.105368.

Data availability

Data will be made available on request.

References

Akbar, F., Khan, A., Gilani, S., Al-Harrasi, A., Al-Sadi, A., Shinwari, Z., 2019. Genetic differentiation in different endemic Boswellia sacra (Burseraceae) populations from Oman. Pakistan J. Bot. 51 (18). https://doi.org/10.30848/PJB2019-1.

Al-Aamri, M., 2014. Sustainable Harvesting of Frankincense Trees in Oman. LAP Lambert Academic Publishing.

Al-Saidi, S., Rameshkumar, K.B., Hisham, A., Sivakumar, N., Al-Kindy, S., 2012. Composition and antibacterial activity of the essential oils of four commercial grades of Omani luban, the oleo-gum resin of Boswellia sacra FLUECK. Chem. Biodivers. 9 (3), 615–624. https://doi.org/10.1002/cbdv.201100189.

Al-Sarmi, S., Al-Yahyai, S., Al-Maskari, J., Charabi, Y., Choudri, B.S., 2017. Recent Observed Climate Change over Oman, pp. 89–100. https://doi.org/10.1007/978-3-319-51856-5_6.

Attorre, F., Taleb, N., Sanctis, M.D., Farcomeni, A., Guillet, A., Vitale, M., 2011. Developing conservation strategies for endemic tree species when faced with time and data constraints: Boswellia spp. on Socotra (Yemen). Biodivers. Conserv. 20 (7), 1483–1499. https://doi.org/10.1007/s10531-011-0039-7.

Bait Said, A.S.M., Abahussain, A.A., Abido, M.S., Mohammad, H.A., 2014. Integrated environmental assessment of frankincense tree associations in the jabel samhan reserve of the sultanate of Oman. Scientific Journal of King Faisal University (Basic and Applied Sciences) 15 (1).

Ball, L., MacMillan, D., Tzanopoulos, J., Spalton, A., Al Hikmani, H., Moritz, M., 2020. Contemporary pastoralism in the dhofar mountains of Oman. Hum. Ecol. 48 (3), 267–277. https://doi.org/10.1007/s10745-020-00153-5.

Ball, L., Tzanopoulos, J., 2020. Livestock browsing affects the species composition and structure of cloud forest in the Dhofar Mountains of Oman. Appl. Veg. Sci. 23 (3), 363–376. https://doi.org/10.1111/avsc.12493.

Bongers, F., Groenendijk, P., Bekele, T., Birhane, E., Damtew, A., Decuyper, M., Eshete, A., Gezahgne, A., Girma, A., Khamis, M.A., Lemenih, M., Mengistu, T., Ogbazghi, W., Sass-Klaassen, U., Tadesse, W., Teshome, M., Tolera, M., Sterck, F.J., Zuidema, P.A., 2019. Frankincense in peril. Nat. Sustain. 2 (7), 602–610. https://doi.org/10.1038/s41893-019-0322-2.

Canney Davison, S., Bongers, F., Phillips, D., 2022. The future of frankincense: understanding the plant's diversity is key to its conservation. HerbalGram 133, 40–59. https://www.herbalgram.org/media/17303/hg133-frankincense.pdf.

Cherenet, E., Abiyu, A., Getnet, A., Sisay, K., Dejene, T., 2020. Tapping height and season affect frankincense yield and wound recovery of Boswellia papyrifera trees. J. Arid Environ. 179, 104176. https://doi.org/10.1016/j.jaridenv.2020.104176.

Condit, R., Sukumar, R., Hubbell, S.P., Foster, R.B., 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. Am. Nat. 152 (4), 495–509. https://doi.org/10.1086/286186.

Coppi, A., Cecchi, L., Selvi, F., Raffaelli, M., 2010. The Frankincense tree (Boswellia sacra, Burseraceae) from Oman: ITS and ISSR analyses of genetic diversity and implications for conservation. Genet. Resour. Crop Evol. 57 (7), 1041–1052. https://doi.org/10.1007/s10722-010-9546-8.

Cousins, S.R., Witkowski, E.T.F., Pfab, M.F., 2014. Elucidating patterns in the population size structure and density of Aloe plicatilis, a tree aloe endemic to the Cape fynbos, South Africa. South Afr. J. Bot. 90, 20–36. https://doi.org/10.1016/j.sajb.2013.09.012.

Cunningham, A.B., DeCarlo, A., 2022. Boswellia species in international trade: identification, supply chains, & practical management considerations (Information Document CoP19 Inf. 10. Convention on International Trade in Endangered Species of Wild Fauna and Flora, p. 203. https://cites.org/eng/node/133556.

Daracan, V., Mendoza, R., Torres, A., Jara, A., Manalo, R., Batallones, C.H., Razal, R., 2020. Comparison of Agathis philippinensis resin tapping and collection practices in three selected sites in the Philippines. Biodiversitas Journal of Biological Diversity 21 (12). https://doi.org/10.13057/biodiv/d211204. Article 12.

DeCarlo, A., Ali, S., Ceroni, M., 2020. Ecological and economic sustainability of non-timber forest products in post-conflict recovery: a case study of the frankincense (Boswellia spp.) resin harvesting in Somaliland (Somalia). Sustainability 12 (9). https://doi.org/10.3390/su12093578. Article 9.

Farah, A.Y., 1994. Milk of the Boswellia forests: frankincense production among the pastoral Somali. In: af Ornas, T.H. (Ed.), Environmental Policy and Society.

Farah, M., 2008. Non-Timber Forest Product (NTFP) Extraction in Arid Environments: Land-Use Change, Frankincense Production and the Sustainability of Boswellia Sacra in Dhofar (Oman). University of Arizona [PhD Dissertation]. http://arizona.openrepository.com/arizona/handle/10150/195762.

Friesen, J., Zink, M., Bawain, A., Müller, T., 2018. Hydrometeorology of the Dhofar cloud forest and its implications for groundwater recharge. J. Hydrol.: Reg. Stud. 16, 54–66. https://doi.org/10.1016/j.ejrh.2018.03.002.

Ghazanfar, S.A., 1992. Quantitative and biogeographic analysis of the flora of the sultanate of Oman. Global Ecol. Biogeogr. Lett. 2 (6), 189–195. https://doi.org/10.2307/2997660.

Hernández-Barrios, J.C., Anten, N.P.R., Martínez-Ramos, M., 2015. Sustainable harvesting of non-timber forest products based on ecological and economic criteria. J. Appl. Ecol. 52 (2), 389–401. https://doi.org/10.1111/1365-2664.12384.

Hulshof, C.M., Stegen, J.C., Swenson, N.G., Enquist, C.A.F., Enquist, B.J., 2012. Interannual variability of growth and reproduction in: the role of allometry and resource variability. Ecology 93 (1), 180–190. https://doi.org/10.1890/11-0740.1.

Hull, B.Z., 2008. Frankincense, myrrh, and spices: the oldest global supply chain? J. Macromarketing 28 (3), 275–288. https://doi.org/10.1177/0276146708320446.

Ibrahim, A.A., 2023. Local knowledge and attitudes of frankincense communities in northeastern Somalia. Global Ecology and Conservation 48, e02748. https://doi.org/10.1016/j.gecco.2023.e02748.

JASP Team, 2024. JASP (version 0.19). https://jasp-stats.org/.

Johnson, S., Davison, S.C., Ablard, K., Bongers, F., Cunningham, A.B., DeCarlo, A., Van Wyk, B.-E., 2024. Good intentions meet complex realities: CITES listing of diverse frankincense (*Boswellia* species) might do more harm than good. For. Pol. Econ. 163, 103207. https://doi.org/10.1016/j.forpol.2024.103207.

Johnson, S., DeCarlo, A., Bongers, F., Cunningham, A.B., 2023. To list or not to list: governance challenges and complexities in global frankincense supply chains. In: Cordonier Segger, M.-C., Wardell, D.A., Harrington, A. (Eds.), CITES for Sustainable Development. Cambridge University Press. https://www.cambridge.org/core/books/cites-as-a-tool-for-sustainable-development/22CDF8213CA9509172A6FD67AC17050C.

Kusters, K., Achdiawan, R., Belcher, B., Pérez, M.R., 2006. Balancing development and conservation? An assessment of livelihood and environmental outcomes of nontimber forest product trade in asia, africa, and Latin America. Ecol. Soc. 11 (2). https://www.jstor.org/stable/26266010.

Lemenih, M., Feleke, S., Tadesse, W., 2007. Constraints to smallholders production of frankincense in Metema district, North-western Ethiopia. J. Arid Environ. 71 (4), 393–403. https://doi.org/10.1016/j.jaridenv.2007.04.006.

Lvončík, S., Vahalík, P., Bongers, F., Peijnenburg, J., Hušková, K., van Rensburg, J.J., Hamdiah, S., Maděra, P., 2020. Development of a population of Boswellia elongata Balf. F. in Homhil nature sanctuary, Socotra island (Yemen). Rendiconti Lincei. Sci. Fis. Nat. 31 (3), 747–759. https://doi.org/10.1007/s12210-020-00936-4.

Maděra, P., Vahalík, P., Hamdiah, S., Hušková, K., Sekava, J., Attorre, F., La Montagna, D., De Sanctis, M., Netek, R., Bongers, F., Rivers, M., Šebesta, J., Amar, M., Keybani, S., Shanayeghen, M., Van Damme, K., 2024. Distribution, ecology, and threats assessment of 11 endemic frankincense tree taxa (Boswellia) in the Socotra Archipelago (Yemen). PLANTS, PEOPLE, PLANET. https://doi.org/10.1002/ppp3.10563.

Mengistu, T., Sterck, F.J., Anten, N.P.R., Bongers, F., 2012. Frankincense tapping reduced photosynthetic carbon gain in Boswellia papyrifera (Burseraceae) trees. For. Ecol. Manag. 278 (Suppl. C), 1–8. https://doi.org/10.1016/j.foreco.2012.04.029.

Mengistu, T., Sterck, F.J., Fetene, M., Bongers, F., 2013. Frankincense tapping reduces the carbohydrate storage of Boswellia trees. Tree Physiol. 33 (6), 601–608. https://doi.org/10.1093/treephys/tpt035.

Negussie, A., Gebrehiwot, K., Yohannes, M., Aynekulu, E., Manjur, B., Norgrove, L., 2018. An exploratory survey of long horn beetle damage on the dryland flagship tree species Boswellia papyrifera (Del.) Hochst. J. Arid Environ. 152, 6–11. https://doi.org/10.1016/j.jaridenv.2018.01.011.

Ostrom, E., 2009. A general framework for analyzing sustainability of social-ecological systems. Science 325 (5939), 419–422. https://doi.org/10.1126/science.1172133.

Patzelt, A., 2014. Oman Plant Red Data Book. Oman Botanic Gardens.

Pickenhagen, W., 2017. History of odor and odorants. In: Springer Handbook of Odor. Springer, Cham, pp. 5–6. https://doi.org/10.1007/978-3-319-26932-0_1.

Raffaelli, M., Mosti, S., Tardelli, M., 2003. The frankincense tree (Boswellia sacra flueck., burseraceae) in dhofar, southern Oman: field-investigations on the natural populations. Webbia 58 (1), 133–149. https://doi.org/10.1080/00837792.2003.10670749.

Raffaelli, M., Mosti, S., Tardelli, M., 2006. Boswellia sacra flueck. (Burseraceae) in the Hasik area (eastern dhofar, Oman) and a list of the surrounding flora. Webbia 61 (2), 245–251. https://doi.org/10.1080/00837792.2006.10670804.

Rijkers, T., Ogbazghi, W., Wessel, M., Bongers, F., 2006. The effect of tapping for frankincense on sexual reproduction in Boswellia papyrifera. J. Appl. Ecol. 43 (6), 1188–1195. https://doi.org/10.1111/j.1365-2664.2006.01215.x.

Schmiech, M., Lang, S.J., Werner, K., Rashan, L.J., Syrovets, T., Simmet, T., 2019. Comparative analysis of pentacyclic triterpenic acid compositions in oleogum resins of different Boswellia species and their in vitro cytotoxicity against treatment-resistant human breast cancer cells. Molecules 24 (11). https://doi.org/10.3390/molecules24112153.

Silpi, U., Lacointe, A., Kasempsap, P., Thanysawanyangkura, S., Chantuma, P., Gohet, E., Musigamart, N., Clément, A., Améglio, T., Thaler, P., 2007. Carbohydrate reserves as a competing sink: evidence from tapping rubber trees. Tree Physiol. 27 (6), 881–889. https://doi.org/10.1093/treephys/27.6.881.

Silpi, U., Thaler, P., Kasemsap, P., Lacointe, A., Chantuma, A., Adam, B., Gohet, E., Thaniswanyankura, S., Améglio, T., 2006. Effect of tapping activity on the dynamics of radial growth of Hevea brasiliensis trees. Tree Physiol. 26 (12), 1579–1587. https://doi.org/10.1093/treephys/26.12.1579.

Soumya, K.V., Shackleton, C.M., Setty, S.R., 2019. Impacts of gum-resin harvest and Lantana camara invasion on the population structure and dynamics of Boswellia serrata in the Western Ghats, India. For. Ecol. Manag. 453, 117618. https://doi.org/10.1016/j.foreco.2019.117618.

Spalton, A., 2020. Agriculture [jabal Al Qara]. In: Al Zubair, M., Mershen, B., Al Saqri, S., Al Ghafri, A., Al Hosni, T., Al Nabhani, Y., Al Rajhi, A., Nasir, S., Patzelt, A., Spalton, A., Anderson, A. (Eds.), The Mountains of Oman. Georg Olms AG.

Strumia, F., Dapporto, L., Dellacasa, M., Scaramozzino, P.L., 2007. Notes on some insects associated to frankincense tree (Boswellia sacra Flückiger, 1867, Burseraceae) in Dhofar (Sultanate of Oman). Atti Soc. Tosc. Sci. Nat., Mem., Serie B 114, 135–139.

Thulin, M., 1998. Boswellia Sacra. The IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T34533A9874201.en, 1998.

Thulin, M., 2020. The genus Boswellia (burseraceae): the frankincense trees. Acta Univ. Upsal. http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-405908.

Torquebiau, E., 1984. Man-made dipterocarp forest in Sumatra. Agrofor. Syst. 2 (2), 103–127. https://doi.org/10.1007/BF00131269.

Varghese, A., Ticktin, T., 2008. Regional variation in non-timber forest product harvest strategies, trade, and ecological impacts: the case of black dammar (canarium strictum Roxb.) use and conservation in the nilgiri biosphere reserve, India. Ecol. Soc. 13 (2). https://doi.org/10.5751/ES-02555-130211.

Woldeamanuel, T., 2011. Dryland Resources, Livelihoods and Institutions. Diversity and Dynamics in Use and Management of Gum and Resin Trees in Ethiopia. Wageningen University [PhD Thesis].

Woolley, C.L., Suhail, M.M., Smith, B.L., Boren, K.E., Taylor, L.C., Schreuder, M.F., Chai, J.K., Casabianca, H., Haq, S., Lin, H.-K., Al-Shahri, A.A., Al-Hatmi, S., Young, D.G., 2012. Chemical differentiation of Boswellia sacra and Boswellia carterii essential oils by gas chromatography and chiral gas chromatography–mass spectrometry. J. Chromatogr. A 1261, 158–163. https://doi.org/10.1016/j.chroma.2012.06.073.