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Development of a population of *Boswellia elongata* Balf. F. in Homhil nature sanctuary, Socotra island (Yemen)

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Abstract

We assessed seven decades of change in the largest known population of the endangered endemic *Boswellia elongata* Balf. F. (Burseraceae) on Socotra Island (Yemen). To quantify the population change we evaluated tree number and locations on digitized images from various sources in the period 1956–2017 and combined this with direct field measurements of the population between 2011 and 2017. Our study reveals that the Homhil Nature Sanctuary *B. elongata* population shows a continuous decline since 1956. The steady but slow natural decline was strongly accelerated by two catastrophic cyclones in November 2015, when 38% of the trees were directly destroyed by strong winds. During the following 2 years 29% of the remaining trees died additionally. The remaining population has a bell-shaped size distribution; most trees are around 40 cm in diameter (range 18 to 70 cm). Tree ring analysis of 11 dead trees with a diameter of 29 to 44 cm without bark, resulted in estimated tree ages between 80 and 101 years. We estimate that similar-sized trees showing strong signs of senescence have a maximum age of a little over 100 years. The age structure of the Homhil population is, therefore, unbalanced with large sized trees prevailing. Natural regeneration is absent for decades. Viable seeds are available and have been shown to germinate, but the development of seedlings into saplings is a bottleneck. If the decline continues at the current rate, only 30 trees will remain there in 2036. Protection, planting and awareness activities are needed to keep this unique frankincense tree in Homhil Nature Sanctuary.

Keywords Socotra · *Boswellia elongata* · Population · Age structure · Regeneration

1 Introduction

The genus *Boswellia* (Burseraceae) is world famous because of the iconic frankincense it delivers to society. The genus is composed of species of which several are under threat of extinction and are included in the list of globally endangered tree species (IUCN 2020). Many current populations are under threat due to land conversion towards agricultural use and grazing (Ogbazghi 2001; Gebrehiwot et al. 2003; Ogbazghi et al. 2006; Eshete et al. 2012), over-harvesting (Mengistu et al. 2012; Groenendijk et al. 2012; Maděra et al. 2017) and fire (Ogbazghi 2001; Bongers and Tennigkeit 2010), among other factors such as mining (Farah 2008). For *B. papyrifera* and *B. serrata* threats have been extensively documented (Brendler et al. 2018; Bongers et al. 2019) but for most other species data are scarce.

Socotra Island, Yemen, has the highest diversity of *Boswellia* species in the world, with ten species documented (Miller and Morris 2004; Lvončík and Řepka 2020; Thulin 2020), all of them endemic. Frankincense trees are endangered on Socotra Island and the populations are declining (Miller and Morris 2004; Attorre et al. 2011; Lvončík et al. 2013). Among other factors, declines are attributed to the strong impact of grazing on tree regeneration (Miller and Morris 2004; Attorre et al. 2011). Besides grazing, frankincense trees have numerous other, including ethnobotanical, uses (Miller and Morris 2004) which together add up and increase the vulnerability of the species to unsustainable harvesting. Also, more frequent occurrence of climatic extremes

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may contribute to population decline of frankincense trees on Socotra Island, for instance through the increased number and intensity of cyclones in recent years. Several Socotran *Boswellia* species are on the IUCN Red List, but the last assessment was done more than 16 years ago (Miller 2004) and the current situation could be different. Natural heritage connected with frankincense trees and other endemic trees is one of the reasons why the UNESCO World Heritage Site was established on Socotra (Van Damme and Banfield 2011).

Boswellia elongata Balf. F., is one of the ten endemic species of *Boswellia* that occur on the Socotra Archipelago (Thulin 2020). It is a ground-rooted tree, characterized by its paper-like bark and umbrella-shaped crown (Miller and Morris 2004; Attorre et al. 2011). It is moderate in size; the largest trunk circumference of 2.2 m (70.1 cm diameter) was recorded for a tree growing in Homhil (in the northeast of Socotra island), while the tallest tree with a height of 8 m was found in Taakes (in central Socotra) (Adolt et al. 2004). Maximum tree age and tree growth are unknown. *Boswellia elongata* grows mostly in small isolated populations in the east, but rare occurrences have been recorded in the west of the island (Miller and Morris 2004; Attorre et al. 2011; Lvončík et al. 2013). It occurs primarily on plateaus and mild slopes with open semi-deciduous shrubland vegetation at an altitude of 172–690 m and mostly on alkaline soils (Attore et al. 2011). The largest populations can be found in three localities, in Homhil, Taakes and Makalhim in the east and central areas of the island (Adolt et al. 2004; Lvončík et al. 2013). The Homhil population is part of a Nature Sanctuary (UNDP/GEF 2000) but without any protection against overgrazing.

This species has a wide ethnobotanical use and is the source of the most valued incense on the island (Miller and Morris 2004). Historical sources indicate that the island of Socotra was part of the incense trade, which was one of the most important luxury items of exchange in antiquity, and was exported to the Mediterranean and Red Sea regions, Mesopotamia, India, and China, mostly in the first and second century (Groom 1981; Gupta 2007). Some studies speculate that *B. elongata* was cultivated in the past (Mies et al. 2000; Jansen van Rensburg and Hopper 2017). Attore et al. (2011) showed that *B. elongata* is the most common species of Boswellia on the island and, based on the absence of saplings, they predicted a decline in its abundance as well as in the abundance of other ground-rooted Boswellia species on Socotra. In the International Union for Conservation of Nature (IUCN) Red List, *B. elongata* was evaluated as vulnerable due to the absence of regeneration, a fragmented population and habitat degradation (Miller 2004).

The current status of many *Boswellia* species populations, especially in the light of the resin over-harvesting during the last decades, is poorly known (Bongers et al. 2019). Here we evaluate the Homhil Nature Sanctuary population as case study of the current situation. We (1) quantify changes in the size of the population of *B. elongata* in Homhil for the period between 1956 to 2017, including a rough extrapolation forecasting future development, (2) assess the age structure of the *B. elongata* Homhil population from annual rings, and (3) evaluate its capability for natural regeneration.

2 Materials and methods

2.1 Study area

The Socotra Archipelago (Yemen) lies in the northwest of the Indian Ocean and is remarkable for its high biodiversity in both fauna and flora (Van Damme and Banfield 2011). The archipelago consists of four islands, Samha, Darsa, Abd al Kuri and Socotra and a few limestone islets. Despite its small size of only ca. 3800 km^2 it harbors more than 827 plant species, 37% of which are endemic (Brown and Mies 2012). Socotra is topographically heterogeneous, with coastal plains, limestone plateaus and highlands at altitude 300–900 m a.s.l. and granitic Hagghier Mountains with its highest peaks around 1550 m a.s.l. (Brown and Mies 2012).

The climate is dry tropical with distinctly separated dry and wet seasons. The summer monsoon brings rainfall in its beginning in May and June. At the end in September, fogs and clouds are very abundant at higher altitudes as a source of horizontal precipitation (Mies and Beyhl 1998). The winter monsoon brings rainfall from October to January, while the potential evapotranspiration exceeds the rainfall for most of the year (Scholte and De Geest 2010). In November 2015, two disastrous cyclones Chapala and Megh came over the island (India Meteorological Department 2015a, b) and heavily affected the *B. elongata* population in Homhil.

The Homhil Nature Sanctuary is located in the northwest of the island (Fig. 1). Homhil is a flat polje at the altitude of 300 m surrounded from three sides by rocky limestone slopes. Its soils are well-developed, deep hypercalcic calcisols, which are silty or sandy (Pietsch and Morris 2010). The size of Homhil Nature Sanctuary (Van Damme and Banfield 2011) is 682 ha of which 125.6 ha were studied. The size of the study area respects the population area that is visible from the aerial photograph from 1956 (Fig. 1b, c). All inventory activities happened inside this locality (all datasets were clipped by the same borders to avoid miscalculations).

2.2 Population dynamics

The total number, the number of newly grown and dead trees of *B. elongata* in Homhil in the years 1956, 2010, 2011, 2014, 2015, 2016 and 2017 were determined. The detectable trees of *B. elongata* with a sufficiently large crown growing

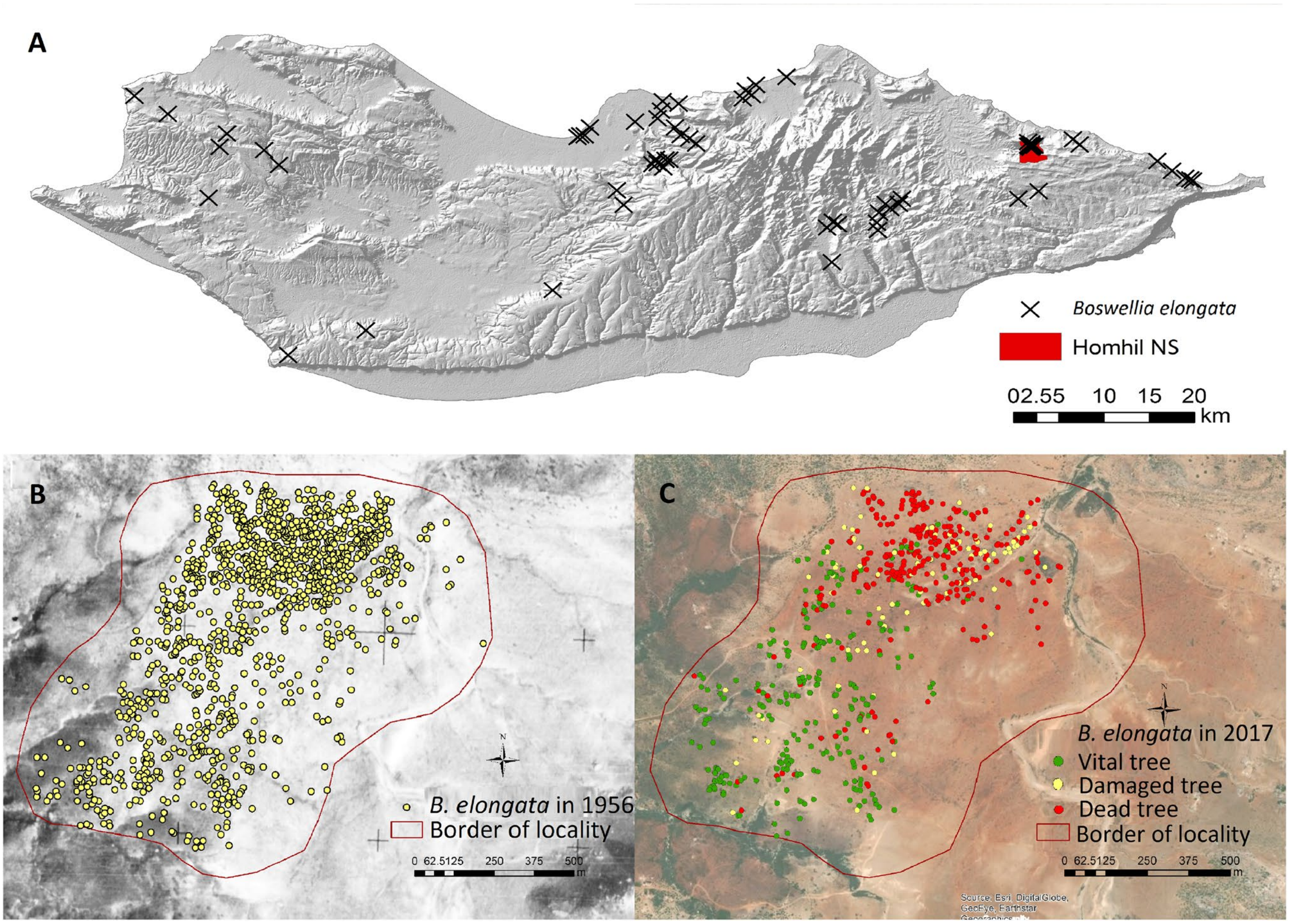

Fig. 1 **a** Socotra Island, distribution of *Boswellia elongata* in 2013, after Lvončík (2013). The study area in the northeast of the island, Homhil Nature Sanctuary, is marked in red. **b** Depiction of *B. elongata* trees on Homhil in 1956. **c** Depiction of *B. elongata* trees in 2017

on Homhil in 1956 were counted from an aerial photograph taken by the Royal Air Force (RAF). To accentuate the tree crown contours, the image was modified by a high-frequency filter using ArcGIS 10.7 and a point vector layer of *B. elongata* specimens was undertaken. The same procedure was applied to images taken by the QuickBird satellite imagery from 2010.

RAF orthophotos were taken together with "georeferencing crosses" that were used as control points in the process of georeferencing and the whole mosaic dataset was orthorectified to the actual position of the Digital Elevation Model (AW3D30 DEM) obtained from the Japan aerospace institute (JAXA). This procedure enabled spatial overlapping of the position of every tree in the RAF orthophotos and QuickBird satellite imagery with no significant spatial distortion.

In November 2011, 2015 and 2016, detailed photos of Homhil were taken from the northern slope of the Hamadero massif. These panoramic photos were first processed by image segmentation using an object-based classification process provided by the eCognition software (Trimble). Thereafter, a point vector layer was created and the number of trees in the individual years was determined above all images. In all the photos, *B. elongata* was distinguished from other tree species based on the characteristic shape and size of its crown and the shadow it casts. Unfortunately, it was impossible to join point vector layers of trees from these panoramic photos with previous aerial and satellite imagery.

In December 2006, 43 randomly selected trees were measured in the population in Homhil. In May 2014 and November 2017, all trees were measured manually in the field (full area inventory). The girth at breast height (GBH) to calculate diameter at breast height (DBH) and the trunk height were measured, and cyclone damage was assessed (uprooted tree, broken stem, crown damaged); the geographic coordinates of all trees were measured in 2017 using the GPS in the mobile phone. The accuracy of this tree positioning was, unfortunately, not good enough to overlap this vector layer with layers from aerial and satellite imageries. The obtained values of DBH were divided into size classes by 5 cm and the frequency percentage was calculated for each class (Fig. 2).

A Kaplan–Meier survival analysis (Efron 1988) was carried out to estimate future development of the *B. elongata* population in the study area. The total number of individuals found; increments and decreases of individuals; the average number of dead trees per year; and the survival probability to the next year (P_x) were calculated. The survival probability was calculated (Eq. 1):

$$P_x = \frac{n(x+1)}{nx}, \quad (1)$$

where n_x is number of living trees at $t = x$ and $n_{(x+1)}$ is the number of survivals to the next year ($t = x + 1$). Based on the calculated P_x a model of future population development was constructed. A theoretical model of how the population could develop without the influence of the cyclones was also created based on average P_x for the pre-cyclone period 2010–2014.

2.3 Age estimation

Samples of wood from 30 randomly selected trees uprooted during cyclones Chapala and Megh were taken in 2015 and their DBH were measured. This random selection is biased towards larger trees (the cyclones uprooted mostly larger trees), undestroyed trunks, and trunks without heart rot. We took full stem discs from 5 trees and increment cores at 130 cm breast height from 25 trees. The presence of decay was evaluated in the cores and the ratio of all cores and cores with a decay or central cavity (rot) were counted.

The increment cores were taken using a Mattson increment borer (5.15 mm diameter, 400 mm bit length) at right angle to the axis of the trunk and were fixated to avoid damage during transport to the laboratory. Before analysis, they were cut lengthwise with a razor blade to remove the cell layer damaged during drilling and the surface of the round cuts was smoothed with P 300 sandpaper. The wood structure in all samples was accentuated by staining with a solution of phloroglucinol and 5% HCl (Clarke 1935). The annual rings in the cores were counted using a LEICA S6 stereomicroscope with a sliding table (TimeTable).

The annual rings in the full stem discs were counted from digital photographs (Keyence VHX-5000 3D digital microscope with a 100× magnification). Annual rings on the full stem discs were counted in three directions to account for incomplete annual rings. The age of the sampled tree was estimated as a number of tree rings counted plus 10 years that we estimated the tree needs to reach breast height.

In the trees, where the phloem and bark were preserved, the width of the wood (W_W) was measured and the wood ratio (R_W) within DBH with phloem and bark was counted (Eq. 2):

$$R_W = W_W/DBH. \quad (2)$$

Furthermore, the average width of tree ring for each bore (W_{TR}) was counted according to Eq. 3:

$$W_{TR} = (0.5DBH \times R_W)/N_{TR}, \quad (3)$$

where N_{TR} is number of tree rings.

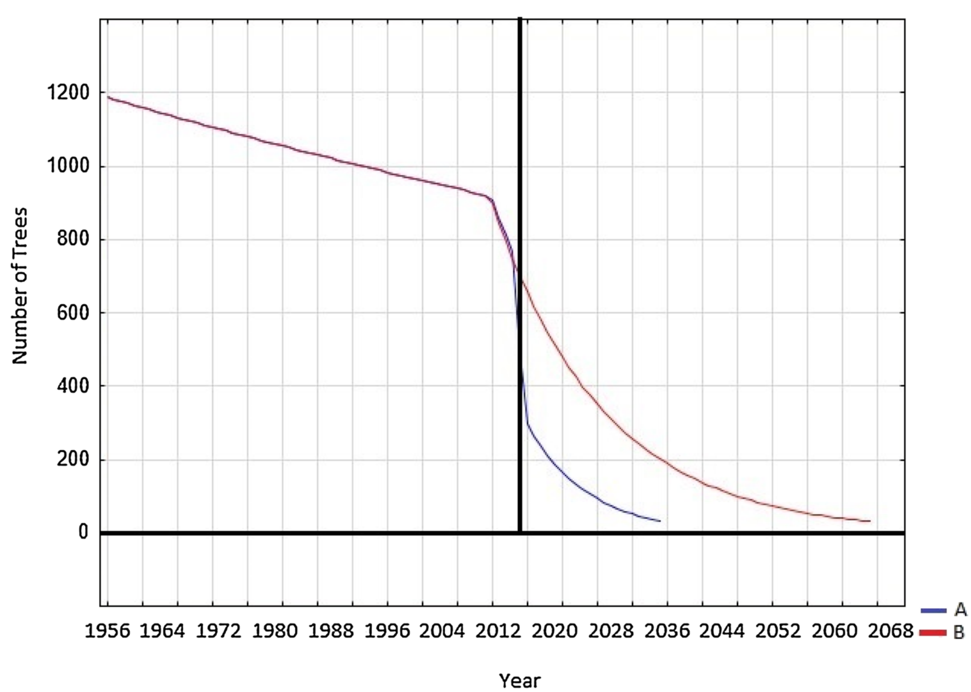

Fig. 2 Modelled changes in the size of *B. elongata* population in Homhil, within the studied area of 125.6 ha, between 1956 and 2064. **a** Theoretical forecasting model with influence of 2015 cyclones (Megh and Chapala). **b** Theoretical forecasting model without the influence of the 2015 cyclones

The average width of a tree ring from all bores (AW_{TR}) was counted using Eq. 4:

$$AW_{TR} = \frac{\sum_{i=11}^{n} \left(W_{TRi}\right)}{11}. \quad (4)$$

In addition, the DBH of one tree planted in 2002 in the Socotra capital Hadiboh and irrigated, since then was measured. The average size of tree rings was calculated, used as growth potential for cultivated trees and compared to annual growth of trees growing in situ.

The Pearson correlation coefficient was used to test the correlation between age and DBH of sampled trees at the significance level $p < 0.05$ using StatSoft Inc (2013).

We estimated age of the trees (A) based on average, minimal and maximal radial annual increment (= average width of tree ring, AW_{TR}) plus 10 years that we estimated the tree needs to reach breast height using Eq. 5 (Fig. 2) and calculated mean age of trees in the population in the years 2006, 2014 and 2017 (Tab. 3).

$$A = (0.5DBH \times R_W)/AW_{TR} + (10) \quad (5)$$

2.4 Natural regeneration and seedling development

Exclosure experiments were established on the same place, where population dynamics and age was studied. Exclosure experiments were established for natural regeneration observations in 2006 and 2012. Treatments were *Boswellia* density (High vs Low Density) and fencing (Fenced vs Wired vs Open). High density forest had all three fencing treatments, Low density forest had only fenced and open, resulting in a total of five treatments, area A (HD-F), area B (HD-W), area C (HD-O), area D (LD-F), area E (LD-O). Each exclosure surface was 49 m^2. Fencing (iron mesh 4.5 × 4.5 cm; 2 m height) excluded all large animals including sheep, goats and humans. Wired exclosures (height 0.8 m) excluded only large grazers like camels, donkeys and cows. Open was accessible to all. The measurements of the 2006 exclosure experiment were carried out at two moments (6-8 December 2006 and 4–6 January 2007). In 2012, the treatments were only "fenced A" (HD-F) and "open C" (HD-O) in high density forest. The measurements of the 2012 experiment were carried out only in May 2014, 21 months after the establishment of the experiment. At the time of establishment, there were no seedlings in both sample plots. The sample plots were situated along transects (within areas A-E in 2006 and only within areas A and C in 2014).

In 2006 the number of seedlings was counted in 1 m^2 contiguous plots in a 2 × 49 m transect (areas A, B and C) and 2 × 29 m^2 for area D and E. Every individual was classified to the number of leaves: 2 cotyledons, 2 leaves, 4 leaves and 6 leaves. For the data analyses, the dataset was transformed to describe the development per seedling during the month of December.

In 2014, in both areas (A, C) 36 sample plots of 1 m^2 were located along transects at 5 m distance. The number of seedlings in the sample plots was counted and their heights measured.

3 Results

3.1 Development of B. elongata population

We recorded 1187 trees in 1956. Of this number, 264 remained in 2017, a 78% decrease in the population size (Table 1). The total number of adult trees decreased continuously since 1956 (Fig. 2), but the rate of decrease varied over time. The highest number of trees died in 2015, 2016 and 2017, most probably as a direct result of the damage caused by the cyclones Chapala and Megh. We observed an infestation by bark beetles directly thereafter, which we speculate further added to the decline of weakened individual trees. However, before the cyclone events, in 2011, many trees died as well, possibly as a result of population over-maturity.

The model of the development of the *B. elongata* population (Fig. 2), based on the probability of its survival to the next year, suggests that if the current conditions remain unchanged and without impacts of new cyclones, only 30 trees would remain in 2036. The theoretical model of the *B. elongata* population development which operates with an average probability of survival from 2011 to 2014 ($P_x = 0.957$) (before the 2015 cyclones and, therefore, without the influence of new extreme weather events) leads us to speculate that there will be only 30 trees in 2065.

3.2 Population structure

The DBH frequency distribution of the population and its calculated age in 2006, 2014 and 2017 (Fig. 3) shows a peak

Table 1 Numbers of trees of *B. elongata* recorded in Homhil between 1956 and 2017 within the studied area of 125.6 ha

Year	Living trees detected	New trees detected	Average number of dead trees per year	P_x (probability of survival to the next year)
1956	1187	.	.	
2010	956	37	3.4	0.9960
2011	898	0	67	0.9393
2014	802	0	32	0.9571
2015	494	0	308	0.6161
2016	296	0	198	0.5995
2017	264	0	32	0.8920

of trees with a DBH of 41–45 cm in 2014, while 2017 shows a peak DBH of 36-40 cm. The average and median DBH in 2014 and 2017 were both 44 cm and 43 cm, respectively. In 2006, based on measurement of 43 randomly selected trees, the highest frequency of trees was in DBH class 36–40 cm, and the average and median DBH were 41 cm and 40 cm, respectively. This suggest an increment of average DBH in the population of 3 cm within 8 years (between years 2006 and 2014) and decrease by 1 cm between years 2014 and 2017 (influence of cyclones in 2015).

Unfortunately, only three full stem discs and eight increment cores had countable tree rings from 30 samples. The rest of the samples were unusable, due to an advanced decay of hard wood or trunk hollows. In 66% of the cores we found proof of a stage of senescence of the tree, through strong wood decay or a large central (pith) cavity.

The R_{PB} ratio was calculated as 12.5%, tree DBH was decreased by this ratio before average tree ring width calculation.

The cored individuals of *B. elongata* were on average 90 years (range 80–101 years) (Table 2). Their average ring width was 2.34 mm (SD = 0.23; range 1.89–2.61 mm). The irrigated Hadiboh tree had a mean annual increment 3.84 times higher than the average tree from Homhil. Counting of the annual rings on full tree discs in three different directions showed a deviation up to 5 rings, up to 6%, respectively.

Using the Pearson Correlation Coefficient a correlation between the number of annual rings and the DBH was shown to be significant ($r = 0.57$, $P = 0.04$).

We estimated that the trees had the highest mean age in year 2014 (105), while in 2006 (98) and 2017 (102), the mean age was lower (Table 3).

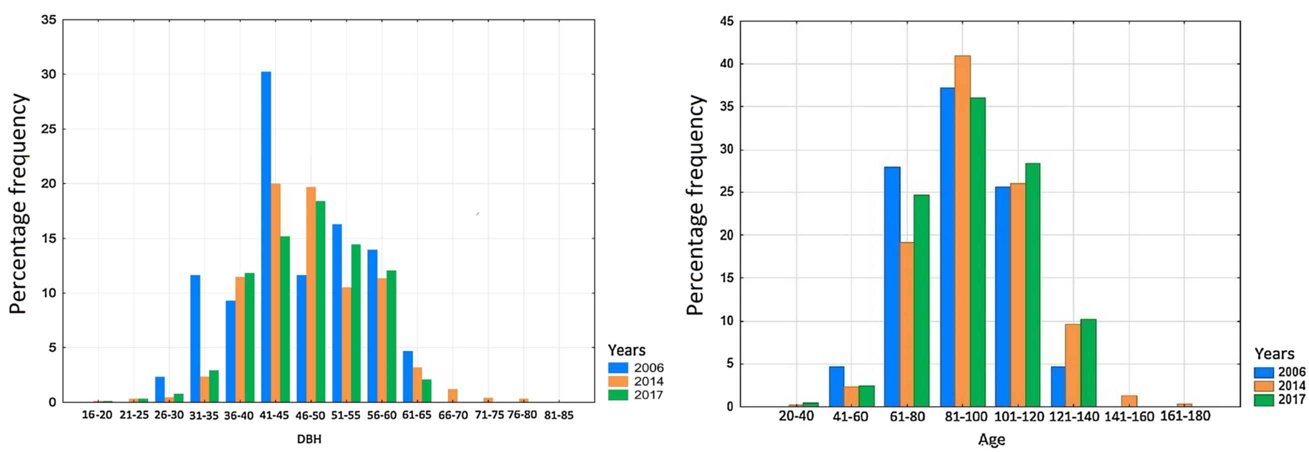

Fig. 3 Frequency percentage of the size of DBH and age classes in 2006 (n = 43), 2014 (n = 802) and 2017 (n = 264)

Table 2 Numbers of detected annual rings and presumed age, DBH and the trunk height of 11 examined *Boswellia elongata* trees from Homhil research area and one from Hadiboh

Sample	Number of annual rings	Presumed age	Average width of annual rings in mm	DBH without bark	Trunk height (cm)
Core 1	88	98	2.32	41	240
Core 2	76	86	2.50	38	270
Core 3	70	80	2.50	35	260
Core 4	91	101	2.41	44	220
Core 5	72	82	2.49	36	210
Core 6	83	93	2.28	38	250
Core 7	79	89	2.46	39	260
Core 8	73	83	2.61	38	230
Stem disc 1	75, 75, 72	84	1.95	29	250
Stem disc 2	85, 84, 80	94	2.28	38	250
Stem disc 3	86, 83, 83	94	1.89	32	260
Average (n = 11)		90	2.34	37.1	245.5
*Hadiboh	15	25	**9	23.6	260

*Irrigated tree

**Calculated value derivated from known tree age and GBH measured (no core was taken)

Table 3 Mean age of *Boswellia elongata* trees in years 2006, 2014 and 2017

Year	2006	2014	2017
Minimal counted age	89	95	93
Mean counted age	98	105	102
Maximal counted age	119	127	124

We found that the biggest tree was 178 years in 2014 (83 DBH, age calculated based on mean radial increment of ring-counted trees) but this tree didn't survive till 2017. Only one tree was younger than 40 years (Fig. 3).

3.3 Natural regeneration and seedling development

In 2006, the total numbers of individuals in the High Density Forest areas (A, B and C) were significantly (ten times) higher than in Low Density Forest (D and E) (Table 4). Most seedlings present in December 2006 disappeared in January 2007 (Table 4). Survival rates over this period are very similar among all areas (approximately 20%) with plot A showing a slightly higher survival (35.4%). The seedlings in the Low Density Forest never developed 6 leaves, suggesting developmental difficulties.

In May 2014, a total of 71 seedlings were found inside the 36 experimental plots (Table 5). Seedling density in the fenced area was on average 1.97 seedlings/m^2 (19722 seedlings/ha). The average height was 13 cm (SD = 9.34 cm), with a maximum of 50 cm and minimum 2 cm. Outside the fenced area there were no seedlings at all. We were not able to distinguish 1- and 2-year-old seedlings, but we can assume that a mixture of 1- and 2-year-old seedlings was measured in May 2014.

4 Discussion

4.1 *Boswellia elongata* distribution

Boswellia individuals are typically distributed in the 2nd and 3rd altitudinal vegetation zones between 100 and 900 m a.s.l. being part of deciduous savannah forests and woodlands and submontane semi-deciduous forests and woodlands (Habrová 2004). The first detailed landcover map of Socotra Island published by Král and Pavliš (2006) mentioned *Boswellia* occurrence in two classes, Frankincense forests and woodlands, but without the possibility to distinguish them from the other tree species using satellite imagery. However, these two landcover classes occupied only 6.6% of the island area. Adolt et al. (2004) showed that, based on remote sensed data, 11,200 ha of Frankincense woodlands and 1130 ha of Frankincense forests occurred on Socotra Island, which is 3.2% and 0.3% of the main island area, respectively. Malatesta et al. (2013) distinguished woodlands of two *Boswellia* species—*Boswellia elongata* and *B. ameero* in their vegetation map. Kürschner et al. (2006) classified the vegetation of the northern mountains of Socotra and reported *Boswellia* occurrence in several plant associations: *Ruellio insignis-Boswellietum ameero* (450–600 m a.s.l.), *Adenio sokotrani-Sterculietum*

Table 4 Number of seedlings of *Boswellia elongata* in the exclosure experiments, divided in types with different number of leaves, found in the different sampling areas to assess the impacts of grazing (see "methods" for A–E) in Homhil on Socotra

Area		2 Cotyledons	2 Leaves	4 Leaves	6 Leaves	Total	No/m^2	Survival rate
A (high density—fenced)	Dec	2	146	94	1	243	2.5	
	Jan	0	10	57	19	86	0.9	35.4%
B (high density—Wired)	Dec	2	96	61	0	159	1.6	
	Jan	1	8	25	3	37	0.4	23.3%
C (high density—open)	Dec	2	48	150	4	204	2.1	
	Jan	0	10	29	1	40	0.4	19.6%
D (low density—fenced)	Dec	2	10	14	0	26	0.3	
	Jan	0	0	5	0	5	0.1	19.2%
E (low density—open)	Dec	2	3	5	0	10	0.1	
	Jan	0	0	2	0	2	0.0	20.0%

These areas were sampled in December 2006 and January 2007

Table 5 Total number of *Boswellia elongata* seedlings within individual height classes in May 2014

Height class	1–5 cm	5–10 cm	10–15 cm	15–20 cm	20–25 cm	25–30 cm	30–35 cm	35–40 cm	40–45 cm	45–50 cm	Total
No of seedlings	16	26	10	6	4	5	2	1	0	1	71

socotranae-boswellietosum socotranae (300–500 m a.s.l.) and *Adenio sokotrani-Sterculietum socotranae-boswellietosum elongatae* (200–300 m a.s.l.).

Attorre et al. (2011) reported 826 individuals of *B. elongata* in 32 sampled plots at an altitude between 172 and 690 m, while Peijnenburg (2007) found 1131 individuals in 103 plots between 1 and 480 m (Fig. 4).

Comparing maps of *B. elongata* potential distribution published by Attore et al. (2011) with the map of known localities published by Lvončík (2013) and Peijnenburg (2007) we observe that *B. elongata* was growing in most of the ecologically suitable localities. Lvončík (2013) showed the occurrence of *B. elongata* also in the western part of the Socotra island in localities, where Attore et al. (2011) and Peijnenburg (2007) predicted them. Our most recent update of the distribution is shown in Fig. 1, although more surveys are needed.

4.2 Population development of *Boswellia elongata* in Homhil

Here we report on seven decades development of one *Boswellia* subpopulation, which is quite unique for Socotra. On Socotra, Habrová et al. (2009) compared a 105-year-old photo of a *Dracaena cinnabari* subpopulation with a recent photo taken from the same position in 2004 and estimated 44% mortality. Our study reveals that the size of the *B. elongata* population in Homhil has been continuously decreasing since 1956 and, if the current speed of decline is maintained, we predict that only 30 trees will remain in 2036. Bongers et al. (2019) predicted that population sizes of *B. papyrifera* in Ethiopia, Eritrea and Sudan will halve within two decades, with also devastating impact for the production of its frankincense. This may increase the pressure to harvest incense from other *Boswellia* species, including those from Socotra.

Extreme weather events related to global warming, the Chapala and Megh cyclones that struck Socotra in 2015 (India Meteorological Department 2015a, b), had the strongest negative impact on the state of the population in Homhil. We estimated that 308 trees were destroyed directly by the cyclones and 230 trees died in the next 2 years. The latter could be partly attributed to our observations of a heavy infestation of the bark beetle *Halystus bimaculatus* (Curculionidae) directly following the cyclones. This species is endemic to the island and naturally occurs on weakened or dying trees of *B. elongata* (Knížek 2012). It is highly probable that the bark beetle infested the trees weakened by the cyclones, a connection shown for various bark beetle species around the world (Schroeder 2001; Bouget and Duelli 2004; Eriksson et al. 2007).

Our results show that many trees were in a late stage of maturity or in senescence before the cyclones, as only 11 of 30 trees we analysed wood samples from in 2016 were free of significant damage by decay (rot) and/or trunk hollowing (Read 2000). The speed of extinction of the Homhil population accelerated as early as in 2011, a few years before the devastating cyclones. We consider this acceleration to be evidence that a large proportion of the trees at Homhil are senescent and natural regeneration is nearly absent due to overgrazing. Because young trees are missing, we predict that this population is moving towards extinction. This is in line with other autochthonous tree species on Socotra, where intensive grazing is seen as the major threat (Adolt and Pavliš 2004; Attore et al. 2011; Brown and Mies 2012; Lvončík et al. 2013; Maděra et al. 2020). Pastoralism has been practised on Socotra for at least several centuries (Miller and Morris 2004; Van Damme and Banfield 2011; Jansen van Rensburg and Hopper 2017). Until the 1960s the Homhil locality was used for grazing only during the rainy seasons, when cattle herders lived in caves in the mountains; after the 1960s they moved with their cattle down to the valley and built permanent stone dwellings around the valley floor. This increased grazing pressure year-round on the valley floor (Morris 2002). Land degradation in Homhil has been directly attributed to the latter cultural shifts as shown in soil erosion studies (Pietsch and Morris 2010). The resulting decrease of tree density has been shown for

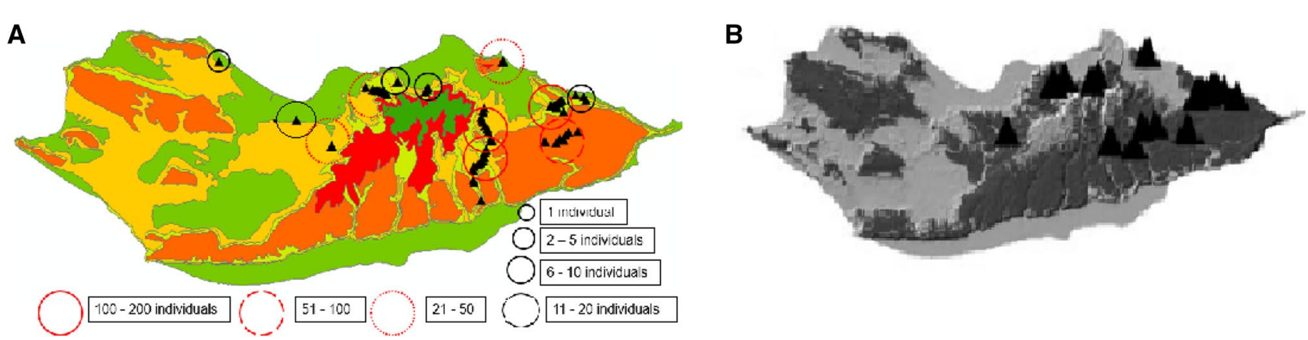

Fig. 4 Occurrences of *Boswellia elongata* on Socotra according **a**—Peijnenburg (2007), **b**—Attore et al. (2011)

other dry tropical woodlands in Africa (Ellis 1988; Vetaas 1993) and from Socotra (Habrová and Pavliš 2017; Maděra et al. 2018, 2019).

The current decline of the population of *B. elongata* shows parallels to the decline of populations of *B. papyrifera* in eastern Africa studied by Bongers et al. (2019). Establishing plantations and enrichment planting in current populations has been put forward as a possible solution to reverse the decline of such populations, as has also been suggested for *B. elongata* (Maděra et al. 2017).

4.3 Age structure of population

One of the most important datasets used to establish suitable measures for tree species conservation is the length of its life cycle and the age structure of its populations (Harcombe 1987) but this information is largely missing for all *Boswellia* taxa from Socotra. The age of woody plants is usually determined by annual rings in the wood, which arise from an irregular function of cambium; the function of cambium is influenced predominantly by climate seasons (Fichtler et al. 2003). Motuma et al. (2012) and Bongers et al. (2019) showed the existence of annual rings in *B. papyrifera* growing in Ethiopia, as well as Worbes (2002); Brienen and Zuidema (2005), did for many other tropical tree species.

We have found tree rings in the wood of *B. elongata* trees, which are most probably annual rings because of the clear climatic seasonality. Our own phenological observation revealed that *B. elongata* has leaves only from April or May to December or January, and is leafless during the long dry period from January to April/May. In the early rainy season large vessels are being constructed for rapid water transport to the flushing leaves, and small ones towards the end of the rainy season. This difference creates clear rings. During the dry season there is hardly any wood formation. We are, therefore, convinced that the rings are annual, comparable to rings in *B. papyrifera* and *B. neglecta* (Tolera et al. 2013; Mokria et al. 2017). As in all ring studies there is a possibility that false or incomplete rings are present (Priya and Bhat 1998; Motuma et al. 2013) leading to slight over- or underestimations of tree age.

The examined trees in Homhil showed between 70 and 91 rings at breast height. To estimate entire age of the tree, we need to add the time that the tree needs to reach the coring height (breast height). Regarding *Boswellia* tree height growth, Tolera et al. (2013) reported that it takes 3–4 years before seedlings of *B. papyrifera* reach a height of 1 m, and Eslemiah (2011) states that saplings of *B. elongata* grow in culture at a speed of 25–30 cm per year. In our field study, growth of *B. elongata* seedlings was slower, average height of all seedlings was 13 cm. But we were not able to distinguish one- and 2-year-old seedlings. If we assume (based on personal observation) that the boundary between 1- and 2-year-old seedlings lies at a height of 10 cm, then the average height of 1-year-old seedlings was 5.6 cm and 21-month-old seedlings 20.95 cm, respectively. Thus, 2-year-old seedlings could reach an average height of 25 cm. This way we roughly estimated 10 years for the trees to approach breast height, and therefore, we estimated the tree age as the number of rings plus 10 years.

The correlation between DBH and number of year rings was proven also. That enables us to estimate the age also of other *B elongata* trees on Homhil, which were not bored but their DBH was known. We found that only one tree is less than 40 years and that the mean age of the population decreased by 3 years between 2014 and 2017. We can conclude that the older trees are more susceptible to the damage caused by extremely strong wind and following insect infestation.

Comparing the mean year-round width between *B elongata* trees on Homhil and Hadiboh shows that the growing speed could differ essentially between localities.

4.4 Natural regeneration

Tree density had a higher impact on seedling abundance than grazing (Table 3). This may be due to better environmental conditions but also to better seed availability. With our design we could not separate these two effects. The high density of surrounding vegetation may serve as nurse trees, as has been described for *Dracaena cinnabari* (Rejžek et al. 2017). Water availability in the soil may be the bottleneck factor here. Horizontal precipitation during summer monsoon may be added to the overall low rainfall as a vital source of additional water (Scholte and De Geest 2010), but together these sources may not be enough for the proper establishment of young plants. The higher tree density captures more horizontal precipitation as well as any other barrier perpendicular to prevailing winds bringing drizzle and mist (e.g., rocks). We found the better developed seedlings often surrounded by stones. Such semiarid seasonal cloud forests have been shown to be important for the hydrological cycle (Hildebrandt et al. 2007; Eltahir 2011; Marzol et al. 2011; Kalivodová et al. 2020; Riccardi et al. 2020). Decline of these forests, therefore, may lead to local desertification and decreasing ability of tree regeneration (Hildebrandt and Eltahir 2006, 2008). Additionally, more trees produce more litter and thereby increase the organic matter in the soil, which on its turn has positive effects on soil water holding capacity which improves the regenerative capacity and growth of species (Shiferaw et al. 2020).

Additional to the improved environmental conditions in the high dense forest, the lack of regeneration and development of seedlings could also result from low seed quality and quantity. Rijkers et al. (2006) found that larger *B. papyrifera* trees have better sexual reproduction than smaller trees. Seeds were heavier and thus have more reserves needed for germination and establishment. For Homhil, the tree size may not be a factor as all trees were fully mature, but tree density may lead to higher quantities of seeds. *Boswellia papyrifera* seed viability was negatively affected by resin tapping, both in Ethiopia (Eshete et al. 2012) and in Eritrea (Rijkers et al. 2006). In Homhil, this could not have played a role as none of the trees are actively tapped, as the local inhabitants collect only naturally oozing resin so far.

In contrast to our expectation, the exclosures in 2006 had no effect on seedling mortality rate in comparison with open grazed areas in the first months of seedling development (Table 3). Probably at the end of winter monsoon (December–January) enough grass and herbs were available elsewhere as food for grazers. In May 2014, at the end of dry period, the result was different. With 1.97 seedlings per square meter in the exclosure and no seedlings outside the exclosure, grazing had a substantially negative impact on seedling development. Heavy impact of grazing has been shown also for *B. papyrifera* in Eritrea (Ogbazghi 2001). The exclusion of livestock has helped to restore natural plant succession and consequent establishment (Namdeo et al. 1989). Overgrazing on Socotra has limited tree regeneration for several species (e.g., Miller and Morris 2004; Habrová and Pavliš 2017; Maděra et al. 2018). Generally, ground-rooted species (including *B. elongata*) are more endangered than cliff-rooted species because of better accessibility to grazers including goats (Attorre et al. 2011).

During the 2006 study none of the fleshy seedlings grew into an eight- (or more) leaved seedling. During the 2014 study, most of the 21-month-old seedlings developed a woody stem and seedlings had a height up to 50 cm. Ogbazghi (2001) reported similarly that the stem transformation from fleshy into wooden seedlings of *B. papyrifera* takes about 2 years.

4.5 What needs to be done

We found that the *B. elongata* population in Homhil is collapsing through the combination of high adult mortality and no recruitment. There are, in the area of the Nature Sanctuary, 6 villages with 295 inhabitants totally. They are keeping 1,445 goats, 634 sheep, 80 cows and 5 donkeys (Mendel University demographic survey 2018-2019, unpubl. data). To avoid collapse leading to local extinction of this species, urgent action is needed. Unsustainable land use, climate change and following insect infestations or other disease all add to the accelerated extinction of the population, and on an island-wide scale, of the entire species. The effects from unsustainable resource use, in this case overgrazing, combined with non-selective catastrophic events such as climate change, can catalyse events on islands and was suggested (before the cyclones) as a likely scenario leading to future extinctions of key species in Socotra (Van Damme and Banfield 2011). As this case study shows, we are now in such a scenario, and human intervention is needed to increase resilience of the local tree populations in the face of land degradation and global warming.

For *B. elongata* in Homhil, we suggest the following. Strict fencing of the area with *Boswellia* is urgently needed to avoid grazing effects on the remaining population and possible recruitment. Actual implementation of the Socotra Conservation Zoning Plan in accordance to the level of formal protection of the Homhil Nature Sanctuary is needed and should come with the protection actions being carried out in the field. Future management plans of the area should incorporate *Boswellia* protection activities. Additional enrichment planting (and consequent protection) of seedlings and cuttings, both in the core area and outside, and consequently protecting them will increase the probability of plants developing into mature trees. Plantings outside the core area could be developed into a source of frankincense, thereby stimulating both economic opportunities and cultural values. These measures should be accompanied with awareness and education involving local and regional communities and stakeholders focusing on long-term sustainable natural resource management. A similar approach has been suggested by Maděra et al. (2019) for *Dracaena cinnabari* conservation on Socotra Island.

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Availability of data and material Data are available on request from the authors.

Code availability ArcGIS 10.55 Mendel University Licence—indica.mendelu.cz:27000.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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