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Overgrazing strongly impedes the natural regeneration of the endemic *Boswellia* species on Socotra Island

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Abstract: Frankincense trees (*Boswellia* spp.) worldwide are affected by a number of threats, including global warming and changing land management practices. On the Socotra Archipelago (Yemen), which harbours eleven endemic *Boswellia* species, grazing is generally assumed to be one of the main threats preventing natural regeneration. To test the impact of overgrazing on natural regeneration, we established an *in situ* experiment on four different *Boswellia* taxa in different areas of Socotra Island. Mortality and the height increment of seedlings were measured for a period of two/three years in five plots excluded from grazing (fenced) and in five paired control (unfenced) plots. Each plot was 50 m × 50 m in size and contained several adult trees as a source of viable seeds. Our results show that seedling mortality was significantly higher, and seedling height increment generally (4 out of 5 sites) lower in open compared to fenced plots. In the fenced plots, the number of seedlings for all species reached up to 772, with 560 surviving seedlings. In comparison, the control plots reached up to 296 seedlings, with 176 seedlings surviving after 2–3 years. The results of our experimental study indicate that grazing directly threatens the natural regeneration of the endemic *Boswellia* on Socotra Island. However, seedling mortality remained relatively high inside the exclosures as well, which indicates that even without the pressure of livestock grazing, other impacts remain a challenge for the future conservation of the archipelago's unique frankincense trees.

Keywords: dryland flora; exclosure experiments; frankincense trees; land management; seedling survival and mortality

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Frankincense trees (*Boswellia* spp.; *Burseraceae*) have high commercial and cultural value due to their resin which is used in incense, perfumes, and medicines (Michie et al. 1991; Lemenih et al. 2003; Tadesse et al. 2007; Davidson et al. 2022). The genus counts approximately 24 different species with a wide distribution range, from the (sub)tropical regions of the Old World, including Africa, the Arabian Peninsula, and parts of East Asia (India); the Horn of Africa and Socotra are the main *Boswellia* diversity hotspots (Thulin 2020). Frankincense trees are strongly linked to human history, which, over many millennia, has resulted in many commercial uses. But this has also had a negative impact on the survival of some species (Bongers et al. 2019; Thulin 2020). Frankincense, an aromatic oleo-gum resin, is extracted from the bark of frankincense trees (Farah 2008; Camarda et al. 2011; Tolera et al. 2013). For thousands of years, oleo-gum resin has been used as incense (Arabic 'liban' or 'luban') and for its medicinal properties, especially in Arabia and Africa (Johnson et al. 2019). There are several species that are well-known for their medicinal uses (e.g. antiseptic properties), for example, *Boswellia serrata*, and indigenous cultures have a wide variety of uses for these plants, including those found in Socotra (Lemenih et al. 2003; Miller, Morris 2004; Camarda et al. 2011; Tošić et al. 2022). The indigenous people of Socotra use the resin of *B. socotrana*, *B. aspleniifolia*, *B. dioscoridis*, *B. elongata*, *B. ameero*, and *B. bullata* also for mouth hygiene by chewing it as a gum (Miller, Morris 2004). They also use the resin as incense to refresh the air and for spiritual purposes (against evil spirits).

The worldwide rise in the demand for frankincense has, however, led to resource overexploitation (Ogbazghi et al. 2006; Maděra et al. 2017; Bongers et al. 2019). As resin is mostly collected in the wild, the demand for frankincense has a huge impact on the natural environment and the livelihoods of the local communities that depend on it (DeCarlo et al. 2020). Among the major threats to the global populations of *Boswellia* are overgrazing, climate change, resin over-exploitation (over-harvesting), and habitat loss (Savithramma et al. 2012; Anitha et al. 2013; Bongers et al. 2019; Thulin 2020). For example, in several areas in Africa, the clearance of land (for agriculture), pressure from livestock and resin extraction, among other factors, have resulted in *B. papyrifera* being under threat (Gebrehiwot et al. 2003; Ogbazghi et al. 2006; Bongers et al. 2019). In Oman, *B. sacra* is threatened due to overgrazing by camels (Farah 2008) as is *B. ogadensis* in southern Ethiopia (Johnson et al. 2022). In addition, they are also threatened by harvesting for firewood and insect infestations (Negussie et al. 2018; Negussie et al. 2021, Johnson et al. 2022). Therefore, overgrazing, as a result of local human population increases, has become a serious threat to the natural regeneration of *Boswellia*, despite the importance of these trees, locally and globally, for the incense trade (Bongers et al. 2019; DeCarlo et al. 2020; Khan et al. 2022) and other ecosystem services such as carbon sequestration and soil formation.

The Socotra Archipelago (Yemen) is well known for its high natural value which includes a high degree of endemism among its plants (Brown, Mies 2012). At the same time, the terrestrial biota of Socotra is under increased pressure from global warming, unsustainable use of resources (overgrazing), and other factors (Van Damme, Banfield 2011; Attorre, Van Damme 2020). The archipelago has eleven endemic species of *Boswellia* and five species of *Commiphora* (four of which are endemic), which represents the highest global diversity of *Burseraceae* species found in an area (Thulin 2020; Lvončík, Řepka 2020; La Montagna et al. 2023). The frankincense trees found on the Socotra Archipelago are facing similar threats affecting the other *Boswellia* species worldwide, and several studies have mentioned overgrazing as an important factor in their decline (Attorre et al. 2011; Lvončík et al. 2013). In addition, the manifestations of climate change have had a large impact on the Socotran *Boswellia*, for example, cyclones (Lvončík et al. 2020), while the branches of the trees are broken off for fodder during the dry season (Miller, Morris 2004). While global warming has a significant effect on adult Socotran frankincense trees in both direct and indirect ways (Lvončík et al. 2020), overgrazing is thought to directly affect young seedlings and, therefore, impedes natural regeneration.

Natural regeneration and seedling establishment in *Boswellia* is better in the absence of grazing in different areas of the world (Gebrehiwot et al. 2003; Ogbazghi et al. 2006; Negussie et al. 2008; Bongers et al. 2019) and protecting woodland areas from livestock pressure has a high conservation potential in Socotra (Habrová, Pavliš 2017). Seeds of the endemic Socotran *Boswellia* species have a healthy

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germination rate under controlled conditions (Hamdiah et al. 2022). Therefore, there is a potential for natural regeneration, guided through conservation efforts. However, in order for ecological restoration to be successful, local environmental threats should be well understood. Disentanglement of the effects of (over)grazing and other potential threats to seedling survival in the wild is therefore important. The protection of the unique *Boswellia* trees of Socotra helps to conserve an important part of the local natural and cultural heritage, protect the island's unique biodiversity, and contribute to the sustainable management of natural resources. This is also the case for other endangered trees on the island, such as the Socotran Dragon's Blood Tree (*Dracaena cinnabari*; Maděra et al. 2019a).

The main aim of our study is to examine the effect of exclosures in order to assess the impact of (over)grazing on the natural regeneration of four *Boswellia* species on Socotra Island. In previous research, mentioned above, overgrazing has frequently been mentioned as a major limiting factor for the natural regeneration of *Boswellia*, but most of these statements were observational, not experimental. Here, an experimental field study was performed to understand the direct effects of grazing pressure on the natural seedling recruitment of frankincense trees by monitoring regeneration in exclosures versus control plots over a two- to three-year timescale in five different localities across Socotra Island.

Study area. The Socotra Archipelago is situated in the north-western Indian Ocean, east of the Horn of Africa and south of the Arabian Peninsula (Brown, Mies 2012). The archipelago has a surface area of about 3 800 km^2. Socotra Island, the largest island with an area of around 3 600 km^2, hosts ten endemic species of *Boswellia*. Recently, a local endemic species from Samha, a smaller island in the same archipelago (ca. 45 km^2), was described (Thulin 2020).

The archipelago has a significant degree of endemism among its terrestrial flora and fauna (Van Damme, Banfield 2011) as a consequence of its long-term isolation from the mainland (Cheung, DeVantier 2006; Culek et al. 2013). The climate of Socotra is mainly controlled by two monsoon seasons (Scholte, De Geest 2010). The summer monsoon lasts from May to September and is accompanied by strong winds (Scholte, De Geest 2010; Beresford et al. 2013); it affects the southern part of the island and mainly brings horizontal precipitation from clouds and fogs (Kalivodová et al. 2020). The winter monsoon mainly affects the northern part of the island, bringing rain (Scholte, De Geest 2010).

The *Boswellia* species on the Socotra Archipelago are divided into two ecological groups: ground-rooting and cliff-rooting species (Attorre et al. 2011; Thulin 2020). Cliff-rooting species (*B. dioscoridis*, *B. bullata*, *B. hesperia*, *B. nana*, *B. popoviana*, *B. scopulorum*, *B. samhaensis*) do remarkably well in very dry and hot situations, they are able to catch water from fog and drizzle during the monsoon season. They also make use of the dew that forms on rocks during the night (Thulin 2020). Ground-rooting species include *B. socotrana*, *B. aspleniifolia*, *B. ameero,* and *B. elongata*, which are also more vulnerable to land-use as they are relatively more accessible to humans and livestock. Our study included three ground-rooting species and one cliff-rooting species. *Boswellia socotrana* s.l. is sometimes considered as one species with two subspecies (*B. socotrana* ssp. *socotrana* and *B. socotrana* ssp. *aspleniifolia*) or these taxa are treated as two different species (*B. socotrana* s.str. and *B. aspleniifolia*; Thulin 2020; Lvončík, Řepka 2020). For practical purposes, we treat these taxa provisionally as two species here (Thulin 2020).

MATERIAL AND METHODS

Site selection and data collection. The study was conducted on *Boswellia* spp. [*B. aspleniifolia* (Balf. f.) Thulin, *B. elongata* Balf. f., *B. socotrana* Balf. f., and *B. dioscoridis* Thulin] at five sites on Socotra Island (Table 1; Figure 1). For all of the species, one population was studied, for *B. elongata* two populations were studied. We selected the five locations in cooperation with the local people for the site to be representative of the typical grazing regime of each area. The design of the exclosure experiment consisted of two plots, each 50 m × 50 m in size, one fenced and one unfenced (control) in each location and for each population. In the control plots free-ranging goat grazing continued, whereas within the fenced plots, grazing was prevented. A similar number of adult trees (2–8 adult trees) grew inside the two plots (Table 1). The exclosures were established in September 2020 and November to December 2021, and seedling appearance and mortality were monitored monthly until February 2023 (Table 1).

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Table 1. An overview of the experimental plots, their locations, species, coordinates and date of establishment for the four *Boswellia* species studied on Socotra Island

Locality*	Species	Coordinates	No. of trees inside fenced/unfenced plots	Start date	End date
Shata Qalansiyah	*B. aspleniifolia*	12°37'43.7"N, 53°35'36.5"E	3/3	21/09/2020	06/02/2023
Diburak	*B. elongata*	12°31'17.8"N, 54°16'41.3"E	2/2	25/09/2020	12/02/2023
Ma'ala (Maleh)	*B. elongata*	12°35'09.9"N, 53°28'29.1"E	3/3	15/11/2021	10/02/2023
Ayhaft Valley	*B. socotrana*	12°36'31.4"N, 53°59'24.9"E	8/8	14/12/2021	03/02/2023
Azgagah (Esgego)	*B. dioscoridis*	12°27'55.0"N, 54°00'24.1"E	3/3	19/11/2021	13/02/2023

* Alternative spellings of toponyms are included

Immediately after the establishment of each exclosure, all *Boswellia* seedlings encountered were recorded from the beginning of the first wet season (the period of germination; Table 1). Each seedling was marked with a wooden stick labelled with an individual code and the initial height was measured

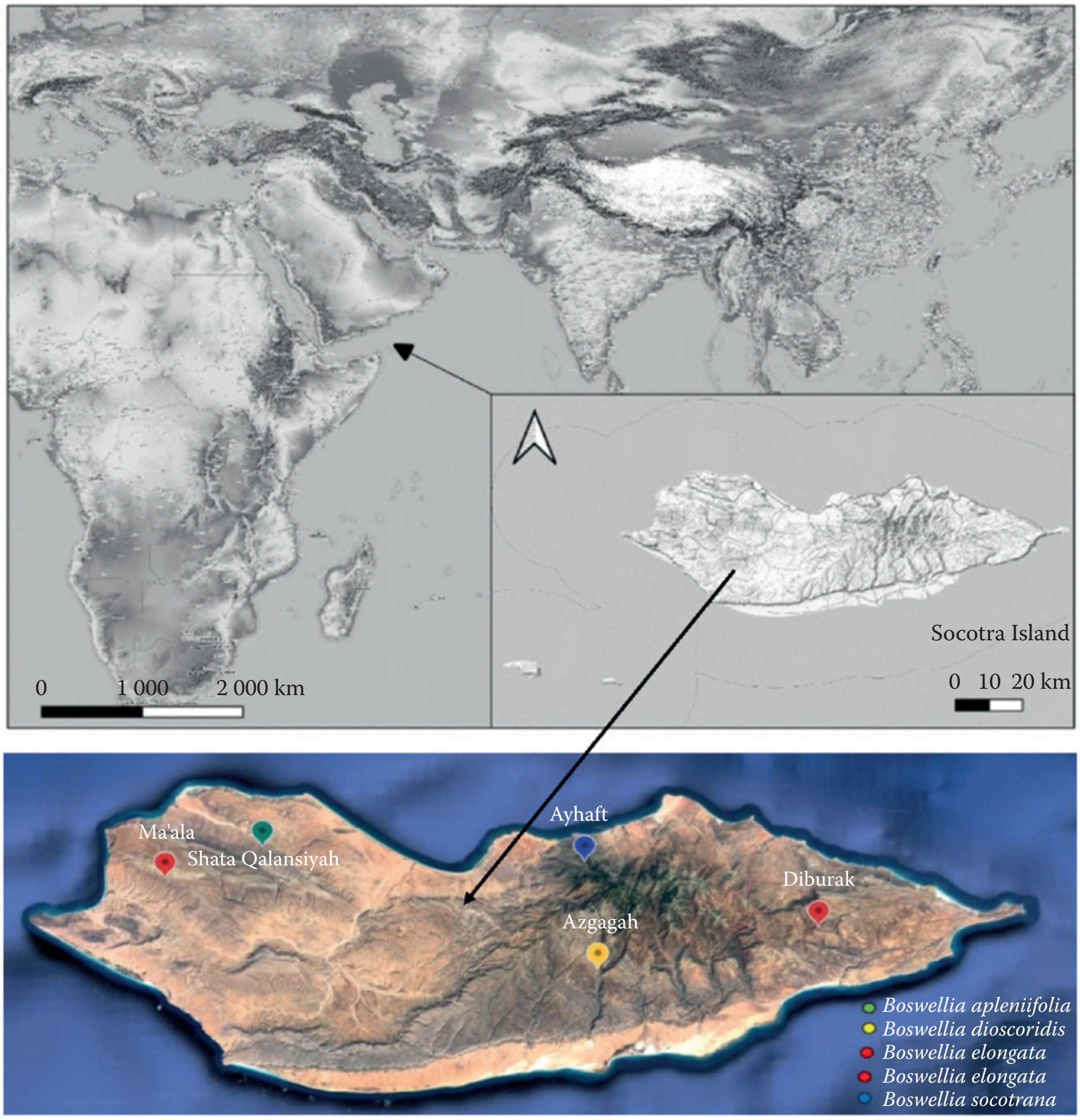

Figure 1. The location of the study area and the exclosure experiments on Socotra Island (Yemen)

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using a tape measure (Figure 2). Individual height measurements, seedling markings and the survival of previously marked seedlings were recorded every month from October to March for the duration of the study including the winter monsoon, the main growing season of *Boswellia* seedlings. The comparison was mainly conducted for three months each year after the start of the rainy season. In some years, the rain arrived in September, October, November, or December. We could not start or continue during the dry season (March to October). It is difficult to observe the seedlings because they do not have leaves, and it is also challenging to distinguish *Boswellia* seedlings from other species due to their appearance as dead sticks. Therefore, we started after the first rains so that we could count the dead and surviving seedlings accurately and measure the new growth as well. The date of the first observation of a new seedling and the date of the first observation of the death of that seedling were recorded in Excel.

Data analysis. Seedling mortality data was analysed using the survival analysis method (Kleinbaum et al. 1996). Seedling survival data was prepared by recording the date of the first appearance of each seedling as the beginning of its life, and the mean time between the last record of a live seedling and the first record of the death/disappearance as the date of death. The seedling longevity was calculated as the difference between these two dates. The seedlings that survived until the end of the study were right-censored in terms of the survival analysis approach (Kleinbaum et al. 1996). Kaplan-Meier survival curves were plotted for each study area at each location with seedlings' longevity (in days) on the x-axis and survival probability on the y-axis. Survival curves were compared using a log-rank test (Harrington, Fleming 1982) between the exclosures and control plots for each location and for each location/species. The survival analysis was performed using the R statistical environment 'survival' package (R Core Team 2022; Therneau 2023).

The total increase in height of each seedling was calculated as the difference between the first and last recorded heights of the seedling. All seedlings were included in this segment of the analysis regardless of whether they survived till the end of the study or died in between, but for the latter, only

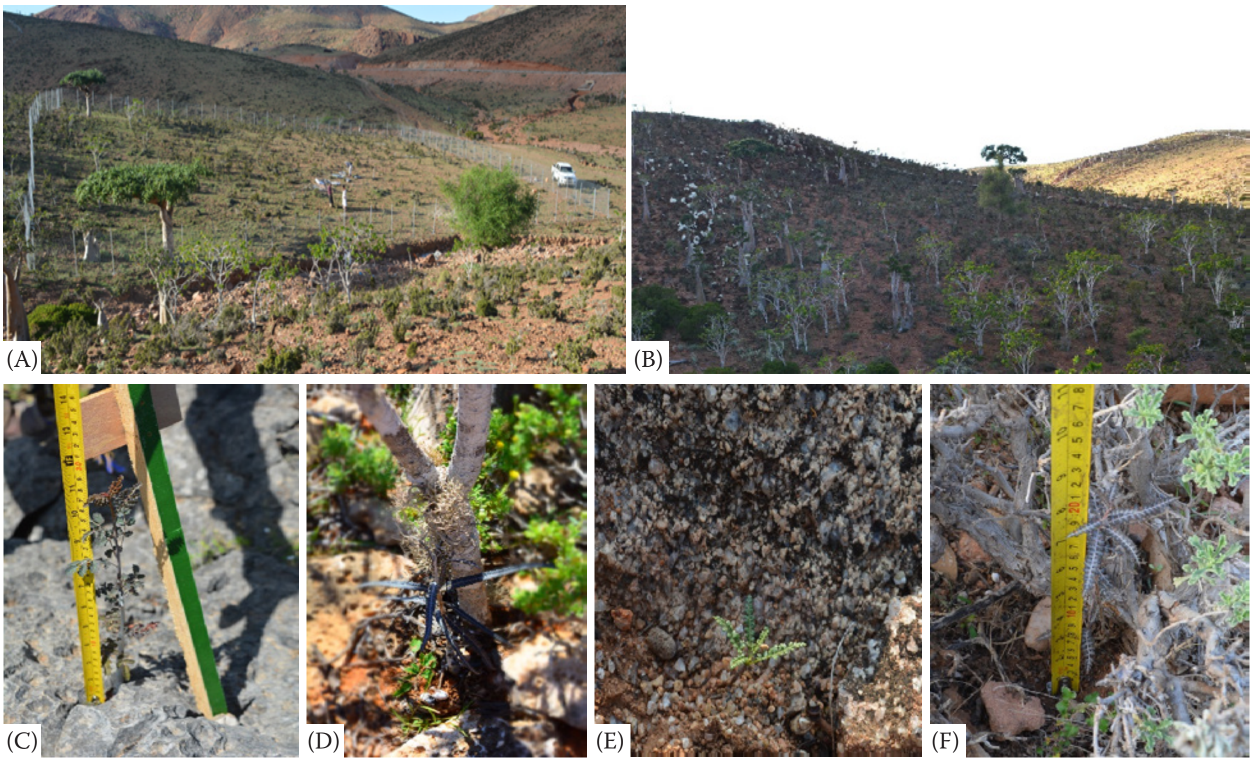

Figure 2. The marking and height measurement of *Boswellia* seedlings within fenced vs unfenced (control) plots on Socotra Island: (A) fenced plot; (B) control plot; (C) *B. dioscoridis* Azgagah; (D) *B. elongata* Ma'ala; (E) *B. socotrana* Ayhaft; (F) *B. aspleniifolia* Shata Qalansiyah

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the period observed alive was considered. Monthly height increments in cm per month (cm·month^{-1}) were then calculated for each seedling by dividing the cumulative increment by the duration of the seedling observed alive. The monthly height increments were then subjected to two-way analysis of variance (ANOVA) with species/location, fencing and their interaction as the effects in the model. Separate tests to compare plots were also performed for each location. The normality and homoscedasticity assumptions for the ANOVA analyses were assessed graphically. The incremental data was also evaluated within the R statistical environment (R Core Team 2022) using the 'lme4' package (Bates et al. 2015).

RESULTS

The results showed that, in general, significantly higher numbers of seedlings survived within the fenced plots than within the control plots (Table 2). Significant differences in the number of seedlings were found among species from different locations despite a similar number of adult trees within each location (Tables 1 and 2). The lowest seedling densities were observed for *B. elongata* at Diburak, but the same species at Ma'ala had much higher densities. The highest densities were observed for *B. dioscoridis* and *B. aspleniifolia* (Table 2).

Table 2 shows the number of seedlings found in the fenced and control plots over two or three years of observation. The number of seedlings that emerged as natural regeneration was generally significantly higher in the fenced plots than in the control plots; however, for some populations, the number of seedlings in both plots was very low (e.g. *B. elongata* in Diburak). For example, in 2020/2021, in Shata Qalansiyah (*B. aspleniifolia*) we found 118 seedlings in the fenced plot and 32 in the control plot, which continued to increase through 2022/2023 to 251 seedlings in the fenced plot and 86 in the control plot. The annual increase in the number of seedlings during the main germination period was equally clear for other locations and species (Table 2).

A comparison of survival probability among species. The general survival patterns between all species and locations, whether fenced or not, were highly significant ($P < 0.0001$). This indicates that cumulatively, the locations affected the species' survival probability. However, no significant differences were noted between *B. aspleniifolia* and *B. elongata* at Diburak ($P = 0.995$) and between *B. dioscoridis* and *B. elongata* at Ma'ala ($P = 0.995$). Both sites with *B. elongata* differed marginally ($P = 0.067$). *B. socotrana* seedlings had the lowest survival probability, less than 10% over 400 days of their life and already had a high level of mortality in the first months after their appearance. *B. aspleniifolia* had a survival of 64% over 400 days but then showed a lower survival probability (less than 40%) over 800 days. Similarly, *B. elongata* seedlings in Diburak had a survival probability of 61% over 400 days but then showed a lower survival probability of around 40% over 800 days. The highest survival probability, close to 70% over 400 days, was recorded for *B. elongata* in Ma'ala and *B. dioscoridis* in Azgagah (Figure 3 and Table 2).

Table 2. The cumulative number of *Boswellia* seedlings observed at different locations and their survival during 2nd or 3rd year from inside the fenced and control plots in Socotra Island from the period 2020–2023

Location	Species	Total number of seedlings						Survival (survival %)	
		2020/2021		2021/2022		2022/2023			
		fenced	control	fenced	control	fenced	control	fenced	control
Shata Qalansiyah	*B. aspleniifolia*	118	32	146	38	251	81	167 (67)	26 (32)
Diburak	*B. elongata*	15	14	16	16	20	16	13 (65)	5 (31)
Azgagah	*B. dioscoridis*	–	–	313	35	359	110	269 (75)	98 (89)
Ma'ala	*B. elongata*	–	–	51	15	106	63	105 (99)	41 (65)
Ayhaft	*B. socotrana*	–	–	20	0	36	26	4 (11)	6 (23)

The total amount of seedlings in the first columns refers to the cumulative numbers of seedlings for each site and each year; the last column (survival) compares the final number of surviving seedlings to the total number of seedlings that appeared over the entire period

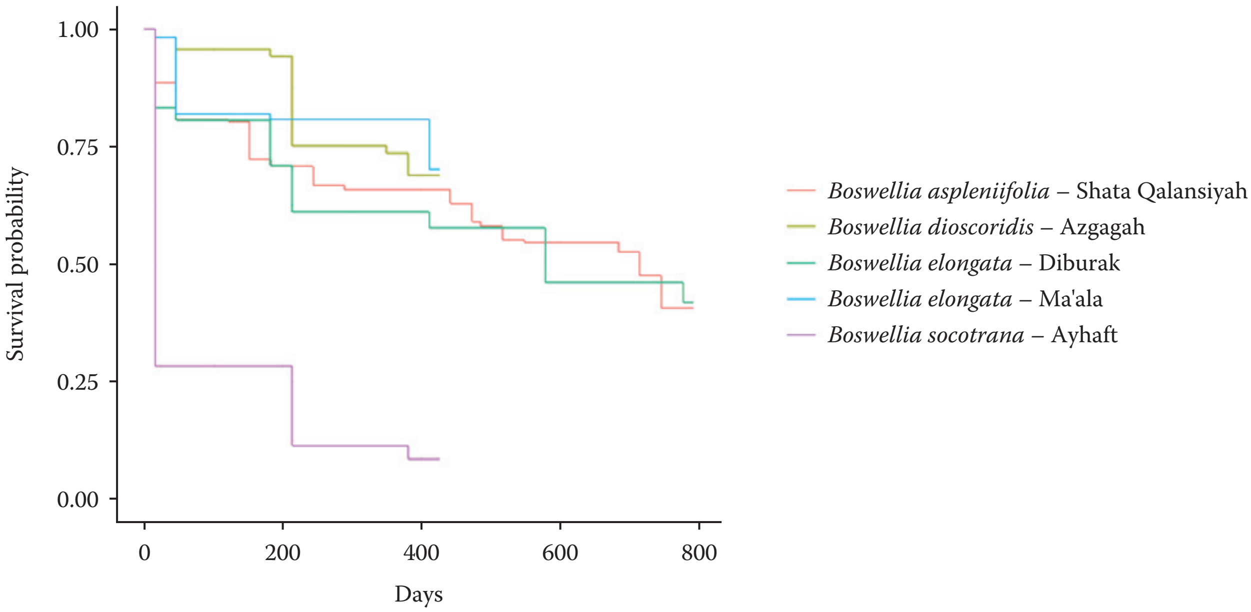

Figure 3. Survival curves for species/locations merged for fenced and control plots

Survival inside and outside the exclosures for all species/localities combined and a comparison of survival probabilities of fenced vs control plots for each species. The survival rate of seedlings in the fenced and control plots for all species and localities combined was highly significant ($P < 0.0001$), decreasing steadily with time, with the mortality rate in the control plots clearly higher throughout the entire observation period reaching about twice the mortality recorded for the fenced individuals. The only exceptions to the above observation were *B. dioscoridis* seedlings in Azgagah and *B. socotrana* seedlings in Ayhaft, where the survival probability of the seedlings in the fenced and the control plots was relatively the same with *P*-values of $P = 0.6547$ and $P = 0.5271$, respectively. It is noteworthy that for all the species and localities, steep declines in survival probability in the first few weeks of life of the seedlings were recorded mostly in the control plots. *B. socotrana* was observed for two years. However, during the first year, no seedlings were found in the control plot, while seedlings were found only in the fenced plot. This observation strongly suggests that there was significant grazing pressure in the control plot for *B. socotrana* (Figure 4 and Table 2). In the second year, we found seedlings both inside the fenced plot and the control plots.

Seedling height increase. All data on monthly height increments (Table 3) were first subjected to two-way ANOVA which showed that the effects of fencing ($P < 0.001$), species/location ($P = 0.065$) and their interaction ($P = 0.002$) were significant or marginally significant. The results for *B. aspleniifolia* – Shata Qalansiyah and *B. elongata* – Diburak (the bottom row of graphs in Figure 5) are treated together here because seedlings were measured for the full three years. We found a significant difference in the increase in height of *B. aspleniifolia* seedlings between fenced and control plots over three years ($P = < 0.001$). A significant difference was found in the height increment of *B. elongata* seedlings between fenced and control plots in Diburak ($P = 0.004$). The maximum monthly increase in height of the *B. aspleniifolia* seedlings was up to 8.2 $cm{\cdot}month^{-1}$ inside the fenced plot, whereas the seedlings in the control plot increased by a maximum of 1.0 $cm{\cdot}month^{-1}$. The maximum increase in height of the *B. elongata* seedlings (Diburak) in the fenced plot was 1.5 $cm{\cdot}month^{-1}$ and 0.4 $cm{\cdot}month^{-1}$ in control plots, respectively.

The increase in height of *B. dioscoridis*, *B. elongata* Ma'ala, and *B. socotrana* seedlings was only observed for two years. Although the increase in height of *B. dioscoridis* seedlings was significantly different for those within the fenced vs those in the control plots ($P = 0.004$), the height difference in that respect for *B. elongata* (Ma'ala) and *B. socotrana* was not statistically signifi-

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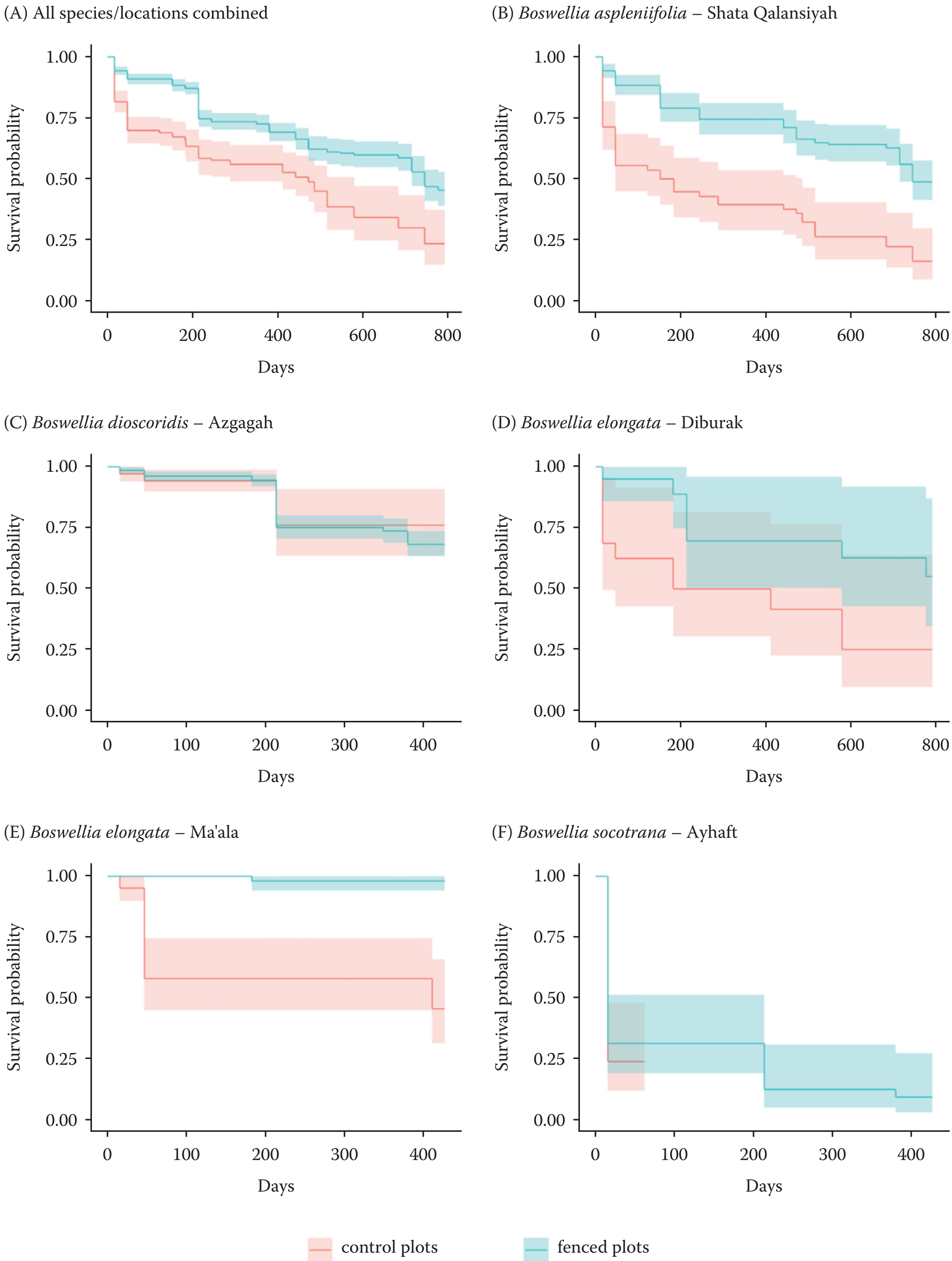

Figure 4. Survival curves for fenced and control plots (A) for all species/localities combined and (B–F) for each species/location separately

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Table 3. The average monthly increase in height (± standard error) of *Boswellia aspleniifolia*, *B. elongata* Diburak, *B. elongata* Ma'ala, *B. dioscoridis,* and *B. socotrana* seedlings in control and fenced plots per species/location

Seedlings	Height increase (cm)		Significance of the difference (P-value)
	control	fenced	
B. aspleniifolia – Shata Qalansiyah	–0.11 ± –0.09	0.45 ± –0.07	< 0.001
B. elongata – Diburak	0.46 ± –0.32	0.15 ± –0.12	0.040
B. dioscoridis – Azgagah	0.06 ± –0.04	0.29 ± –0.04	0.004
B. elongata – Ma'ala	–0.34 ± –0.09	0.22 ± –0.05	0.219
B. socotrana – Ayhaft	0.16 ± –0.30	0.23 ± –0.09	0.795

cant with P-values 0.219 and 0.795, respectively. The maximum monthly increase in height of the *B. dioscoridis* seedlings in the fenced plot was 6.8 cm·month^{-1}, while in the control plot, it was only 1.4 cm·month^{-1}. The Ma'ala *B. elongata* seedlings in the exclosure increased their height by a maximum of 2.9 cm·month^{-1} in both fenced and control plots. The smallest increases in height were recorded for *B. socotrana* (Ayhaft) seedlings in both fenced and control plots (maximum 1.0 cm·month^{-1}). Related to the negative growth increments in the fenced and control plots, some seedlings showed a reduction in height as a result of damage inflicted by goats grazing or other factors leading to the death of the apex part (Figure 5 and Table 3). Within the control plots, it was observed that the apex part of the seedlings was either eaten by goats or subjected to death. In case of the seedlings inside the fenced plots, the apex of some seedlings suffered death by drought or insect infestation, resulting in lowered follow-up measured height.

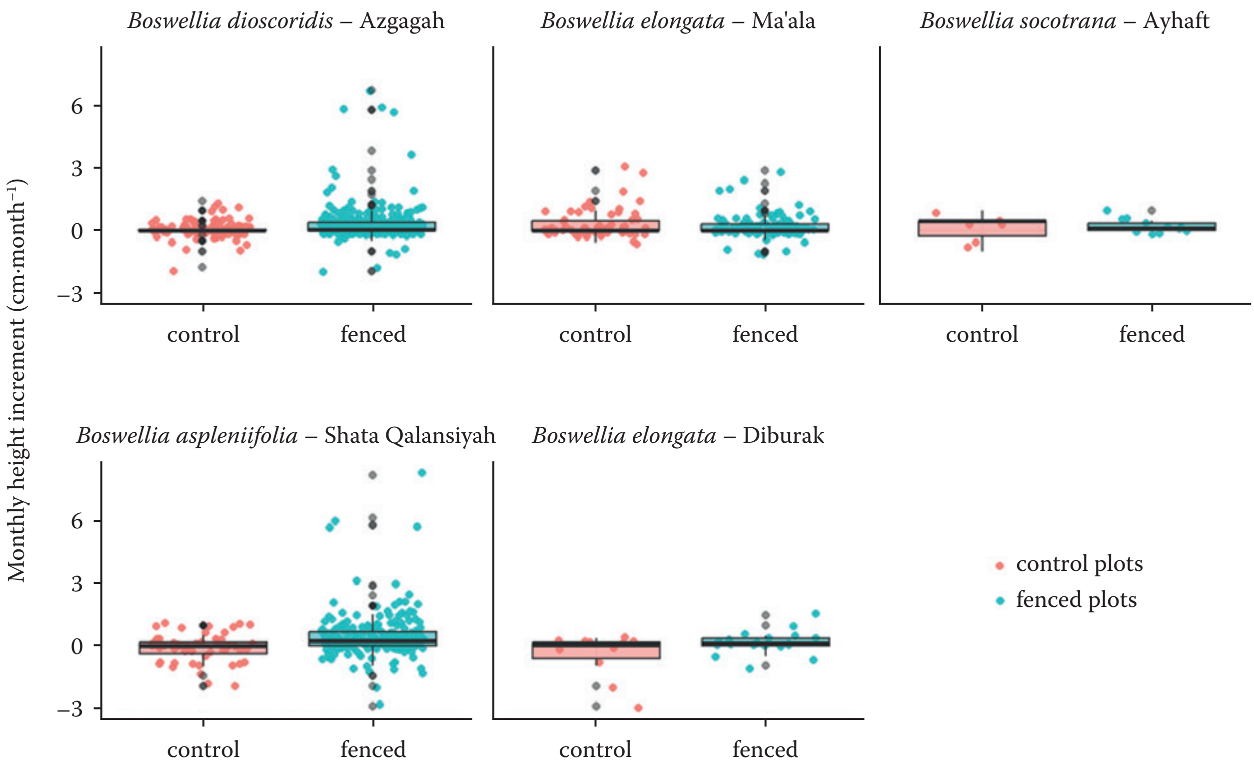

Figure 5. The monthly height increments in *Boswellia aspleniifolia*, *B. elongat*a Diburak, *B. elongata* Ma'ala, *B. dioscoridis*, and *B. socotrana* seedlings in the fenced and control plots for each of the separate species/locations

Boxplots and individual data values are shown; the upper row of graphs is for species with two years of data, the lower row for species of three years of data

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DISCUSSION

The emergence of *Boswellia* seedlings. Natural regeneration of frankincense trees on the Socotra Archipelago has faced many threats over the last few decades, such as increases in the quantity of livestock together with the abandonment of traditional methods of grazing management, which affects the entire terrestrial ecosystems (Scholte et al. 2007; Van Damme, Banfield 2011). In addition to a steady decline, unforeseen natural occurrences, such as cyclones and drought, have a strong impact on Socotran *Boswellia* in the wild (Lvončík et al. 2020), which also affects other species (Bongers et al. 2019). The reasons for decline could also be partly biological. However, all *Boswellia* species in Socotra produce a healthy proportion of viable seeds (Hamdiah et al. 2022). This result demonstrated that there is, at least, good potential for natural regeneration in some species and/or localities of Boswellia stands (Hamdiah et al. 2022). Nevertheless, there is also a large proportion of unfertilised seeds, which may indicate the presence of a problem with pollination or another biological/ecological factor (Raju et al. 2012). In low-density tree populations such as *Boswellia* species on Socotra, individual trees are spread far apart, leading to self-pollination dominating within each tree. However, cross-pollination proves to be more effective in terms of fertilisation and fruit development compared to self-pollination. Consequently, a considerable portion of the flowers on *Boswellia* trees on Socotra Island are expected to undergo self-pollination, leading to a higher number of empty seeds produced by these trees. Once they emerge, seedlings are vulnerable, especially those of ground-rooting species of *Boswellia* (Maděra et al. submitted 2023). Exclosure experiments (Habrová, Pavliš 2017; Fazan et al. 2021) provide an opportunity to examine the effect of specific conditions such as grazing, which is considered to be an important factor that prevents the natural regeneration of *Boswellia* woodlands in Socotra and beyond (Bongers et al. 2019).

The capacity for natural regeneration of *Boswellia* (sub)populations was obvious from our field experiments in Socotra. In both fenced and control (unfenced) plots, we found that *Boswellia* seedlings appeared naturally in every rainy season. It is a well-known fact that insular endemic plants often have spectacular recovery rates when immediate pressure (like grazing) is released. But it may not apply in general; Fazan et al. (2021) found only a few seedlings of *Zelkowa abelicea*, an endemic tree species of Crete Island, in less than 10% of their (both fenced and control) plots. The capacity for natural regeneration of the vegetation on Socotra was illustrated earlier by Habrová and Pavliš (2017), who recorded 49 woody species, of which 23 were endemic, in an exclosure of 1 000 m^2. Their study serves as compelling evidence, demonstrating the presence of regeneration capabilities within these communities. The same authors also mentioned that the number of individual woody plants remained almost the same after five years of fencing, and some died while others appeared (Habrová, Pavliš 2017). In such exclosures, it is typical for unpalatable species to disappear, while more palatable species (e.g. grasses) become more abundant (Habrová, Pavliš 2017). In the rangeland of Socotra, the unpalatable species are selected by goats grazing for centuries (Scholte et al. 2007) but many palatable species keep the ability to regenerate after fencing. The diverse *Boswellia* trees are prime examples of species that experience suppression due to grazing. However, they possess the remarkable ability to bounce back when grazing pressure is reduced or eliminated, such as when the areas are fenced. In our experimental plots (of 50 m × 50 m), the highest density reached was 1 436 seedlings per ha for *B. dioscoridis* and 1 004 seedlings per ha for *B. aspleniifolia*, while the lowest density found was 80 seedlings per ha for *B. elongata* in Diburak.

On the other hand, Negussie et al. (2008)'s study recorded 8 331 and 3 325 per ha of *B. papyrifera* in Jijike (northern Ethiopia) during the rainy season for exclosures and control plots, respectively, representing 19% and 11% seedlings survival in the first dry season during the study. It is noteworthy that Socotra Island records lower seedling densities as compared to other locations, such as Ethiopia, during exclosure studies. According to Habrová and Pavliš (2017), higher regeneration recorded in various exclosure experiments for fenced plots vis-à-vis control plots could partly be due to the buildup of humus layer from dead grass and plant biomass. However, per the high mortality rates especially in the early stages even without grazing pressure, other ecological factors could be at play here. Muchiru et al. (2009) noted that arid areas such as Socotra which have extensively been used by transhuman pastoralists for a long period could

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be the reason for the slow natural regeneration, hence the need to protect seedlings from grazing for a much longer period. This assertion is supported by Maděra et al. (2019b) suggesting that *Dracaena cinnabari* would need to be protected for at least 50 years to escape browsing pressure on Socotra.

Our study confirms that a high number of *Boswellia* seedlings appear after every monsoon in both absence as well as presence of grazing, and that they have a relatively better chance of survival if they are protected from grazing. Important to note here is that regeneration remains possible if there are still adult trees in the area, as the seeds have high germination rates (Hamdiah et al. 2022), as long as the seedlings are well protected.

***Boswellia* seedling recruitment.** Seedling recruitment is a bottleneck in plant population dynamics (Garnier et al. 2021). At the beginning of their lives, seedlings are most sensitive to environmental factors such as light level, competition with other plant species, herbivores, diseases, and resource limitations which cause high mortality rates (Lavine et al. 2002; Negussie et al. 2008). We observe that the *Boswellia* seedling mortality rates for all species and locations in Socotra were at their highest in the first weeks after germination, varying from 2% to 75%. The early-stage mortality was high in both fenced and control plots, which means that other factors, not only grazing, are important in causing seedling mortality in the early stages. The significant differences in the survival probability between species and locations also indicate that local environmental (and perhaps climatic) factors have an important impact on *Boswellia* seedling mortality. Grazing plays an important role during early-stage seedling mortality because in the control plots, the survival rates were always lower than in the fenced plots.

Although it was not studied in detail here, *Boswellia* seedlings survival is likely to increase with the occurrence of nurse plants. Rejžek et al. (2016) and Habrová and Pavliš (2017) showed this convincingly using *Dracaena cinnabari* as a case study, which can act as an important nurse plant on Socotra Island. We saw that *Boswellia* seedlings prefer small unpalatable shrubs as nurse plants, such as *Pulicaria stephanocarpa* or spiny shrubs like *Lycium sokotranum* which were present in some of our study plots (pers. obs.). Nurse shrubs may 'catch' the seeds that are carried by the wind from the mother tree and protect the seedling not only from grazing but also generate an improvement in the local environment by capturing humid air (Kalivodová et al. 2020), providing shade and promoting the humus layer.

At a later stage, grazing plays an even greater role in the survival of the *Boswellia* seedlings in the wild. Our results show that later-stage mortality decreased and the survival probability of seedlings in the fenced plots became significantly higher in comparison to the control plots in all species (except for *B. socotrana*). It means that the effect of livestock pressure became more important than any other environmental factor in later-stage *Boswellia* seedling mortality, after two to three years. This is also related to the fact that during the dry season, grazing pressure on *Boswellia* increases as there is a limited choice of vegetation to browse. This also means that any future climate impacts (e.g. prolonged and increased droughts) will worsen the impact of grazing on the island.

For all the *Boswellia* species studied, a considerable proportion of seedlings survived in the grazed plots, and these were mostly (at least partly) protected by a nursing plant/shrub or rocks/crevices unreachable by goats (pers. obs.). In addition, there is a high regenerative capacity of older *Boswellia* seedlings even after they have been repeatedly browsed. Our observations, in many areas of Socotra Island, of very small (dwarf) browsed forms of different *Boswellia* species (pers. obs.) also support this. Similarly, many other tree species on Socotra have the same regeneration capacity that has been selected for by long-term grazing pressures (Maděra et al. 2019b), probably for several millennia when livestock was thought to be first introduced along with the first human colonisation (Černý et al. 2009).

However, our study also shows that even if livestock browsing is entirely excluded in an area, the survival of the local *Boswellia* populations in Socotra is not guaranteed. After only two to three years, the seedlings in some populations, protected by our fenced plots, had dropped to 10% or less. This indicates that other factors, likely also the local climate (e.g. potentially prolonged droughts), are still important factors that need to be examined, and considered in any local conservation strategy. Although we did not study the difference between cliff- and ground-rooting species in detail, the seedlings of the only cliff-rooting species in our study (*B. dioscoridis*), generally had a remarkably high survival rate with or without grazing (almost 75%) as a consequence of the opportunity to grow in small cracks between boulders which provide a useful micro-climate (also grazing pressure is lower here). Similarly, the higher natural regeneration is mentioned by Attorre et al. (2011) in another cliff-rooting species *B. popoviana.* Ground-rooting species of *Boswellia*, such as *B. elongata*, may generally be more vulnerable, in particular in areas where the substrate and ground vegetation are less-well developed.

The increase in height of *Boswellia* seedlings. The majority of *Boswellia* populations showed significant differences in seedling height increase in the absence of grazing pressure, except for *B. socotrana* in Ayhaft and *B. elongata* in Diburak. In the control plots, goats actively grazed on the seedlings which affected tree growth. Similarly, authors who have used exclosures in other areas consider grazing to be the main factor that negatively affects the growth of *Boswellia* species (Ogbazghi 2001; Farah 2008; Negussie et al. 2008).

The absence of grazing led to significant increases in the height of seedlings, which were quite remarkable in some cases. The results report increments in cm·month^{-1}, whereas cumulative increments are reported here to compare our results with other studies. Within exclosures, we observed average annual height increments ranging from 0.35 cm to 2.45 cm in different *Boswellia* species. However, the growth is not steady and is happening in bursts with respect to water availability. We found that the growth rate is closely related to the occurrence of rainy seasons. The maximum observed growth during these bursts was 8.2 cm·month^{-1}. However, when considering the annual growth, the maximum average rate we observed was 13.3 cm·year^{-1}. These increases in height took place without any additional (artificial) watering, indicating that *Boswellia* seedlings in Socotra can grow rapidly in their natural environment in the absence of grazing pressure, but, in the *B. elongata* seedlings in Diburak, the increase in height of the seedlings did not greatly differ with or without grazing. In the juvenile stage, *Boswellia* species on Socotra are considered to grow quite slowly, similar to *Dracaena cinnabari* (Maděra et al. 2019a). Eslamieh (2011) documented the height of a year-old seedling of *B. elongata* at 30 cm, but this plant was cultivated and regularly watered. Tolera et al. (2013) found that *B. papyrifera* grew much more quickly (seedlings reached heights of 1 m after 4 years). However, in general, the growth of some of the individual seedlings in our study, in natural conditions, was remarkably quick.

CONCLUSION

Frankincense trees are a vital asset in Socotra because of their medicinal properties and their place in the island's natural history and cultural heritage. Therefore, their survival is crucial to the local human population and culture. Our study confirms that grazing has an undeniably negative impact on the survival and growth of the seedlings of the endangered and endemic *Boswellia* species on Socotra. We demonstrate that employing exclosures can be an important strategy in future conservation efforts. This technique, to some extent, helps to promote the growth and survival of *Boswellia* trees. However, long-term monitoring of the impact is crucial as shorter-term measurements (here 2–3 years) may represent over or underestimations of the long-term survival and growth. We observed that even in the absence of grazing, seedling mortality during the early stages can still be high for some populations (50–90%). Therefore, the effects of other factors (potentially drought or habitat quality) should be taken into account to help and protect these important tree species in the future. The protection of adult trees remains crucial, as they are the annual source of seeds. The use of exclosures in cooperation with the indigenous people can be applied to the local *Boswellia* populations. The approach will not only be beneficial to produce more seedlings of frankincense trees and enhance natural regeneration, but it will also benefit other endemic plant and animal species which all contribute to providing a thriving ecosystem, and to the local people who benefit from the many ethnobotanicals uses.

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