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Frankincense in peril

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The harvest of plant parts and exudates from wild populations contributes to the income, food security and livelihoods of many millions of people worldwide. Frankincense, an aromatic resin sourced from natural populations of *Boswellia* trees and shrubs, has been cherished by world societies for centuries. *Boswellia* populations are threatened by over-exploitation and ecosystem degradation, jeopardizing future resin production. Here, we reveal evidence of population collapse of *B. papyrifera*—now the main source of frankincense—throughout its geographic range. Using inventories of 23 populations consisting of 21,786 trees, growth-ring data from 202 trees and demographic models on the basis of 7,246 trees, we find that over 75% of studied populations lack small trees, natural regeneration has been absent for decades, and projected frankincense production will be halved in 20 yr. These changes are caused by increased human population pressure on *Boswellia* woodlands through cattle grazing, frequent burns and reckless tapping. A literature review showed that other *Boswellia* species experience similar threats. Populations can be restored by establishing cattle exclosures and fire-breaks, and by planting trees and tapping trees more carefully. Concerted conservation and restoration efforts are urgently needed to secure the long-term availability of this iconic product.

Worldwide, tens of thousands of plants and animals are exploited from wild populations[1,2]. These natural products provide income, safeguard livelihoods and contribute to food security of millions of people[3]. Over-exploitation of wild populations causes population collapses, imperils resource supply and is a major threat to global biodiversity[4,5]. Natural ecosystems harbouring wild populations are threatened by habitat loss and a variety of anthropogenic disturbances, including grazing, fire and conversion to other land uses. Sustainable management of wild populations and their ecosystems is a major global conservation challenge, with direct implications for international treaties on species trade (Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES) and biodiversity conservation (Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services, IPBES).

Frankincense, an iconic product harvested from wild populations, is obtained by tapping natural resins from the bark of several species of *Boswellia* trees. For millennia, frankincense resin has been harvested, traded and used during cultural and religious ceremonies and as an ingredient in perfumes. In classical times, huge amounts of frankincense were supplied to the Greeks and Romans through well-organized 'frankincense trails' from the Southern Arabian Peninsula and the Horn of Africa[6].

Here we study threats and future production of the main frankincense-producing species of this time, *Boswellia papyrifera*. To put our study in context, we first review distribution, threats and production of the main frankincense-producing *Boswellia* species.

Frankincense sourcing: production and threats

Frankincense is chiefly produced by five *Boswellia* species, distributed from West Africa to India, with highest diversity in the Horn of Africa (Fig. 1). Frankincense production differs widely among species: *B. papyrifera* is the main producing species at present, while the contribution of *B. sacra* from the Arabian Peninsula to resin trade is currently negligible (Supplementary Table 1). All *Boswellia* species are threatened by habitat loss, fire, grazing, heavy exploitation and/or insect infestations (Fig. 1).

For the past millennia, *B. sacra* was the main source of high-quality frankincense, a shrub-like tree growing in dry habitats in Oman, Yemen and Somalia. Habitat loss, droughts, strong winds and intense tapping have greatly reduced populations of this species[7], resulting in its inclusion in the International Union for Conservation of Nature (IUCN) Red List as near threatened. In Somalia, the situation of *B. sacra* (and *B. frereana*) populations is alarming[8] with ample evidence of careless tapping and full debarking (Fig. 1), resulting in tree death and increasing scarcity. *B. serrata* is widely distributed and has been a major source of resin for many centuries. However, studies of wild populations show that populations are affected by grazing, fire, high adult tree mortality and lack of regeneration[9–11], resulting in low production and declining

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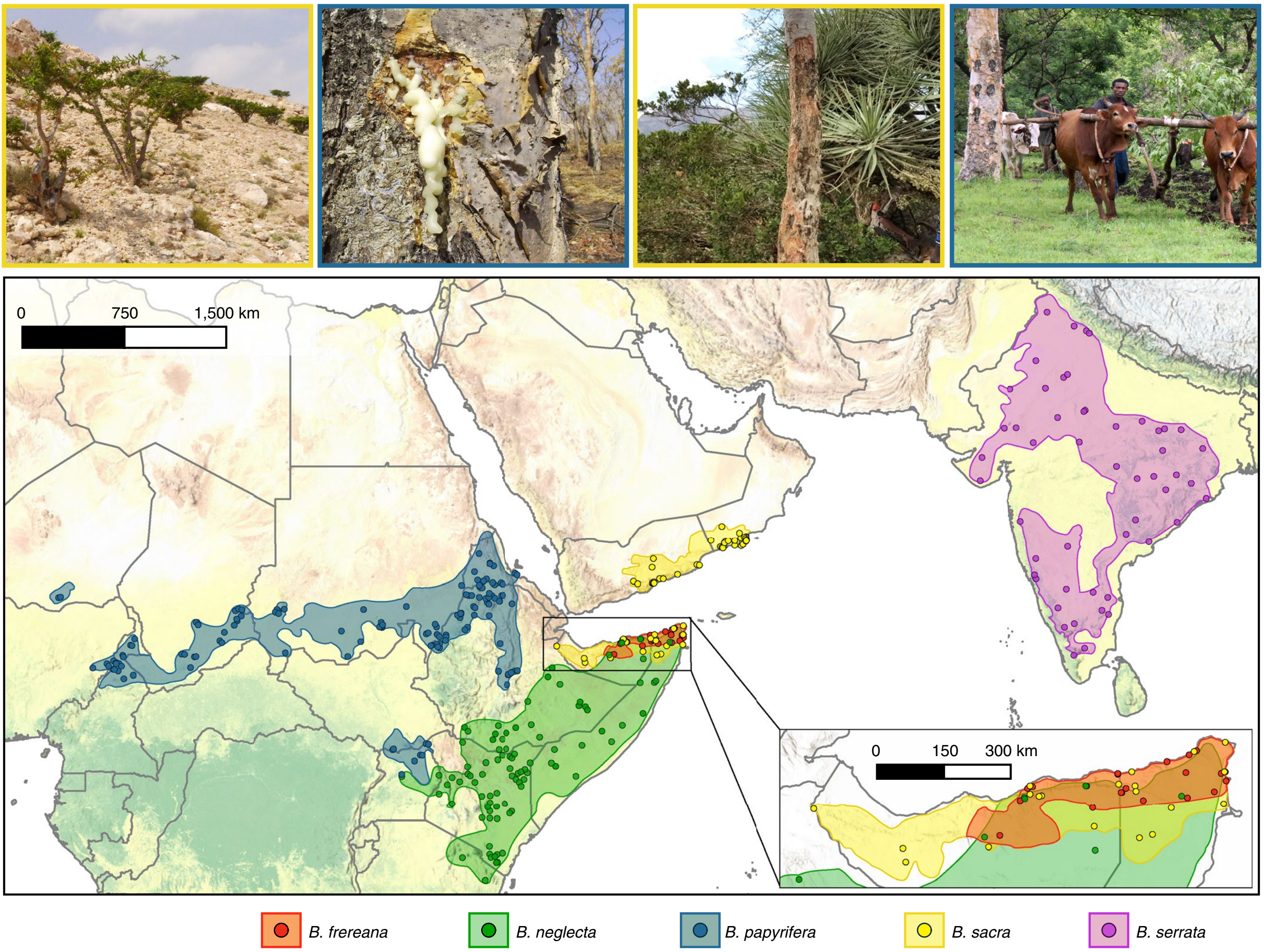

	🟥 *B. frereana*	🟩 *B. neglecta*	🟦 *B. papyrifera*	🟨 *B. sacra*	🟪 *B. serrata*
Trade (ton yr^{-1})	200	100–300	3,500–4,000	1,400–2,000	~100
Habitat loss	some	yes	yes	some	yes
Grazing	no	yes	yes	no	yes
Over-exploitation resin	yes	no	yes	yes	yes
Over-exploitation wood	no	yes?	yes	no	yes
Fire threat	no	no?	yes	no	yes
Insects	yes	no	yes	yes	no?
Lacking regeneration	no	no?	yes	no?	yes

Fig. 1 | Distribution of major frankincense-producing species and main threats to existing populations. Dots represent known locations of *Boswellia* species on the basis of several sources (Global Biodiversity Information Facility, www.gbif.org; herbarium and tree inventories). The table includes estimated international resin trade and threats to all species. *B. sacra* from Oman and from Somalia (*B. sacra-carteri*) are pooled. Photographs show species and their threats (from left to right): *B. sacra* shrubs (Oman), frankincense from *B. papyrifera* trees (Ethiopia), debarked *B. sacra-carteri* tree (Somaliland) and conversion to agriculture of *B. papyrifera* forest (Ethiopia). Photo credits from left to right: F. Bongers, F. Bongers, A. DeCarlo, F. Bongers. Hillshade layer credit: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS user community.

populations[12]. Frankincense collection from *B. neglecta* does not require tapping but is obtained by natural oozing from stems and branches, with little impact to populations. Yet, these populations are affected by land use change, tree killing for firewood and seedling mortality due to cattle browsing.

Frankincense sourcing has shifted over the past decades: *B. sacra*, *serrata* and *frereana* used to be the main producing species. Since the 1990s, *B. papyrifera* has been the main source of frankincense globally, accounting for about two-thirds of production[7,12,13] (Fig. 1 and Supplementary Table 1). In Ethiopia, production from *B. papyrifera* is affected by conversion of woodlands into agricultural land, initially in the highlands but in recent years also in the lowlands bordering Sudan[14]. Forest conversion is associated with rapid increase in human population and accompanying

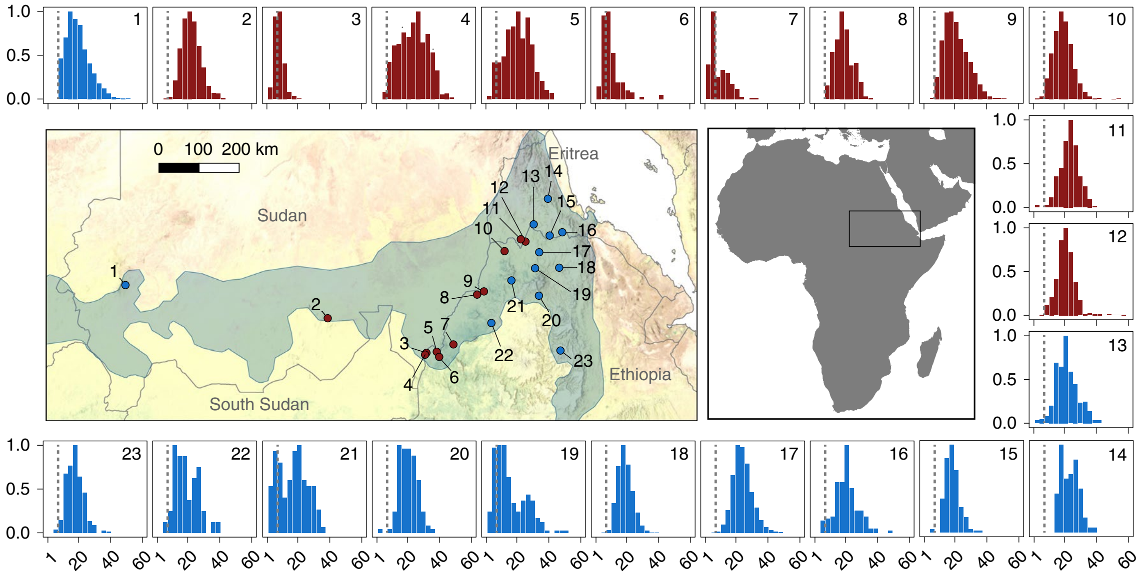

Fig. 2 | Distribution and size structures of *Boswellia papyrifera* populations. Map shows distribution of *B. papyrifera*, the main global source of frankincense, and locations of 23 *B. papyrifera* populations included in this study from highland (blue) and lowland (red) sites. Size structures are on the basis of relative abundance (highest class, 1) in 3-cm-wide tree diameter classes (minimum diameter, 1 cm). Size structures show that small, juvenile trees (<7 cm stem diameter, grey dashed vertical lines) are often missing, potentially due to cattle ranging and frequent fires. Site information is given in Supplementary Table 2. Hillshade layer credit: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS user community.

expansion of cattle and goat herds. Forest loss causes remaining woodlands to be heavily exploited[14,15], impacted by grazing and frequent fires and susceptible to disease and insect attack[16,17]. In Eritrea, *B. papyrifera* has disappeared from >40% of villages over the past decades[18,19]. Agricultural expansion and increased grazing pressure especially affected *B. papyrifera* at the northern limit of its distribution in Eritrea. In Sudan, the three frankincense regions are under heavy pressure from forest loss and fuel wood extraction due to war (Darfur, Kordofan), refugee camps (Blue Nile) and conversion to agricultural lands[20].

Cryptic changes in the main frankincense species

Conversion of *Boswellia* woodlands to other land uses can be observed by remote sensing[14,20] and used to estimate productivity loss. The effects of cryptic changes such as fire, grazing and insect infestation on frankincense production are probably also large but quantifying these is challenging. Empirical evidence is scarce: first reports suggest effects on regeneration, tree mortality and population decline of *B. papyrifera* at local scale in Ethiopia[13,21]. A key question is whether cryptic collapse of *B. papyrifera* populations has the potential to threaten frankincense production globally.

Here we assess evidence of demographic collapse of *B. papyrifera* throughout its distribution range and evaluate implications for global frankincense production. We do so using a combination of demographic field studies, tree-ring analyses and modelling (see Methods). We studied size distributions of 23 populations in Eritrea, Ethiopia and Sudan (Fig. 2) to evaluate regeneration status. Together these populations cover 157 ha, contain 21,786 individuals and include the full altitudinal (604–1650 m above-sea-level, a.s.l.), rainfall (489–1263 mm yr^{-1}) and temperature (mean annual temperature, 16.5–27.7 °C) ranges experienced by *B. papyrifera* (Supplementary Table 2). In four of these populations, we collected tree-ring data ($n = 202$ individuals; Supplementary Table 3) to quantify the period of the regeneration failure. In another four populations, we performed demographic studies on 7,536 trees and constructed demographic models[22] (Supplementary Table 4) to simulate the development of populations and frankincense production for the next 50 yr.

Results

We found evidence of strong regeneration failure across the distribution range of *B. papyrifera*. The population recruitment index (fraction of saplings, 1–4 cm in stem diameter, in the population) was <4% in 78% of the study populations (Fig. 2 and Supplementary Table 5). In 57% of the populations not a single small tree was found, indicating complete regeneration failure (Fig. 2). Thus, in spite of the typically large seed crops produced[23], high germination rates[23] and local abundance of young seedlings[19,24], seedlings do not transition to saplings (>1 cm stem diameter) in most populations.

How long has this regeneration failure gone on? As *B. papyrifera* produces annual growth rings, we could answer this question using tree-ring analyses[21]. We established age–diameter relationships (Supplementary Fig. 1) and used these to estimate the year of recruitment of all individuals in four populations. Age distributions revealed that regeneration was entirely absent during the past half-century in two populations (means of year at which youngest individual recruited: 1951 and 1956, and 95% confidence intervals (CI: 1944–1958 and 1950–1961 respectively) and virtually absent during the past quarter-century in two others (mean 1967 (CI 1956–1978) and 1988 (CI 1970–2006); Fig. 3). If age–diameter relations of these four populations are representative for those of the other 19 study populations, these results suggest regeneration failure during several decades across the Horn of Africa (Fig. 2). Regeneration failure could also explain why most *B. papyrifera* populations are currently dominated by large, old trees.

As altitude is a proxy for climatic conditions in the study areas, we grouped the study sites in a lowland (<1100 m a.s.l.) and in a highland class (>1100 m a.s.l.; see Methods). Lowland and highland populations differed in growth (stem diameter growth is 3.30 versus 1.48 mm yr^{-1}, $P < 0.001$, adjusted $R^2 = 0.08$, d.f. = 15,072) and fecundity (30.6% versus 92.7%, $P = 0.04$, d.f. = 443) but not survival (89.3% versus 94.9% per year, $P = 0.238$; see Methods,

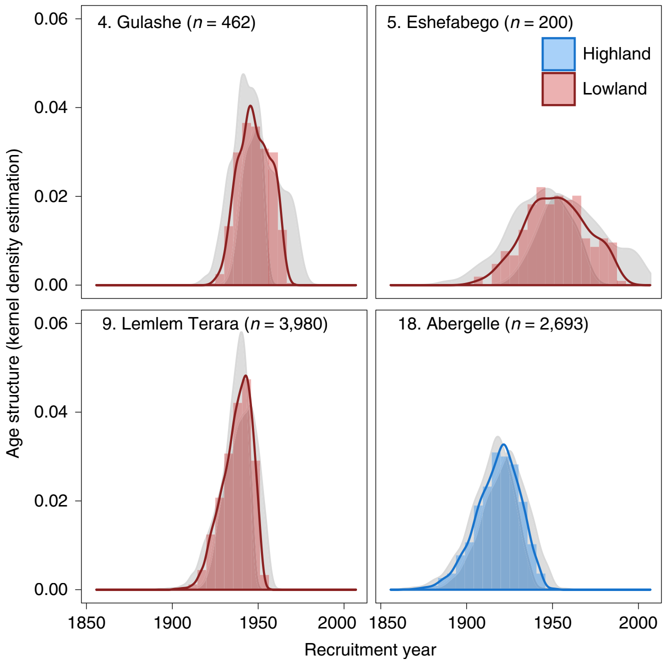

Fig. 3 | Regeneration failure in *Boswellia* populations obtained from tree-ring analysis. Distributions of the estimated calendar year of recruitment (bars and coloured lines) for four populations and their 95% CI (shaded area) on the basis of uncertainty in the age–diameter relations (Supplementary Fig. 1). Population numbers as in Fig. 2.

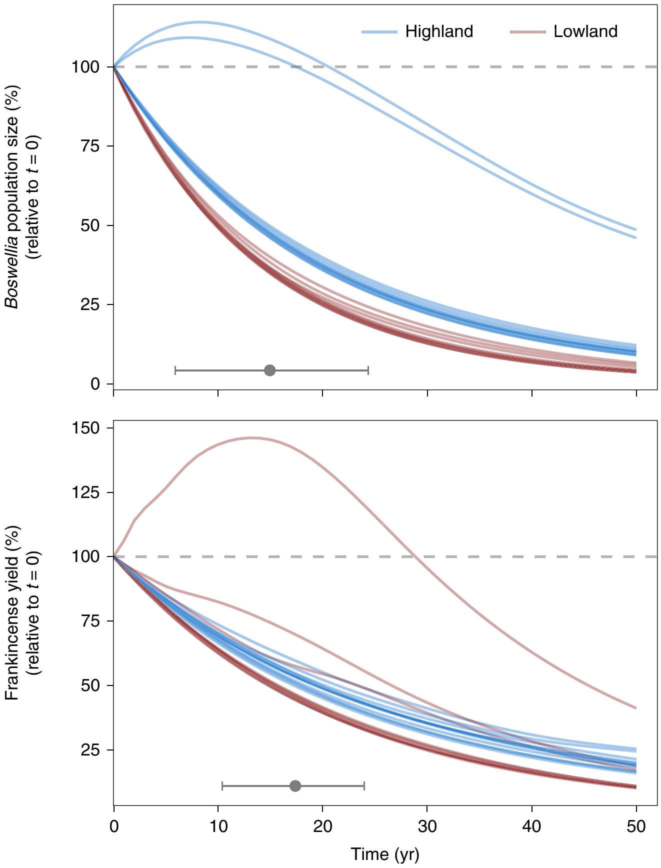

Fig. 4 | Projected development of *Boswellia* populations and frankincense yield at 23 sites. Projections show rapid decline of both population size and frankincense yield across the Horn of Africa, in both highland (blue; $n = 12$) and lowland (red; $n = 11$) classes. Each line represents the average population and yield projection of the 250 bootstrapped Integral Projection Model runs. Lines are semitransparent to allow for visualization of overlapping projections (see Supplementary Fig. 4 for individual graphs per site). Dots represent average time (whiskers, 1 s.d.) to reach 50% of initial population size and yield.

Supplementary Table 5 and Supplementary Figs. 2 and 3). We therefore constructed separate demographic models for lowland (11 populations) and highland (12 populations) populations. We also distinguished between 5 regenerating (recruitment index >4%) and 18 non-regenerating populations. To simulate development of regenerating populations, we included recruitment of saplings; for non-regenerating populations, we assumed no saplings recruited during the 50-yr simulation period.

All model versions (for highland and lowland, regenerating and non-regenerating populations) projected rapid declines of our study populations for the coming decades. After 25 yr, projected population size declines by 71.2% on average. A 50% reduction in population size is reached in 15.2 ± 9.6 yr (average ± s.d.; Fig. 4). As expected, populations without recruitment declined faster (75.7% reduction in 25 yr) than regenerating populations (52.2%; Fig. 4). Lowland populations declined faster (80.5% reduction in 25 yr) than highland populations (61.5%), mainly due to a higher mortality of adult trees (Supplementary Fig. 3). The only populations showing temporary increases are regenerating highland populations but their initial increase is nullified by high adult mortality after two decades.

To evaluate the implications of population decline for frankincense production we combined population projections with information on resin production of individual trees. An average highland tree produces 464 g of frankincense per year, while a lowland tree produces less (342 g yr^{-1})[25,26] (Supplementary Fig. 2c). Using the projections of population development, frankincense production will drop drastically and rapidly in all but one populations over the next decades (Fig. 4, Supplementary Fig. 4 and Supplementary Table 5). Averaged across populations, frankincense production will drop by 50% in 19.0 ± 7.0 yr (average ± s.d.), with slightly longer periods in lowland (21.3 yr) than highland (17.0 yr) classes. Frankincense production decreases more slowly in regenerating (50% reduction in 27.8 yr) compared with non-regenerating populations (16.6 yr) but the presence of regenerating trees is insufficient to sustain productivity at present-day levels.

Our simulation results are robust to variation among individuals in our datasets and to the separation into lowland and highland sites. First, the 250 population trajectories resulting from bootstrap analysis show very little variation (Fig. 4), indicating high robustness of our results to demographic variation. Second, we evaluated the robustness to lowland versus highland separation by performing simulations of all 23 sites using either lowland or highland models, and its effect on frankincense yield. The projections show robustness to this major modelling change. The years needed to reach 50% of initial population shifted only slightly: from 15.2 ± 9.6 yr (standard simulations) to 16.7 ± 9.0 yr when using highland models and 10.2 ± 0.5 yr when using lowland models for all populations. Time to 50% reduction in frankincense yield shifted even less: from 19.0 ± 7.0 yr (standard simulations) to 18.0 ± 5.7 yr (highland rates) or 19.5 ± 6.8 yr (lowland rates) (Supplementary Fig. 5).

Our 23 study sites are representative for *B. papyrifera* woodlands in general, as quantified through woodland tree cover and changes in tree cover for our sites compared to those obtained for other locations with known occurrence of *B. papyrifera*, and through comparison with *B. papyrifera* presence locations, random locations in *B. papyrifera* distribution area and GBIF herbarium collection locations (Supplementary Method 1, Supplementary Note 1 and Supplementary Fig. 6).

Discussion

Magnitude of population collapse. Our projections show fast collapsing *B. papyrifera* populations and a 50% reduction of frankincense yield in the next two decades. The study sites were mostly located in dense, relatively intact, frankincense woodlands. The evaluation of forest cover change on the basis of Global Forest Watch (GFW) facility[27] suggests low rates of forest conversion for our sites (Supplementary Fig. 6b). Yet, this remote-sensing product only detects tree cover (changes) for trees >5 m high, which is taller than many *Boswellia* woodlands. Caution is needed in its interpretation[28] as actual cover change is probably considerably higher, including in *Boswellia* areas[14,20].

Our estimate of population decline is conservative because: we did not account for conversion of *B. papyrifera* woodland to agricultural land; and we ignored possible effects of woodland fragmentation on population development. The overall decline of *B. papyrifera* populations across its distributional range is probably considerably larger than projected.

The projected population declines of *B. papyrifera* are sufficient to consider inclusion of this species as vulnerable in the IUCN Red List, following its criteria[29]. With an estimated >30% area reduction over the past three generations, and ongoing severe threats, the species would classify as vulnerable in the specific category of VU-A2cd +3 cd. So far, 13 out of the 19 *Boswellia* species are red-listed (Supplementary Table 1). During the 2019 CITES meeting, the *Boswellia* genus received special attention. Our results for *B. papyrifera* provide useful empirical data and arguments to support policy development both through CITES and other mechanisms.

Drivers of population collapse. What explains the population collapse of *B. papyrifera* found here? First, lack of regeneration for extended periods of time is a factor. Lack of favourable climatic conditions has been shown to cause regeneration failure of woody plants in arid environments[30] but this is probably not the case for *Boswellia*. Wet episodes that would have allowed regeneration in *B. papyrifera* populations did occur in the region over the past 50 yr[31–33]. Also, past episodes of tree regeneration reconstructed from tree-ring analyses did not coincide with periods of high rainfall[21]. Therefore, the most plausible explanation for regeneration failure is reduced recruitment due to intensified cattle grazing pressure and associated higher burning frequency, in addition to unsustainable tapping practices that have weakened trees, reduced seed production and lowered seed quality[23,34].

Second, high mortality of adult trees affects population size. Elasticity analyses show that projected population growth rate during the next 50 yr was highly sensitive to changes in survival (97–99% of total elasticity; Supplementary Fig. 7). High mortality occurs naturally in aging populations but this is unlikely to be the only explanation. *Boswellia* trees are currently tapped at much higher intensity than before, with dramatic consequences for seed production and size[23], and for carbon reserves[35], diminishing tree survival and future resin production[15]. Reduced tree vitality may induce a high sensitivity to insect damage, especially to longhorn bark beetles[17,36], probably contributing to mortality. Tapped trees are also easily infested by a pathogen fungus known to cause stem cancer[16]. High mortality and low recruitment of *B. papyrifera* may lead to change in species composition of woodlands. *Boswellia* woodlands are reported to gradually shift into woodlands dominated by less sensitive species, such as *Acacia*[20,37].

Measures to reverse yield decline. The projected collapse of *B. papyrifera* populations indicates a 50% decline in frankincense production in 20 yr. What can be done to counteract this yield decline? We issue a stark warning against short-term tapping intensification as a means to mitigate gradual yield decline, as more intense tapping damages trees and is unsustainable[23,35]. Counteracting yield declines requires tapping intensity to be reduced, rather than increased. We suggest immediate reduction of tapping intensity, application of low-damage tapping techniques, and implementation of tapping-rest years. Although tapping guidelines exist (in Ethiopia[38]) and most tappers receive some basic training, tapping activities are not controlled or monitored in the field. Multiple techniques exist to reduce tapping impact on trees: reducing the number of tapping spots; reducing the size of tapping spots; preventing deep cuts; reducing the tapping cycles in one season[38]; application of different tapping devices; and installing permanent tapping systems instead of repeated damaging of trees during tapping cycles. The implementation of such methods can be readily monitored in the field, possibly linked to certification schemes. Another issue is that current payments are on the basis of the amount of resin tapped, creating an incentive to maximize extraction intensity and not to sustain tree health and long-term production. To sustain yields, this incentive needs to be shifted to one that also values the quality of the resin and aspects of sustainable tapping. Resin quality can be assessed in terms of drop size, hardness, and the percentage of bark and dirt in the resin.

We suggest the application and enforcement of tapping-rest years, as this improves the vitality of tapped trees and prolongs their lifespan. Such years are part of tapping guidelines and are respected by some companies, but need to be controlled in the field and enforced strictly. Current guidelines[38] recommend 1−2 yr rest after 3−5 yr tapping, in addition to maintaining a percentage of trees untouched. Insect control measures may also help to reduce tree mortality but pilot studies are needed to evaluate the effectiveness and environmental implications of potential measures (for example, chemical pesticides).

To enforce the above measures, appropriate legislation needs to be in place and (more importantly) enforced. Third-party verification and certification is a possible means to improve resin exploitation but has not been applied to *B. papyrifera* frankincense yet. Overall, developments towards sustainable production of frankincense are just starting.

***Boswellia* woodland restoration and protection.** In addition to reduction of extraction intensity, we call for the restoration of declining *Boswellia* populations. Passive restoration measures include (temporary) fencing of *Boswellia* populations to reduce livestock grazing[39], implementing fire-breaks around frankincense-producing forests, and improving control of field-cleaning fires. Cattle exclosures need to be maintained for 5–10 yr to allow establishment of saplings that are robust to high light levels, browsing and occasional fires, on the basis of restoration trials in exclosures in the Ethiopian highlands[40,41]. Fire-breaks and improved fire control should be conducted on a yearly basis. Potentially effective active restoration measures include planting of seedlings or saplings in extant *Boswellia* populations, followed by protection from livestock and fire. Enrichment planting with seedlings and small saplings has not been successful so far, possibly due to slow growth, prolonged dry season, livestock grazing, and lack of post-planting care. Recently, tissue culture techniques are being developed to produce small *B. papyrifera* plants. Planting of branch cuttings is promising[42], especially when latex of *Euphorbia abyssinica*[43] is applied to speed up root growth, and has been partly successful when applied in livestock exclosures.

Creating an enabling environment. To be effective, improved management and restoration measures need to be implemented in concert with important socio-economic changes. First, the profit structure in the frankincense production chain needs to be fundamentally changed. At present, most profit is made by intermediaries and traders, while tappers earn very little[44]. Improved management and restoration of populations can only be effective if the value chain of frankincense production is restructured. Tapper incentives need to be on the basis of quality of tapping and resin, instead of the quantity of product. Valuation systems of sourcing of the product and of improved compliance with socio-ecological sustainability criteria need to be implemented, for instance in a certification scheme; this should lead to higher prices all along the chain. The international market seems ready for such upgrading and market demand is pushing for more sustainable ways of production. In Ethiopia, sourcing of species and regions has started. Product upgrading in producing countries may lead to a higher share in profit. Separation of the raw product in specific-use-targeted upgraded products is being implemented, and producing countries could take a stronger role in that. Another opportunity for increasing profit share is by reducing the number of intermediaries.

Second, the current tenure systems of frankincense-producing woodlands induces 'tragedy of the commons' dynamics[45,46]. Farmers do not own *Boswellia* trees and therefore are less interested in long-term management of trees on their land. The largest share of *B. papyrifera*-derived frankincense is sourced from state-controlled concessions, where state-owned companies and increasingly private companies are the concession holders. In Ethiopia, new regional governance structures recognize local communities as primary stakeholders and grant them rights of ownership and shared benefits[47,48]. Such new governance structures will probably stimulate success of woodland management and restoration measures but only if national laws, regional and local rules support this and are effectively enforced.

Third, political unrest, warfare (including civil wars and threats by local warlords), and large-scale economic developments (construction of dams, main roads and mines) impede development of sustainable frankincense use. For instance, Eritrea implemented woodland exclosure areas during the 1990s but these were abandoned during and after the 1998–2000 border war with Ethiopia. The current peace has led to an upsurge of frankincense tapping in the border regions but conversion to agriculture is likely with the increasing human population. In Ethiopia, *Boswellia* woodlands will probably be converted to agricultural land in several lowland regions; such as the Sudan border of Amhara and Beneshangul-Gumuz, where the new Millenium Dam attracts people and boosts agricultural investments. In Sudan, the three frankincense regions are under heavy pressure: the Jebel Marra in Darfur experienced war; the Blue Nile region currently experiences large influx of people into refugee camps, with all kinds of related issues such as excessive tree cutting for fuel; the Nuba Mountains in Kordofan is an area with ongoing fights between government and rebels. These conditions impede sustainable use and management of the *Boswellia* woodlands.

Towards sustainability in other frankincense-producing species. Sustainability of production and management of *Boswellia* is high on national and international agendas but implementing and enforcing rules, regulations, suggestions and guidelines locally is challenging. *B. sacra* frankincense production in Oman has changed radically: export of raw materials has ceased since the mid-1990s and is replaced by more valuable resin-derived products such as perfume constituents and essential oils. Following low levels of frankincense extraction in the 1980–1990s, attention to frankincense production and development has increased, leading to guidelines for sustainable production and harvest[49], research on frankincense genetics and chemistry[50–53], vegetative propagation, plantations, and ground-water-fed frankincense farms. Preliminary results of agronomic initiatives are promising: good establishment, fast growth and resin production in several years. Prospects for *B. sacra* and *B. frereana* in Somalia and Somaliland are showing positive shifts as more relaxed political conditions may support sustainable frankincense exploitation. For instance, new initiatives were taken to intensify control of wild frankincense production, to improve tapping and resin treatment practices, and to install frankincense plantations[54]. Extraction of *B. serrata* in India was banned in the 1980s but the ban was lifted again in 1995, allowing controlled extraction in certain areas. A national guideline for gum resin collection and post-harvest practices is available[55] but without sustainability issues included[56]. While most *B. serrata* frankincense is sourced from wild populations, new plantations are being constructed[12]. The wild populations are strongly affected by anthropogenic activities (Fig.1), leading to populations with lower densities, regeneration problems, and replacement of *Boswellia* woodlands by thorny shrubby vegetation. *B. serrata* is not red-listed but has been assigned a conservation status of vulnerable (VU) in some areas in India and critically endangered (CR) in Sri Lanka. A recent review[12] proposes adding *B. serrata* to Appendix II species of IUCN. The *B. neglecta* naturally oozing frankincense collection is clearly less harmful, although general threats affect the future and potential of the species (Fig. 1). In Kenia, in some areas the resin collection is Fairwild Organic certified; current production levels are far below potential ones (H. Sommerlatte, personal communication).

Worldwide frankincense demand is increasing, especially due to the recent higher demands for essential oils in human care products. Several large companies now push for more sustainable use and management, partly in response to pressure by their customers. In addition, resin use in medical applications is promising, adding to the increasing international demand. These international demands often interfere with the use of frankincense by local communities for a variety of domestic, cultural and religious ceremonies. Balancing national and international demands of frankincense will be an important challenge in the near future.

Conclusion

Frankincense is in peril. Our study shows that remaining *B. papyrifera* populations will collapse and frankincense production will drop drastically in the coming decades. Actual decline in global frankincense production may be more severe than predicted here, as our projections do not include effects of woodland loss. We propose a series of measures to sustain yields in the long run but acknowledge that reduced frankincense yield over the next decades cannot be avoided. Such measures have not been implemented yet because stakeholders insufficiently recognize the risk of collapse, socio-economic conditions impede the implementation of new management and restoration, and *Boswellia* forests and woodlands in the Horn of Africa are not effectively protected at this moment. The situation for other *Boswellia* species is similar and concerted action at genus level is needed. Our study thus calls for active protection and restoration of the remaining *Boswellia* woodlands to ensure that the iconic frankincense will be available for future generations.

Methods

Data collection. We compiled information from four different datasets: (1) tree size distributions obtained from static population studies in plots at 23 sites; (2) tree ages and tree growth rates on the basis of tree-ring measurements at 4 sites; (3) demographic rates (tree growth, survival, reproduction and recruitment) obtained from dynamic population studies in permanent sample plots at 4 sites; and (4) annual frankincense yield obtained from repeated measurements of experimentally tapped trees at two sites.

Tree size distributions. Population structures were obtained from population censuses conducted by us (46.9% of all trees) or from published sources (scientific publications, reports, theses, Supplementary Table 2). All plots included trees >1 cm diameter at breast height (d.b.h.). A total of 21,786 individuals were censused with a maximum tree size of 64 cm d.b.h. We pooled data from plots <20 km apart to obtain sufficiently large samples to construct representative population structures per site. We made one exception: sites 3 (Kurmuk) and 4 (Gulashe) exhibited strongly contrasting size distributions (Fig. 2), possibly reflecting a different history of disturbance. Although we recognize that our study sites are located along an altitudinal gradient, we categorized sites as lowland (<1100 m a.s.l., 11 sites) or highland (>1100 m a.s.l., 12 sites) since environmental conditions and exploitation history differ strongly between lowland and highland populations.

For 14 populations (representing 46.9% of all individuals) we had data of sizes for individual trees, for the remaining 9 populations we read abundances from published size distributions and assigned random diameter values in these size classes, assuming a uniform in-class size distribution. For all 23 populations, we categorized individuals into 18 diameter classes (1–4 cm, 4–7 cm, and so on) and calculated a recruitment index as the percentage of the population (>1 cm d.b.h.) that is in the 1–4 cm d.b.h. class. High values indicate good recruitment, while zero reflects complete regeneration failure.

Tree ages and tree growth rates on the basis of tree-ring measurements. Annual ring formation in *B. papyrifera* was demonstrated[21], using pinning at Lemlem Terara (site 9). Anatomically, the ring boundaries of *B. papyrifera* are characterized by radially flattened fibre cells. In addition, density changes of vessels and tangential rows of vessels can be used to mark ring boundaries[21].

Tree-ring data and tree ages were obtained from 202 fully cross-dated trees from four sites (Supplementary Table 3), including the 100 trees sampled at Lemlem Terara[21]. At each site, we sampled trees in one to four 2-ha plots, across the entire diameter range. We first classified trees into five to six size categories of 5-cm width in d.b.h. From each of these categories, five trees were randomly selected per 2-ha plot. For the Abergelle site, five additional trees were sampled from the plot and its direct surroundings to include the largest and smallest trees at the site. Tree-ring samples were obtained from tree discs (taken at 0.4 m height) or from increment cores (two cores per tree, at opposite sides of the tree and at 0.4–0.5 m height). Sample preparation and measurements followed standard dendrochronological methods[57] and protocols developed for *B. papyrifera*[21]. Discs and increment cores were air-dried and prepared for tree-ring measurements: discs were sanded using 80–1,200 grit sand paper; cores were first cut using a microtome and sanded afterwards. Ring boundaries were identified and marked macroscopically using a microscope (Leica MS-5) at Wageningen University Dendrolab. Width of growth rings was measured to the nearest 0.001 mm using a Leica MS-5 microscope coupled to a LINTAB 5 measurement table associated with TSAP software[58]. Ring-width measurements were visually cross-dated to detect missing or false rings. This visual cross-dating was followed by statistical tests (GLK, Gleichlaufigkeit[59]) to quantify common temporal growth variation among trees. Only trees that had significant ($P<0.001$) GLK coefficients—hereafter 'cross-dated' trees—were included in further analyses. Across sites, 75% of the individuals could be cross-dated, allowing further analyses to be performed for 24–84 trees per site.

Age–diameter relations were established by regression for each of the four sites (Supplementary Fig. 1); 43–76% of the variation in ages was explained by stem diameter. We used these regression equations (and their 95% CI) to estimate the age of all trees included in the population size distributions at these four sites. This allowed us to reconstruct age distributions (and CI) for these sites and to quantify the period of recruitment scarcity or absence.

We calculated annual stem growth rates of all cross-dated trees across their entire lives by averaging radial growth (ring width) from two increment cores multiplied by two (Supplementary Fig. 2). These annual diameter growth rates were used to construct demographic models.

Demographic rates obtained from dynamic population studies. Rates of tree growth, tree survival and seedling recruitment, and information on reproductive status of *Boswellia* trees were obtained from population dynamics studies at four sites in permanent plots of 2.4–19.8 ha, monitored for 2–3 yr and containing 246–3,980 marked individuals per site (Supplementary Table 2). We installed plots at two sites in lowland (<1,100 m a.s.l.; Lemlem Terara site 9; Kuara site 8; refs. [13,60]) and at two sites in highland (Abergelle site 18; Adi Arkay site 19; ref. [60]), in 2007. In all plots, all *Boswellia* individuals >1 cm d.b.h. were identified, tagged and their d.b.h. was measured.

To study reproductive status and seed production, we randomly selected 25 adult trees (>10 cm d.b.h.) in each plot and noted their reproductive status (seed-bearing or not). To determine whether trees are seed-bearing, we also verified that seeds are viable, using germination trials. Trees are only considered reproductive if they bear viable seeds in 1 of the 2 yr of measurements. Annual re-measurements were conducted to record survival and d.b.h. (for all trees), and to record reproductive status and seed production (for selected trees) (Supplementary Figs. 2 and 3). Growth rates (Supplementary Fig. 2) in d.b.h. were calculated, both per year and averaged over the total monitoring period (2–3 yr). A large proportion of trees, especially among highland populations, exhibited negative d.b.h. growth values. These negative growth rates were probably caused by fluctuations in stem water content due to seasonal rainfall patterns or in-season fluctuations in rainfall, and are commonly observed for tree species in dry forests[61–63]. When conducting re-measurements, we also searched for newly recruited trees (into the >1 cm d.b.h. class) in the entire plots but only found recruiting trees in Adi Arkay (site 19).

We tested the differences in growth, survival and fecundity rates between highland and lowland populations. Growth rate differences (total differences and interaction) between regions were tested using the tree-ring data only, as tree-ring data provide more accurate and longer time series than plot-derived data. We log-transformed the growth data before analysis, to normalize data and stabilize variance. Growth rates for lowland populations were higher than highland populations ($P<0.001$, adjusted $R^2=0.0795$, d.f. = 15,072). Growth rates increased with tree size in both populations but this increase was stronger for lowland populations (a larger slope, $P=0.0134$).

We tested for differences in fecundity between sites using a logistic regression between size and reproductive status (binomial yes, 1 or no, 0). We used a generalized linear model with a binomial family using the glm function in base R (ref. [64]) between size and reproductive status and included an interaction factor for highland and lowland populations. Trees in the lowland populations had a lower probability of being reproductive than trees in highland populations at similar size ($P=0.04$, d.f. = 443). The probability of being reproductive increased with size ($P=0.0252$), and the slope of this relationship was similar between highland and lowland populations ($P=0.3492$).

We tested for differences in survival between sites using a logistic regression mixed effect model, a generalized linear mixed-effects model with a binomial family (glmer function of lme4 library in R; ref. [65]). We tested for the relationship between survival and size and included an interaction factor for highland and lowland. As survival was measured in several plots in both highlands and lowlands and over 3 yr in the highlands and 4 yr in the lowlands (Supplementary Fig. 3), we included plot and year as random factors in the model. Survival probability increased slightly with tree size (marginally significant, $P=0.0878$, d.f. = 18,420). Highland and lowland sites had similar survival probability ($P=0.238$) and similar relationship between survival and size ($P=0.2693$).

The rates of growth, survival, reproduction and recruitment were used to construct demographic models.

Frankincense yield obtained from experimental tapping. We measured resin yield of *B. papyrifera* trees at one lowland site (Lemlem Terara, site 9) and one highland site (Abergelle, site 18)[25]. At each site, we selected 40 trees for each of five d.b.h. categories (range 12–43 cm d.b.h.), outside the plots to perform experimental harvesting. We tapped selected trees using commonly used intensity (6–12 tapping spots per tree) during two consecutive tapping seasons (2008/2009 and 2009/2010). We dried and weighed resin and calculated annual resin production per tree. The resulting frankincense yield data were related to tree size (linear regression) and this relation was combined with results of demographic simulations to simulate future frankincense production.

Construction of demographic models. We used Integral Projection Models (IPMs) to project the future development of populations for the 23 sites for which we collected population size structures. IPMs are extensions of matrix models that simulate future population development of populations with a continuous size structure[66]. IPMs are powerful and flexible tools for demographic modelling, especially for long-lived species, as they allow to construct models with many size categories and to explicitly include variation in growth rate among individuals, and as they are built from a few coefficients[22].

We constructed separate IPMs for lowland (<1,100 m) and highland (>1,100 m) populations, since environmental conditions, and in many cases also exploitation history, differ strongly between elevations (Supplementary Fig. 8). Both IPMs are constructed using demographic data from permanent sample plots, tree-ring measurements and experimental tapping at two sites: for the lowland IPMs Kuara (site 8) and Lemlem Terara (site 9); for the highland IPMs Abergelle (site 18) and Adi Arkay (site 19). We set the minimum tree size of these IPMs to 1 cm d.b.h. as trees above this size were searched in all of the 23 sites for which we had population structure (seedlings are usually not included in these studies); and as small trees (1–4 cm d.b.h.) occur at low density (or are absent) from many populations.

We constructed IPMs using regression functions (linear, quadratic and logistic) that relate rates of survival, growth and fecundity to tree size for all trees >1 cm d.b.h. Logistic regressions for survival versus d.b.h. were on the basis of pooled data from two plots for lowland and two plots from highland populations. Regressions were calculated for each of 2–3 yr and these annual survival–d.b.h. relations were averaged to obtain one relation for lowland and one for highland populations. Linear and quadratic regression of d.b.h. growth versus d.b.h. were based either on growth rates obtained from tree-ring measurements ('ring-only' model) or on rates obtained from plot studies and tree-ring measurements combined ('ring + plot' model). The 'ring-only' model has the advantage that negative growth due to stem shrinkage was not included, while the 'ring + plot' model has the advantage of a larger number of trees included. Because of the high proportion of negative growth rates in the plot-derived data, we choose to present results for the 'ring-only' model in the main results; and present the 'ring + plot' model to evaluate the robustness of our model to a change in the source of our growth data (Supplemenatry Fig. 4).

We constructed logistic regressions of reproductive status versus d.b.h. for lowland and highland sites. We set the lower limit for trees to be reproductive at 10 cm d.b.h., in accordance with the minimum size of selected trees included in the reproduction study. As no new recruits were observed in three of the four sites, we quantified recruitment for just one site (Adi Arkay, site 19). The number of new recruits entering the population per year was calculated, as well as the d.b.h. distribution of these recruits. These annual values were then averaged.

We also constructed separate IPMs for populations with and without recruitment. We categorize populations at the 23 sites into those that showed recent recruitment (5 sites with recruitment index >4%) and those that showed (virtually) no recruitment (remaining 18 sites). The simulations for populations at regenerating sites were conducted using an IPM in which recruitment rates were on the basis of the annual recruitment rates from the Adi Arkay population. For the other population, recruitment values were zero, thus assuming that the recent lack of recruitment into the 1 cm-d.b.h. category prevails during the period of simulation. To test the robustness of our simulation results to recruitment, we also tested to what extent results of simulations would change when the Adi Arkay recruitment values were applied to all 23 sites. This resulted in only very small changes in simulation output (results not shown).

We then combined the continuous functions for survival, growth, reproduction and recruitment into one kernel that describes the transitions among tree sizes. Size ranges (lower, L, to upper, U) of this kernel were 1–55 cm d.b.h. for lowland and highland IPMs. Upper d.b.h. values were determined on the basis of the maximum diameter measured for any *Boswellia* tree plus 5%. To project population dynamics, this kernel needs to be discretized into a large number of categories (m, 'mesh size'), each of width h (in cm d.b.h.), such that $h = (\mathrm{U} - \mathrm{L})/m$. In IPMs, m should be large enough such that model output is not affected when increasing m. We set m at 500, as no effects of m on model output were found beyond $m = 250$ (data not shown). Thus, each of the four IPMs (low/highland × 'ring-only'/'ring + plot') was a 500 × 500 matrix with annual transitions. We accounted for unintentional eviction in our IPMs.

Simulations of population size and yield. For each site, we projected population size and population structure over 50 yr, using IPMs. For the 11 lowland sites, we used the lowland IPM, both the 'ring-only' and 'ring + plot' versions. For the 12 highland sites, we used the highland IPM. We projected 50-yr frankincense yield for all 23 populations by combining information from the projected population structures with the d.b.h.–yield relationship (Supplementary Fig. 4).

To assess the robustness of our projections to uncertainty in demographic rates, we performed an extensive and rigorous bootstrap analysis. We removed 1% of the individuals from the demographic datasets, re-ran all statistical analyses to construct new IPMs and performed new projections. This procedure was repeated 250 times. We performed bootstrapping for all 23 populations. We present 50-yr projections of population sizes and frankincense yield for all 250 replications (Supplementary Fig. 4); plus average values of population sizes and frankincense yield at start and after 50 yr (Supplementary Table 5).

To evaluate how sensitive population growth is to changes in the vital rates, we performed a demographic elasticity analysis for four example populations[67]. We did so for three broad size classes of trees (1–10, 10–25 and >25 cm diameter), by increasing growth rate, survival probability or recruitment rate by 1%. We evaluated the effects of these changes on population growth during 50 yr (λ_{50}), which we calculated as $(N_{50}/N_0)^{1/50}$, with N_{50} being the simulated population size at $t = 50$ and N_0 the starting population size. For each combination of size class and vital rate we calculated transient elasticity (e_{50}) as: $(\Delta\lambda_{50}/\lambda^*_{50})/0.01$, where $\Delta\lambda_{50}$ is the change in λ_{50} due to the change in the vital rate and λ^*_{50} is population growth for the unchanged situation. We deliberately choose to calculate elasticity of transient (instead of asymptotic) population growth as we are interested in population development for the next 50 yr. We choose to calculate elasticity of vital rates (instead of matrix elements) as we wanted to separate the importance of survival and growth on population growth (Supplementary Fig 7.)

To further evaluate robustness of our models and model results we simulated population development for all 23 sites using either highland or lowland IPM models. We also calculated the implications of this shift for resin yield data (Supplementary Fig. 5)

All IPM analyses were performed in R, using the IPMpack package[68].

Land use change and representativeness of our sites. See Supplementary Methods

Data availability

The data reported in this paper are tabulated in the Supplementary Data and can be accessed in the Github repository (https://github.com/groenendijk/Frankincense-demography).

Code availability

The R script used for the IPM analysis can be accessed in the Github repository (https://github.com/groenendijk/Frankincense-demography).

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Author contributions

F.B., F.J.S., P.A.Z. and P.G. conceived the study. F.B. and P.G. compiled the data. P.G. and P.A.Z. performed the demographic modelling. M.D. evaluated forest change. F.B., P.A.Z., F.J.S. and P.G. wrote the paper. All authors contributed data and commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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