Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations

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Summary

1. Resins are highly valued non-timber forest products (NTFP). One of the most widely traded resins is frankincense, tapped from several *Boswellia* tree species (Burseraceae). Exploited *Boswellia* populations often show poor regeneration, but the demographic consequences of these bottlenecks are unknown. Here we report on the first large-scale demographic study of frankincense-producing trees.

2. We studied 12 populations of *Boswellia papyrifera* in northern Ethiopia, varying in altitude and productivity. Six of these populations had been tapped before and were tapped during the study. Survival, growth and fecundity were determined for 4370 trees and 2228 seedlings, in 22.8 ha over a 2-year period. We also studied a remote population where no grazing and tapping took place. Matrix models were used to project population growth and frankincense production under four restoration scenarios.

3. Population structures of both tapped and untapped populations showed clear gaps. Small seedlings were abundant in all populations, but none developed into persistent saplings. Such saplings were only present in the remote population. Fire and grazing are the likely causes of this regeneration bottleneck.

4. Adult mortality was high (6–7% per year) in both tapped and untapped populations, probably caused by beetle attacks and fire. Unexpectedly, tapped populations presented higher diameter growth rates and fecundity compared to untapped populations. These differences are probably caused by non-random selection of exploited populations by tappers.

5. Under the 'business as usual' scenario, population models projected a 90% decline in the size of tapped and untapped populations within 50 years and a 50% decline in frankincense yield within 15 years. Model simulations for restoration scenarios revealed that populations and frankincense production could only be sustained with intensive management leading to full sapling recruitment and a 50–75% reduction in adult mortality.

6. *Synthesis and applications.* Regeneration bottlenecks and high adult mortality are causing rapid decline in frankincense-producing tree populations in Ethiopia. This decline is unlikely to be a consequence of harvesting and is probably driven by fire, grazing and beetle attacks. Fire prevention and the establishment of non-grazing areas are needed. Our results show that other factors than exploitation may seriously threaten populations yielding NTFP.

Key-words: *Boswellia papyrifera*, Ethiopia, frankincense, matrix model, non-timber forest products, regeneration bottleneck, resin, restoration, sustainable use, tapping

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Introduction

Resins are some of the most valuable non-timber forest products (NTFP), particularly those tapped for fragrances and flavours. Frankincense from several *Boswellia* spp. of the Burseraceae family is an important oleo-gum resin on the local and international markets (Lemenih, Abebe & Olsson 2003). In the Horn of Africa, frankincense is tapped from adult trees of *Boswellia papyrifera* (Del.) Hochst. in natural woodlands. It is traded world-wide for the production of perfumes and incenses (Chikamai 2002). Tapping of resins can form a substantial sink of carbohydrates for a tree (Silpi *et al.* 2007) and can reduce diameter growth (Silpi *et al.* 2006). In *Boswellia*, tapping was found to reduce seed production and viability (Rijkers *et al.* 2006), but the effects on tree growth and population dynamics are unknown.

Many populations of *B. papyrifera* are threatened by conversion into agricultural land (Ogbazghi *et al.* 2006b) and present a hump-shaped population distribution, dominated by small seedlings and adult trees but lacking the sapling and treelet stages (Ogbazghi 2001; Gebrehiwot *et al.* 2003; Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010). This gap in the population structure may be caused by the low production and viability of seeds of tapped trees (Rijkers *et al.* 2006), recurrent droughts (Ogbazghi 2001), increased fire frequency, uncontrolled livestock grazing (Ogbazghi *et al.* 2006a) or a combination of all of these (Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010). Alternatively, the lack of regeneration may be a consequence of unfavourable conditions during the recent past and to episodic recruitment, as sometimes occurs in arid environments (Walker 1993).

Blocked regeneration poses a potential threat to the maintenance of *Boswellia* populations and the production of frankincense in the long term. Despite the economic importance of this species, virtually nothing is known about the demographic consequences of tapping and blocked regeneration in *Boswellia* populations. Such information can be obtained from stage-based population matrix models (Caswell 2001) that project population development over time. Matrix models are powerful tools to study population dynamics and have often been applied to study consequences of timber and NTFP harvest (Ticktin 2004; Verwer 2008; Schmidt *et al.* 2011).

Here we assess the consequences of frankincense exploitation for *Boswellia* populations and future frankincense production. This is one of the first studies to assess the population-level consequences of resin tapping (Schmidt *et al.* 2011). We hypothesize that tapped *Boswellia* populations exhibit stronger regeneration bottlenecks and lower rates of diameter growth, fecundity and survival compared to untapped populations. As a result, we expect lower population growth rates in tapped populations.

We studied population dynamics in six tapped and six untapped stands between 2007 and 2009. In addition, we obtained data from a remote study area where no tapping and grazing occurs, to quantify the dynamics of saplings, unavailable in the 12 main study plots. We constructed matrix models for tapped and untapped populations and used these to project population development and frankincense yield under four restoration scenarios.

Materials and methods

EXPERIMENTAL SITES AND STUDY SPECIES

Data collection was carried out in northern Ethiopia, in the Metema (12°40′N, 36°17′E) and Kuara (12°34′N, 36°7′E) districts, situated ca. 30 km apart. This site is referred to as 'Metema'. Twelve stands were selected based on the presence of relatively intact *B. papyrifera* stands and to cover altitudinal and 'production' gradients (based on visual observations of stand characteristics and nearby cropland production; Eshete, Sterck & Bongers 2011). The region has a uni-modal rainfall distribution, with a rainy season in June-September and an annual rainfall of 884 mm (range 660–1100). Populations in Metema only contain small seedlings and trees with a Diameter at Breast Height (DBH) of > 6 cm (Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010).

A second site was selected near the village of Adi Arkay (13°27′N, 38°4′E), in the Adi Arkay district, ca. 210 km north-east of Metema. Located at an altitude of 1415 m, the area is characterized by steep cliffs with presence of *Boswellia* populations. In Adi Arkay, *B. papyrifera* seedlings and saplings of all sizes are present, presumably because poor accessibility of the area prevents grazing and agriculture.

Boswellia papyrifera is a small deciduous tree, occurring from northern Nigeria to the highlands of Ethiopia and Eritrea in woodlands and wooded grasslands at an altitude of 800–1850 m. It often occurs on shallow soil in semi-arid conditions on steep, rocky slopes, in sandy river valleys or on lava flows (Ogbazghi *et al.* 2006b). The phenological cycle of the species is mainly controlled by the distribution of precipitation: reproductive activity takes place during the dry season. In our study region, *B. papyrifera* trees reached a maximum height of 14–16 m and a maximum DBH of 51.5 cm. The region is one of the main *Boswellia* growing areas in the Horn of Africa and is subject to commercial extraction of frankincense (Eshete, Teketay & Hulten 2005). Tapping occurs during the dry season using a special axe ('mngaf') to make incisions in the bark. Trees are revisited periodically (every 15–21 days) to collect resin clumps and reopen tapping wounds. Tapping intensity (the amount of incisions) and frequency (the amount of rounds of frankincense collection) varies. The 'traditional' tapping intensity – applied in this research – involves 6–8 tapping incisions for trees of 10–30 cm DBH and 8–12 incisions for larger trees, applied over 8–12 rounds (Ogbazghi 2001).

DATA COLLECTION

In Metema, 12 plots of 1.6–2.0 ha (total area 22.8 ha) were installed: six plots in areas where frankincense tapping is conducted (T1–T6) and six in untapped areas (U1–U6). *Boswellia* trees in untapped areas are not tapped at present because of lack of infrastructure (e.g. roads), non-availability of drinking water, and/or because the trees had a lower total basal area (Eshete, Teketay & Hulten 2005; Eshete, Sterck & Bongers 2011). Measurements took place during the rainy season (July) in 2007, 2008 and 2009. During the first census, a total of 4370 trees > 1 cm DBH were identified, tagged and their DBH and height were also measured. For each tree of < 150 cm height (*n* = 2228), diameter at stem base (hence called 'root collar diameter', RCD) and height were measured. In subsequent years, growth and survival were

recorded for all individuals. To estimate the reproductive status, we randomly selected 25 adult trees in each plot, stratified over all size categories. For each tree, we recorded whether it produced seed-containing fruits during 2 years (2008 and 2009).

A similar demographic study was carried out in the Adi Arkay plot to quantify growth and survival rates of the missing tree size classes in the Metema plots. Two plots (total 2.4 ha) were established and all individuals present ($n = 327$) were measured in the rainy season in 2007, 2008 and 2009. Seedlings were not measured in these plots and reproductive status was not assessed.

In addition, we also conducted a tapping experiment to relate frankincense production per tree to diameter (DBH). In two of the Metema plots, we selected approximately five trees per 5-cm wide DBH category just outside the plots and tapped them at an average intensity of nine incisions in 2008 and 2009. Resin clumps produced by each tree were collected and their dry weight was measured.

CATEGORIZATION AND POPULATION STRUCTURES

The life cycle of *B. papyrifera* can roughly be split into seedlings, saplings, juvenile trees and adult trees, further subdivided into 12 size classes (Fig. 1). Seedlings are 0–2.0 cm in RCD, with a height of 0–2.6 cm. We observed that the aboveground part of seedlings died back every dry season and that it reappeared during the rainy period as a rosette of leaves. Presumably, seedlings in this stage (hereafter 'non-permanent seedlings') invest in storing reserves below-ground and not in height growth. Indeed, non-permanent seedlings were found to possess root systems of > 2 m length (P. Groenendijk and A. Eshete, unpublished data). It is unclear what triggers the switch from non-permanent seedlings to permanent sapling. We estimate that this shift takes place at approximately 2.0 cm RCD (Fig. S1, Supporting Information).

Saplings are individuals with a RCD > 2.0 cm and a DBH of < 6 cm. Three sapling size classes were distinguished: 2–4 cm RCD; > 4.0 cm RCD and < 150 cm height; > 150 cm height and < 6 cm
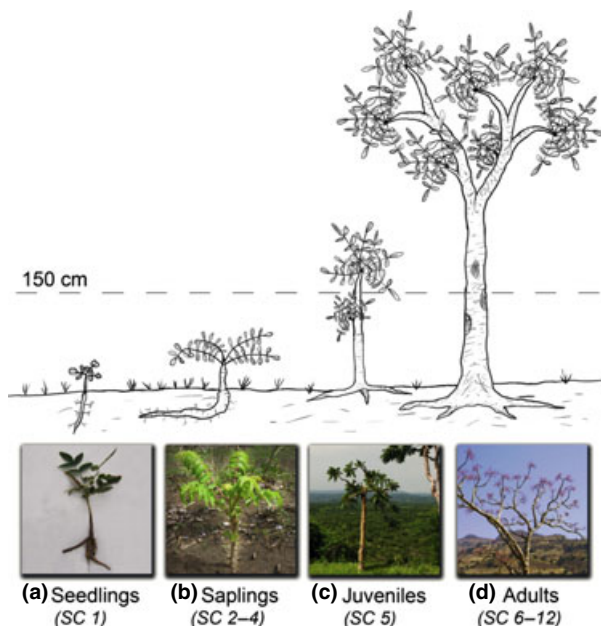
DBH. Individuals of 6–10 cm DBH were categorized as juvenile (non-reproductive) trees. Reproduction started at approximately 10 cm DBH and individuals > 10 cm DBH were classified as adults. Seven adult classes were distinguished: 10–14 cm DBH, 14–18 cm DBH, 18–22 cm DBH, 22–26 cm DBH, 26–30 cm DBH, 30–35 cm DBH and > 35 cm DBH.

To obtain representative population structures for tapped and untapped populations, we pooled abundance data from the six populations per tapping treatment. We compared the shape of these population structures using a Kolmogorov–Smirnov test and tested for differences in adult and seedling densities using a *t*-test (with plots as replicates).

CALCULATION OF VITAL RATES

We used regression models to test for relationships between vital rates (growth, survival and reproduction) and size (RCD, height or DBH). In these models, data of all size categories were combined. We used dummy variables to analyse differences between plots (tapped: T1–T6 and untapped: U1–U6) and included plot*DBH interactions to check for differences in size-dependent relations across plots. Linear regressions were used for increment in RCD of seedlings and small saplings (Metema and Adi Arkay data 2008–2009), for sapling height growth (Adi Arkay data; 2007–2009) and for diameter growth (Metema data; 2007–2009). We used multiple logistic regressions to analyse the relationship between survival and diameter and that between the probability of reproduction ($Prob\{f\}_i$) and diameter. For the experimentally tapped trees, annual frankincense production per tree (in kg) was related to DBH by a linear regression.

MATRIX MODEL CONSTRUCTION

We constructed stage-based matrix models (Caswell 2001) to analyse the population dynamics of *B. papyrifera*. Matrix models use the equation: $\mathbf{n}(t + 1) = \mathbf{A} \times \mathbf{n}(t)$, where $\mathbf{n}(t)$ and $\mathbf{n}(t + 1)$ represent the population structure at time t and $t + 1$, and $\mathbf{A}$ is the square matrix containing the transition probabilities between size classes for one time step (1 year).

Matrix elements in $\mathbf{A}$ can be grouped into progression, stasis and fecundity. Progression elements (G) represent the probability of an individual to grow from one size class (g_i) to the next: $G_i = \gamma_i * \sigma_i$, where γ_i is the probability that a surviving individual in size class i grows to the next class ($i + 1$) and σ_i is the annual survival probability in class i. We calculated γ_i as g_i/c_i, where g_i is the DBH or RCD growth rate for category i (in cm year^{-1}) and c_i is the category width (in cm). Stasis elements (P) represent the probability that a surviving individual stays in the same size class: $P_i = \sigma_i - G_i$. Fecundity elements (F) represent the seedling production per individual in an adult category: $F_i = \sigma_i \times Prob\{f\}_i \times f_i$, where $Prob\{f\}_i$ is the probability for an individual in class i of being reproductive and f_i the quotient of annual seedling recruitment in the current year (per ha) and the abundance of reproductive trees in the previous year (per ha). As *Boswellia* does not form a seed bank (Eshete, Teketay & Hulten 2005), we could estimate f_i directly from these measures.

To determine vital rate values for every category, we filled in midpoints of each size class in the regression equations. Subsequently, we averaged the category-specific vital rate values of the six tapped plots to obtain one value for a tapped population. In the same way, we also obtained the average for an untapped population. This procedure ensures that we obtain realistic and representative transition matrices for both tapped and untapped stands, in which plots that differ in tree densities have an equal weight.

150 cm

(a) Seedlings
(SC 1)

(b) Saplings
(SC 2–4)

(c) Juveniles
(SC 5)

(d) Adults
(SC 6–12)

Fig. 1. Life stages of *Boswellia papyrifera*: (a) seedlings with non-permanent stem (Size Class 1); (b) saplings (Size Classes 2–4); (c) juveniles (Size Class 5) and (d) adult trees (Size Classes 6–12).

RESTORATION SCENARIOS

We developed four modelling scenarios for which we simulated consequences of various restoration activities on populations and yield: a 'business as usual' scenario and three restoration scenarios. All scenarios were simulated for both tapped and untapped populations, as the latter are also projected to decline over time.

The 'business as usual' scenario (BAU) was based on the observed dynamics of the Metema populations, that is without regeneration of saplings. Transition matrices for this scenario contain zeroes for progression from size class 1–2 and for all transitions of sapling classes (2–4). We used these matrices as a basis for alternative restoration scenarios described below.

The first restoration scenario allows full regeneration (REG), for example as a result of creating cattle exclosures. Under this scenario, non-permanent seedlings grow into permanent saplings. The annual transition probability from seedlings (size class 1) to small saplings (2) was estimated to be 0.1 based on observations on planted seedlings, which remain non-permanent for at least 8 years (E. Birhane, personal communication). To calculate progression and stasis transitions for sapling classes, we used vital rates from the remote Adi Arkay population. Secondly, we also developed restoration scenarios in which restoration activities (e.g. fire prevention, prevention of insect attack) would reduce adult mortality. The REGMOR50 and REGMOR75 scenarios simulate the effect of full regeneration (as in REG) combined with a 50% or 75% reduction in adult mortality. Finally, we also tested the effect of doubling or halving the probability that seedlings grow into saplings. As this led to very small changes in model output, we do not present results of these simulations.

MATRIX MODEL ANALYSES

The dominant eigenvalue (λ) of a transition matrix represents the asymptotic population growth rate of the population once it has reached the stable stage distribution (Caswell 2001). In the case of exploitation and restoration, it is more appropriate to analyse population development over the next decades to century, i.e. the transient population dynamics. We projected the development of population structures over 100 years and used these to calculate population sizes and frankincense production. We did so for both tapped and untapped populations, and for all four scenarios. We also calculated the transient population growth rate over a period of 100 years (λ_{100}):

$$\lambda_{100} = \sqrt[100]{\frac{n_{100}}{n_0}}$$

where n_0 and n_{100} are the population sizes at $t = 0$ and at $t = 100$, respectively. The 95% confidence intervals for λ_{100} were estimated using the series approximation method (Caswell 2001), which uses information on variation and sensitivity of vital rates. We used vital rate sensitivity for λ (Zuidema & Franco 2001) as a proxy for that of λ_{100} as differences between λ and λ_{100} were small (average difference = 0.005, $n = 8$).

Results

POPULATION STRUCTURE

All tapped and untapped populations in Metema lacked individuals in the size classes 2–4 and exhibited a hump-shaped distribution of adult trees (Fig. 2). Seedling densities varied widely across plots in tapped (2–93 ha^{-1}) and untapped populations (10–94 ha^{-1}). The density of seedlings (*t*-test) and the shape of the population structure (Kolmogorov–Smirnov test) did not differ between tapped and untapped populations, but adult tree densities were higher in tapped (227.2 ± 44.1, mean ± SD) compared to untapped stands (139.8 ± 47.0; *t*-test, $P = 0.003$, $T = 3.319$, d.f. = 10).

All stands presented newly recruited seedlings in both years, but none of the seedlings was observed to grow into a persistent sapling. Annual seedling recruitment per reproductive tree was 0.39 ± 0.55 in tapped and 0.79 ± 0.57 in untapped stands.

VITAL RATES

Diameter growth of adult trees was higher in two tapped plots (T4 and T5) and one untapped plot (U2) compared to the reference plot (U1). The relationship of ΔDBH and DBH differed significantly from that of the reference plot for four tapped
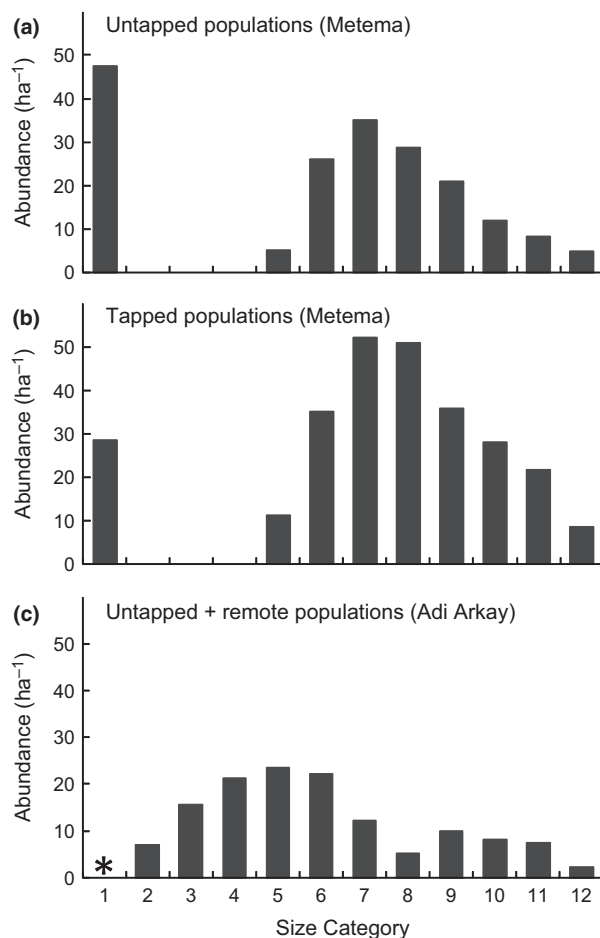

Fig. 2. Population structures of *Boswellia papyrifera* for six untapped (a) and six tapped stands (b) in Metema and for an isolated untapped population (c) in Adi Arkay. See Fig. 1 and text for size categories. Seedlings were not enumerated in the remote untapped study site (* in panel c).

plots (T1–T4). When averaged over the six replicate plots, diameter growth in the six tapped plots was higher than in untapped plots and showed a stronger increase with DBH (Fig. 3).

Survival increased with tree diameter, but the explained variation in the logistic regression model was very low (Nagelkerke $R^2 = 0.035$). We therefore chose to discard the model and to use the average annual survival rate of the 12 plots: 93.7% ($\pm 2.1\%$, $n = 12$) for tapped and 93.3% ($\pm 3.8\%$, $n = 11$) for untapped stands. One of the untapped plots (U7) had a very high ($\sim 25\%$) mortality rate for 2008–2009 because of a windfall event. As we were interested in normal mortality rates, this plot-year was discarded.

The chance of being reproductive differed significantly in three tapped (T1, T3 and T6) and one untapped (U4) plot compared to the reference (U1), in the first measurement year (Multiple logistic regression model, $R^2_{\text{Nagelkerke}} = 0.171$, $n = 293$, $P < 0.001$). In the second year, four tapped (T1, T3, T5 and T6) and two untapped plots (U7 and U8) differed from the reference plot (Multiple logistic regression model, $R^2_{\text{Nagelkerke}} = 0.458$, $n = 293$, $P < 0.001$). On average, individuals in tapped populations had a higher probability of being reproductive than those in untapped plots (Fig. 3).

Seedling survival did not differ between plots (Logistic regression, $P > 0.05$), so we used the average of the six tapped and untapped plots to calculate annual survival rates: $85.2 \pm 9.8\%$ for tapped plots ($n = 10$) and $84.4 \pm 13.1\%$

($n = 12$) for untapped plots. For saplings (data from the Adi Arkay plot), variation in growth rate was not explained by diameter (RCD) and the average growth rate was used for all sapling size classes (0.493 cm year^{-1}, $n = 113$). The probability of survival was significantly related to diameter (Nagelkerke $R^2 = 0.238$; $P < 0.05$), and this logistic regression was used to estimate survival rates for sapling classes.

Annual frankincense production increased with tree size ($R^2 = 0.351$, $n = 242$, $P < 0.001$; Fig. 4). The linear regression was used to estimate the yield at the midpoint of each size class.

MATRIX MODEL OUTPUT

Under the BAU, populations were projected to strongly decrease: by 93% in 50 years for untapped populations and 87% for tapped populations (Fig. 5a,b). Population growth rates for the next 100 years (λ_{100}) were 0.942 for untapped and 0.950 for tapped stands (Table 1, transition matrices Table S1, Supporting Information,). Confidence intervals were narrow and did not include the value of 1, indicating that population decline is quite certain (Table 1). As no regeneration was present and mortality was equal for all adult size classes, population growth in fact reflected adult survival rates ($\sim 93\%$). The projected frankincense yield based on the 'business as usual' scenario showed a rapid decline: yield was halved within 15 years in tapped stands (Fig. 5c).
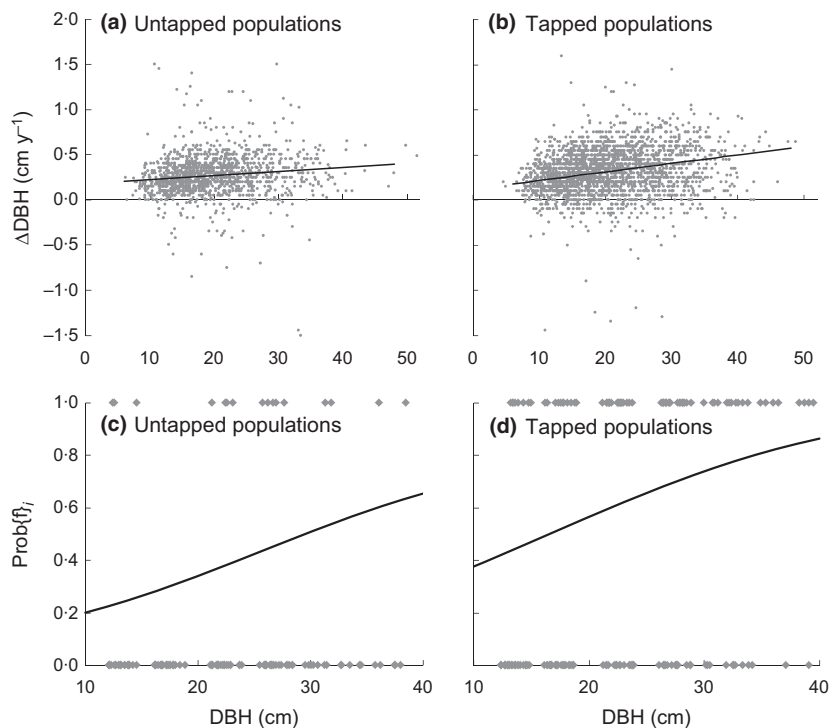
Fig. 3. Relationship between annual diameter growth rate (ΔDBH; a,b) and probability of reproduction (*Prob*{f}$_i$, c,d) with diameter at breast height (DBH) for untapped (a,c) and tapped populations (b,d) of *Boswellia papyrifera*. Lines denote the average of six linear (a,b) and logistic (c,d) regressions (one for each population). Each dot represents one tree. Linear regression: $R^2 = 0.164$, $n = 1361$ (untapped) and 2431 (tapped), $P < 0.001$; effect of DBH: $P < 0.001$. Logistic regression: $R^2_{\text{Nagelkerke}} = 0.330$, $n = 123$ (untapped) and 171 (tapped), $P < 0.001$; effect of DBH: $P < 0.001$.
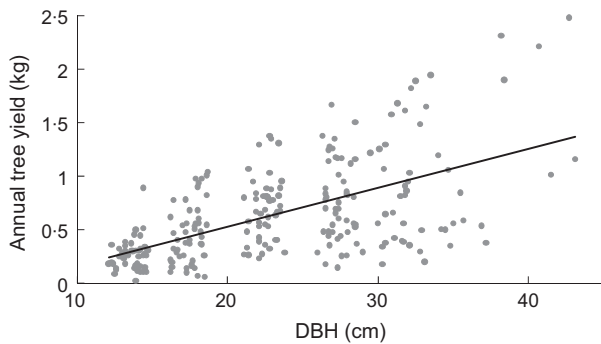
Fig. 4. Relationship between annual yield of frankincense and diameter at breast height of experimentally tapped *Boswellia papyrifera* individuals. Each dot represents one experimentally tapped tree; the line denotes a linear regression ($R^2 = 0.351$, $n = 242$, $P < 0.001$).
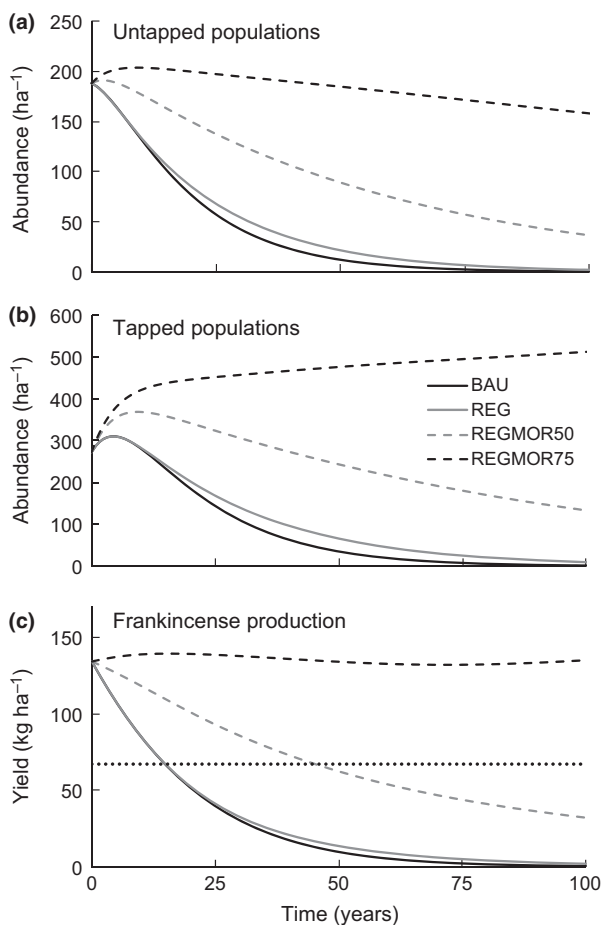
Fig. 5. Projected abundance (a,b) and frankincense yield (c) from untapped (a) and tapped (b,c) populations of *Boswellia papyrifera* under four restoration scenarios. See Table 1 and text for explanation of scenarios. The horizontal dotted line in panel c denotes 50% of current frankincense yield.

In the full regeneration scenario (REG), λ_{100} increased to 0.956 for untapped and 0.967 for tapped stands (Table 1). These values still indicate a considerable decrease in population size over time. Confidence intervals of λ_{100} did not include the value of 1 for both untapped and tapped stands (Table 1).

Time to halving of frankincense production was the same as for the BAU, that is 15 years.

When – in addition to allowing full regeneration – adult mortality was decreased by 50% (REGMOR50; adult survival = 96.7%), λ_{100} of the untapped stands increased to 0.984 (Table 1, Fig. 5a). For tapped stands, λ_{100} increased to 0.993 and frankincense production halftime increased to 51 years (Fig. 5c). Reducing adult mortality by 75% (REGMOR75: survival rates of 98.3%) resulted in slightly declining populations ($\lambda_{100} = 0.998$) for untapped stands and slightly growing populations ($\lambda_{100} = 1.01$) for tapped stands (Table 1, Fig. 5). Under both REGMOR50 and REGMOR75 scenarios, confidence intervals included 1 for tapped and untapped stands (Table 1), suggesting that significant population decline (or increase) is unlikely.

Projected population structures after 15 and 50 years show strongly contrasting results for the BAU and the most intensive restoration scenario (REGMOR75; Fig. 6). Using the observed dynamics in tapped and untapped plots in Metema and departing from observed population structures in these plots, strong population shrinkage was projected resulting in populations containing only seedlings and large adult trees after 50 years (Fig. 6). Under the most intensive restoration scenario (REGMOR75), projected population structures would become continuous because of sapling recruitment (Fig. 6, panels in lower two rows). Simulations for tapped and untapped populations resulted in very similar population structures.

Discussion

We present the first large-scale study on population dynamics of a frankincense-producing tree. Our results suggest that a lack of regeneration and high adult mortality – and not resin tapping – is causing strong population declines in *B. papyrifera*. As a result, strong drops in frankincense production are predicted, with a 50% reduction within 15 years.

VITAL RATES AND POPULATION DYNAMICS IN TAPPED VS. UNTAPPED POPULATIONS

We expected lower rates of tree growth, fecundity and survival of *B. papyrifera* in tapped populations as the resin extraction leads to a significant loss of carbohydrates and to investments in restoring damaged bark tissue. Surprisingly, tapped populations presented higher diameter growth rates and a higher proportion of reproductive trees compared to untapped populations. These results contrast with experimental studies on the effect of tapping: Rijkers *et al.* (2006) showed that tapping of *Boswellia* had a negative effect on reproduction, reducing flower and fruit production and increasing the proportion of non-viable seeds. Also, studies on the rubber tree *Hevea brasiliensis*, the most widely tapped tree species globally, have shown that tapping constitutes a substantial sink of carbohydrates (Silpi *et al.* 2007), leading to a 50% decline in diameter growth (Silpi *et al.* 2006). On the other hand, recruitment rates in populations of *Copaifera*

Table 1. Results of matrix model projections for four restoration scenarios of untapped and tapped populations of *Boswellia papyrifera*. Annual population growth rates λ_{100} (and corresponding 95% confidence intervals) are shown. BAU is business as usual (i.e. no management), REG is full regeneration, REGMOR50 is full regeneration plus a 50% reduction in adult mortality and REGMOR75 is full regeneration plus a 75% reduction in adult mortality
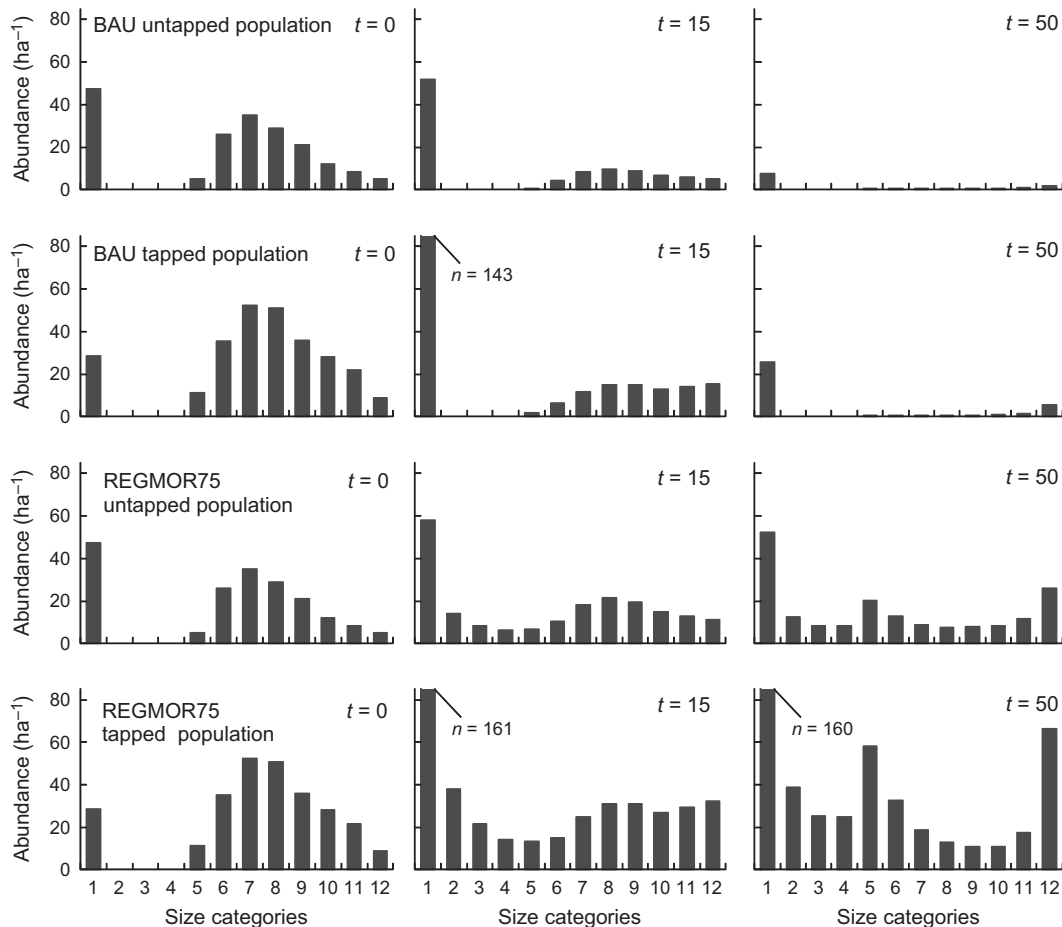
Restoration scenario	Untapped populations	Tapped populations
BAU	0.942 (0.932–0.951)	0.950 (0.938–0.962)
REG	0.956 (0.922–0.989)	0.967 (0.935–0.999)
REGMOR50	0.984 (0.951–1.016)	0.993 (0.962–1.024)
REGMOR75	0.998 (0.966–1.030)	1.006 (0.976–1.037)

reticulate in Brazil remained unaffected by harvesting of oleo-resins (Herrero-Jauregui *et al.* 2011) and reproductive output of *Khaya senegalensis* trees was not affected by partial debarking (Gaoue & Ticktin 2007).

Why were diameter growth rates in tapped populations higher than those in untapped populations? There are two possible explanations for this finding. First, higher growth rates in tapped populations may be found if diameter measurements are taken close to the tapping spot, as increased bark forma-

tion may take place around the incisions (cf. Silpi *et al.* 2006). We do not expect that such measuring biases have influenced our data, as there were no signs of increased callus thickness or wound tissue at the spots of diameter measurements. Secondly, tapped populations may differ in other respects than just the exploitation. In our study, we deliberately choose to compare the demography of tapped and untapped populations rather than performing a large-scale tapping experiment in formerly untapped populations (as performed by Rijkers *et al.* 2006). Farmers select stands based on their intuitive judgement of the potential resin production, based on average tree size, tree density, distance to roads and availability of drinking water during the dry season. Therefore, tapped populations constitute a non-random sample of *Boswellia* populations in the region, possibly located on more productive soils (Eshete, Sterck & Bongers 2011) or at locations with higher water availability (Ogbazghi *et al.* 2006b). It is likely that the observed differences in tree performance are a reflection of this non-random selection and that the favourable conditions in tapped stands have masked the likely negative effects of tapping on tree growth and reproduction.

Mortality rates did not differ significantly between tapped and untapped populations. Rijkers *et al.* (2006) suggested that resin tapping does not affect tree mortality, as long as it is

Fig. 6. Current and projected population structures of tapped and untapped stands of *Boswellia papyrifera* under two contrasting restoration scenarios. See Table 1 and text for explanation of scenarios.

performed at a moderate intensity. Tapping in our exploited populations was conducted in the traditional way, that is at moderate intensities. More intensive tapping, involving more and deeper incisions or complete debarking and exposure of cambium, is known to occur in regions under high commercial pressure (Eshete 2002). Damage from intensive tapping is probably comparable to that inflicted by bark harvesting, which substantially increased mortality risk in *Prunus africana* and *Garcinia lucida* (Guedje *et al.* 2007; Stewart 2009).

As a result of the higher rates of diameter growth and fecundity, tapped stands had a slightly higher population growth rate than untapped stands (Table 1). This difference in population growth is much smaller than that between the business-as-usual scenario (which led to strong population decline) and the best restoration scenarios (optimal regeneration and strongly reduced adult mortality, REGMOR50 and REGMOR75). This suggests that factors other than tapping are governing *Boswellia* populations in the study region.

CAUSES AND CONSEQUENCES OF THE REGENERATION BOTTLENECK

Both tapped and untapped populations showed clear regeneration bottlenecks. Population structures presented gaps in the juvenile size classes, and none of the monitored seedlings (*n* = 2228) grew into permanent saplings during 2 years of observations. In our study, only the remote untapped population (Adi Arkay) contained saplings and small juvenile trees. Such gaps in population structure have been observed for unharvested (Walker 1993; Wassie *et al.* 2010) and over-exploited tree species (Peres *et al.* 2003). Our model simulations for *Boswellia* showed that gaps in population structures will worsen under a business-as-usual scenario (Fig. 6).

What are the plausible explanations for the blocked regeneration in our study populations? First, apparent lack of regeneration may occur if regeneration takes place sporadically, for example during periods of favourable (climatic) conditions (Holmgren *et al.* 2001). Such erratic regeneration may be sufficient to replace the standing population and does not necessarily result in a decline in population viability (Wiegand, Jeltsch & Ward 2004). However, in our study region we did find a continuous distribution of individuals over size classes in the Adi Arkay plot where climatic variability is supposed to be the same as in the Metema area. Thus, there are no indications that gaps in population structure are the result of erratic sapling establishment.

A second possible cause of regeneration failure is high seedling mortality because of fires or grazing. Natural fires occur occasionally in dry tropical forests and woodlands (Eriksson, Teketay & Granström 2003) and are a major determinant of tree population dynamics in these forests (Swaine 1992; Nangendo *et al.* 2010; Suresh, Dattaraja & Sukumar 2010). In *Boswellia*, non-permanent seedlings are unlikely to be affected by fires as they do not possess aboveground structures during the dry season, but permanent saplings may be severely impeded by fire. Grazing and browsing are known to affect natural regeneration in *Boswellia*: significantly higher seedling

densities can be found in fenced compared to open areas (Ogbazghi 2001; Gebrehiwot *et al.* 2003). *Boswellia* seedling leaves are an important source of fodder, and fodder collection leads to seedling damage and mortality (Gebrehiwot *et al.* 2003). Grazing is also thought to block regeneration of *Prunus africana*, another important African tree species that yields NTFP (Stewart 2009).

It is likely that the incidence of fires and the intensity of grazing in our study area has increased over the last decades because of a strong increase in cattle population (Eshete, Teketay & Hulten 2005). Farmers customarily burn grasses in the forest understorey at the end of the dry season to stimulate nutrient-rich regrowth. A large part of the previously undisturbed forests containing *Boswellia* populations are now grazed and frequently burned. Studies on (changes in) fire frequency and the effect of fire and grazing on tree populations are urgently required.

CAUSES AND CONSEQUENCES OF HIGH ADULT MORTALITY

Adult tree mortality was high, in both tapped and untapped populations. Annual mortality rates for trees > 10 cm DBH equalled 6–7%. These rates are almost ten times higher than those in an Indian dry forest (Suresh, Dattaraja & Sukumar 2010) and probably also substantially higher than those in other dry forests. A large proportion of the trees in our study were killed after having been attacked by the long-horn beetle *Idactus spinipennis* (Eshete 2011). High infection rates (up to 85%) of *Boswellia* trees by larvae of this beetle have been reported for our study region (Metema) and elsewhere (Tigray: Negussie 2008). High incidence of fire may weaken trees and make them more susceptible to beetle attack. In this context, it is interesting to note that adult trees in the remote Adi Arkay population, where no burning or grazing was applied, presented lower rates of annual mortality ($\sim$3.6%; *n* = 246), showed fewer signs of beetle attack and no detectable signs of fire (A. Eshete, personal observation). Clearly, there is a pressing need to obtain clarity on the causes of the elevated adult mortality in *Boswellia* stands.

Our simulation results suggest that high adult tree mortality severely limits population growth and is one of the two main causes of the projected decline in *Boswellia* populations under the business-as-usual scenario. This elevated mortality seems to be unrelated to tapping, as mortality levels are very similar in tapped and untapped stands. Population growth of long-lived tree species is highly susceptible to changes in adult mortality (Guedje *et al.* 2007; Zuidema *et al.* 2010). Thus, enhancing adult survival will be crucial to the long-term persistence of *Boswellia* populations and sustainability of frankincense production.

IMPLICATIONS FOR MANAGEMENT

Clearly, restoration interventions are necessary to reverse the projected trend of declining populations and frankincense yield. In the short term, it is essential to reduce adult mortality.

Fire and beetle attacks are the most likely causes of tree death and need to be controlled. Fire breaks should be established and fire frequency should be strongly reduced. Control of beetle attacks is more difficult as basic information on beetle life cycle, densities and impact is lacking.

In the long term, it is important that *Boswellia* saplings recruit naturally in tapped and untapped populations. Set-aside areas that are protected from ground fires and grazing for long enough (5–10 years) are needed to allow sapling establishment. Increased regeneration of *B. papyrifera* trees has been found in enclosures in other parts of Ethiopia and in Eritrea (Ogbazghi 2001; Gebrehiwot *et al.* 2003), and this approach could be followed more widely. Furthermore, *Boswellia* stands could be supplemented with saplings raised in nurseries. Experimental planting of tree cuttings has shown promising results (Negussie *et al.* 2009), but successful raising of seedlings requires specific care and protection (E. Birhane, personal communication).

The restoration of Ethiopian *Boswellia* stands is complicated by the fact that multiple groups of users exploit frankincense woodlands for different resources. In our study area, these forests are used by local people for grazing and by labourers from elsewhere for frankincense tapping (Eshete, Teketay & Hulten 2005; Lemenih, Feleke & Tadesse 2007). Ultimately, the responsibility for forest management in these areas lies with the state as it holds jurisdiction over forest resources. We believe that widespread and strong management incentives are necessary to sustain and restore *Boswellia* populations and safeguard future frankincense production.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Height-root collar diameter relation.

Table S1. Transition matrices of tapped and untapped populations.

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