The Effects of Herbivory by a Mega- and Mesoherbivore on Tree Recruitment in Sand Forest, South Africa

D. D. Georgette Lagendijk*, Robin L. Mackey, Bruce R. Page, Rob Slotow

Amarula Elephant Research Programme, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, South Africa

Abstract

Herbivory by megaherbivores on woody vegetation in general is well documented; however studies focusing on the individual browsing effects of both mega- and mesoherbivore species on recruitment are scarce. We determined these effects for elephant *Loxodonta africana* and nyala *Tragelaphus angasii* in the critically endangered Sand Forest, which is restricted to east southern Africa, and is conserved mainly in small reserves with high herbivore densities. Replicated experimental treatments (400 m²) in a single forest patch were used to exclude elephant, or both elephant and nyala. In each treatment, all woody individuals were identified to species and number of stems, diameter and height were recorded. Results of changes after two years are presented. Individual tree and stem densities had increased in absence of nyala and elephant. Seedling recruitment (based on height and diameter) was inhibited by nyala, and by elephant and nyala in combination, thereby preventing recruitment into the sapling stage. Neither nyala or elephant significantly reduced sapling densities. Excluding both elephant and nyala in combination enhanced recruitment of woody species, as seedling densities increased, indicating that forest regeneration is impacted by both mega- and mesoherbivores. The Sand Forest tree community approached an inverse J-shaped curve, with the highest abundance in the smaller size classes. However, the larger characteristic tree species in particular, such as *Newtonia hildebrandtii*, were missing cohorts in the middle size classes. When setting management goals to conserve habitats of key importance, conservation management plans need to consider the total herbivore assemblage present and the resulting browsing effects on vegetation. Especially in Africa, where the broadest suite of megaherbivores still persists, and which is currently dealing with the 'elephant problem', the individual effects of different herbivore species on recruitment and dynamics of forests and woodlands are important issues which need conclusive answers.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: georgette.lagendijk@gmail.com

Introduction

Different-size herbivores have different feeding preferences [1]; however, some overlap, and hence competition, might exist between different trophic guilds [2]. Megaherbivores (body mass ≥1000 kg [3]) compete with mesoherbivores (medium-size herbivores with body mass between 50 and 450 kg [1,2]) for food [2] as they feed in overlapping height ranges [4,5]. Through their browsing activities, both mega- and mesoherbivores have the capacity to alter structural diversity (e.g. height class distributions) of forests and woodlands [6,7]. Some megaherbivores open up the canopy by changing the vertical structure from top down, by impacting on large trees and browsing at higher levels [3]. On the other hand, mesoherbivores may have considerable effects as (1) controllers of the state induced by megaherbivores, by suppressing woodland or forest recovery through browsing after megaherbivore impact has altered woodland to shrubland [8] or (2) top down control of recruitment into taller height classes by browsing of seedlings [9,10]. Individual species or entire communities may disappear over time when there is no adequate recruitment and hence regeneration into taller height classes to compensate natural die-offs, impact of fire [11] and megaherbivores.

While numerous studies have focused on megaherbivore impact on woody communities (e.g. [3,12–16]), and on the effects of herbivores in general on community structure and composition [17–21], the combined effects of both mega- and mesoherbivore species on different height classes have received scant attention. Exclosure experiments in savanna landscapes have tried to separate effects on vegetation by different groups of herbivores [22–26]. However, effects observed in these studies can not be positively ascribed to one species only, when distinguishing between groups of herbivores of similar sizes. Consequently, the specific browsing effects of both mega- and mesoherbivores on regeneration of woody vegetation, especially in the African context where the broadest suite of megaherbivores still persists, still remain largely unknown.

Here we focus on the impacts on seedling and sapling recruitment by a mega- and mesoherbivore within the critically endangered Sand Forest community [27]. This deciduous dry forest type is restricted to the Maputaland Centre of Endemism in north-eastern KwaZulu-Natal, South Africa and southern Mozambique [28–30]. Sand Forest generally occurs in a mosaic of patches enclosed by mixed woodland or savanna bushveld [31,32], and includes a large number of rare and endemic species

[29,30,32]. Its restricted geographic range and unique species composition makes Sand Forest one of the most important habitat types for conservation in southern Africa [28,31,33]. Sand Forest is susceptible to fire and selective species utilisation by both man and herbivores, the effects of which are exacerbated by Sand Forest's low resilience to disturbance and poor recruitment rates of its tree species [29,34,35]. While foraging, browsing herbivores create pathways which open up the forest [36,37]. Once savanna vegetation enters these gaps within the Sand Forest, successive changes to savanna woodland may be irreversible [31,34].

The dynamics of Sand Forest are poorly understood [32]. The structural diversity in the Sand Forest system in some protected areas has changed drastically over the past decade, particularly in Tembe Elephant Park (Matthews pers. comm.) and Phinda Private Game Reserve (Pretorius pers. comm.). The main reason for this is thought to be herbivory [5,38], affecting both the recruitment phase and taller height classes. Both elephant Loxodonta africana and nyala Tragelaphus angasii became locally abundant in protected Sand Forest areas after (re)introductions of these species in the early 1990s.

Conservation of the Sand Forest community is of critical importance, and it is therefore imperative to assess potential drivers affecting the tree community and its low recruitment rates. Management questions have been raised regarding the impact of herbivores, in particular elephants [39], on the vegetation, such as whether elephants or other herbivores are causing irreversible damage to the Sand Forest ecosystem, and if densities of these species need to be reduced in order to conserve the forest. We hypothesise that both mixed feeders have had, and are having, substantial impact on the vegetation [5,29,38], as densities of both elephant and nyala have increased since (re)introduction with concomitant changes to Sand Forest structural diversity. Therefore, the aim of this study was to assess the role of elephant and nyala on Sand Forest structure through their individual and combined browsing effect, particularly on recruitment. While impala Aepyceros melampus have been linked to recruitment limitation [10,40], this has not been studied for nyala. To our knowledge, this is the first study to experimentally separate the browsing effects of a mega- and mesoherbivore.

Methods

Study area

Phinda Private Game Reserve (hereafter Phinda) is a 180 km^2 (27°92′–27°68′S; 32°44′–32°20′E) conservation area in Maputaland, northern KwaZulu-Natal, South Africa. The reserve includes a wide range of habitat types, such as western Maputaland sandy bushveld as well as several patches of the endemic Sand Forest [27]. The climate is subtropical with hot, humid summers and warm, dry winters. Temperatures range from a minimum of 10°C in winter to a maximum of 35°C in summer. Annual rainfall ranges between 350 mm and 1100 mm, and varies spatially from west to east.

Before Phinda was created in 1991, the area consisted of private and small game farms. Game was introduced following the establishment of the park [38], with fifty-eight elephants being released into Phinda between 1992 and 1994 [41]. At the start of this study (2005) 81 elephants were present in the reserve, increasing to 98 individuals in 2007 (based on an individually identified and monitored elephant population (e.g. [42])). Nyala numbered approximately 1100 and 1750 individuals in 2005 and 2007, respectively (based on annual aerial game counts). Other browsing ungulates in Phinda include giraffe Giraffa camelopardalis (154), kudu Tragelaphus strepsiceros (188), impala (1690), red duiker

Cephalophus natalensis (23), common duiker Sylvicapra grimmia (no count available) and suni Neotragus moschatus (no count available). Counts in parentheses are approximate and reflect the 2007 annual helicopter game count.

This study was conducted in the endemic Sand Forest, which occurs in the northern section of Phinda. Sand Forests occur on acidic, sandy soils with very little clay [29]. The Sand Forest is a dense vegetation type, with a closed canopy, 5 to 12 m high, without a significant understorey. Characteristic woody species include Balanites maughamii, Cleistanthus schlechteri, Cola greenwayi, Croton pseudopulchellus, Dialium schlechteri, Drypetes arguta, Hymenocardia ulmoides, Newtonia hildebrandtii and Pteleopsis myrtifolia [28,31,33]. Few mammal species utilise Sand Forest [31]. In Phinda, elephant and nyala are the only mega- and mesoherbivore utilising the Sand Forest patches (Lagendijk pers. obs.).

Experimental design

The effects of elephant and nyala on Sand Forest recruitment were tested using exclosures. In November 2005, elephants were excluded from part of the Sand Forest using electrified (7000 volts per second) high tension galvanized wires (2.4 mm thick) erected at 1.8 m and 2 m above the ground, enclosing 3.09 km^2 of the 5.2 km^2 Sand Forest patch (Fig. 1). To determine the effects of both elephant and nyala separately, twelve exclosures of 20 m×20 m using 1.8 m high bonnox fencing (a coarse wire mesh with 30×20 cm openings) were erected inside the elephant-free area. This type of fencing allowed passage for small-size herbivores such as duiker and suni, but excluded nyala. Adjacent to this exclosure, another 20 m×20 m area was marked out and opposite these two treatments just outside the elephant fence a third 20 m×20 m area was marked for sampling. This resulted in an experimental design of a set of three 400-m^2 treatments in close proximity, consisting of: (1) unfenced area available to all herbivores (open access "+E+N"); (2) area fenced to exclude only elephant (partial exclosure, nyala present "−E+N"); (3) area fenced to exclude both nyala and elephants (full exclosure "−E−N"), but providing access to smaller herbivores. There
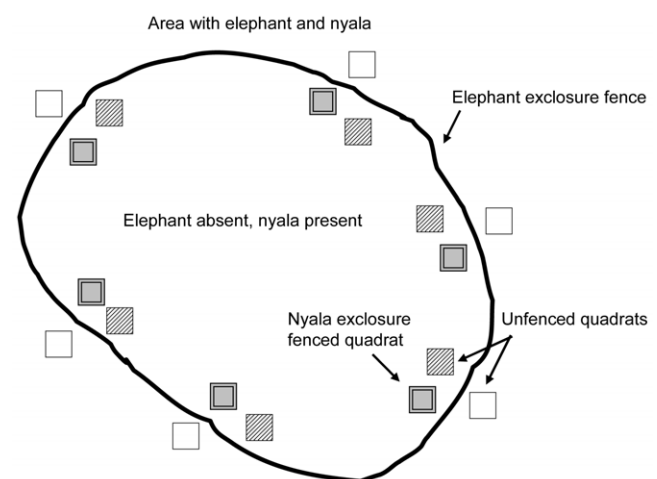

Figure 1. A schematic representation of the exclosure experiment with the three treatments. (1) open access, accessible for all herbivores (+E+N, open bars); (2) partial exclosure, elephant excluded, nyala present (−E+N, diagonal hatching); (3) full exclosure, both elephant and nyala excluded (−E−N, grey bars) (not to scale). The sets of three treatments were replicated 12 times.
doi:10.1371/journal.pone.0017983.g001

were a total of 12 replicates of this set of three treatments. Distance between replicates ranged between 0.12 km and 2.75 km.

A base-line study was conducted in 2005. In each quadrat (n = 36) all woody individuals (including seedlings; >0.02 m and ≤0.5 m tall; and saplings, >0.05 m and ≤1.5 m tall) were identified to species and counted. Diameters above the buttress swelling of all stems (including seedlings and saplings) and all tree heights were recorded. Diameters and the heights of trees to 2 m were measured, the heights of trees between 2 m and 4 m estimated to the nearest 20 cm, and the heights of taller trees estimated to the nearest 50 cm using the height of an observer as a scale following Shannon et al. [16]. Two years after implementation of the experiment, quadrats were sampled again during June–July or November–December 2007, with the three treatments from a replicate being sampled during the same sampling trip. Five open access plots were repositioned in 2007, therefore when doing pair-wise comparisons between the two sampling years, only 7 open access plots (+E+N) were included in the analyses. The analyses are of 2007 data unless otherwise stated.

Statistical analyses

Following recommendations by Clarke and Warwick [43], tree species contributing less than 4 percent of the abundance per plot in 2005 were discarded and only species present in both sampling years were included. Given that recruitment is dependent on a local seed source, we believe that excluding the rare species provides a more robust test of recruitment patterns across treatments. Consequently a total of 26 tree species were included in the analyses (Table 1); all of these species were browsed upon by the herbivore guild during the course of the experiment.

Because there are two possible demographic responses to browsing viz. mortality or a coppicing response (i.e. the production of new stems after the terminal part of the main stem has been removed [44]), changes in both the density of individual trees (which measures mortality, but also reflects recruitment) and stem density (which measures the coppicing response or mortality of vertical stems) were investigated. Individual and stem densities were scaled up from 400 m^2 to 1 ha. Individual trees and stems were allocated to seven height classes (≤0.5 m, 0.51–1.5 m, 1.51–3 m, 3.01–5 m, 5.01–8 m, 8.01–12 m, >12 m), which roughly correspond to the limits at which browsing by different-size herbivores occurs.

ANOVAs were used to test for differences in overall tree and stem densities among treatments in 2007, for which data were pooled for all species and height classes. Differences in seedling (≥0.02 and ≤0.5 m in height) and sapling (>0.5 m and ≤1.5 m in height) abundance, as well as stem densities in these height

classes, among treatments were also analysed using ANOVA. Pairwise comparisons of individual overall tree densities and seedlings per treatment between 2005 and 2007 were also analysed using ANOVA.

Tree populations are regenerating when the population structure displays an inverse J-shaped frequency distribution [45,46]. This translates to a relatively high abundance of seedlings, which represents sufficient recruitment, and a relatively low abundance of tall trees. A distribution of a different shape is indicative of disturbance [47]. Following previous work in Sand Forest [48,49], we used 18 different size classes with 1 cm intervals to 7 cm diameter, thereafter 2 cm intervals to 15 cm diameter, 5 cm intervals to 30 cm diameter and 10 cm intervals to 60 cm. The diameter limits that are equivalent to the height categories we used are 1, 4, 9, 15, 25, 40 and >40 cm diameter (derived from a quadratic regression of diameter vs height for all Sand Forest species ($r^2 = 0.73$)). A G-test was used to determine whether size distributions differed among treatments for the pooled data. To prevent compounding of Type 1 errors from running three pair-wise G-tests, alpha of 0.05 was Bonferroni-adjusted to 0.017.

At the tree species level, we focused our analyses on the three most common Sand Forest species in our study area (Salacia leptoclada, Uvaria caffra and Tricalysia junodii) and on three characteristic Sand Forest trees (D. schlechteri, N. hildebrandtii and P. myrtifolia) to determine the effect of elephant and/or nyala on recruitment. Seedling and sapling abundance were analysed separately among treatments per focus species using a two-way ANOVA. When ANOVA assumptions were not met, densities were analysed with a Kruskal-Wallis test. Size class distributions (SCD), which reflect population structures, were analysed for each of these six species using linear regressions (cf. [45,50]). Data were pooled per treatment. The number of individual trees per diameter class was divided by the width of the diameter class, giving an average density (D_i) for the class midpoint (M_i). These variables were 'ln+1' – transformed prior to regression analyses. All size classes up to the largest size class containing individuals were included in the analyses. We used SCD slopes to interpret population structures. An inverse J-shaped curve is represented by a steep negative slope, while species with little regeneration show a negative slope close to zero.

For all the abovementioned statistical tests the significance level was set at P = 0.05, unless otherwise stated. All significant ANOVAs (assumptions of normality and homoscedasticity being met) were followed-up with Tukey's post-hoc tests. All statistical analyses were performed using SPSS 15.0 (SPPS Inc., Chicago, USA).

Table 1. List of 26 species included in the analyses.

Cola greenwayi Brenan	Hymenocardia ulmoides Oliv.	Rhus natalensis Bernh. Ex Krauss
Combretum celastroides Welw. Ex Laws.	Hyperacanthus amoenus (Sims) Bridson	Salacia leptoclada Tul.
Combretum mkuzense Carr & Retief	Landolphia kirkii T.-Dyer	Strychnos henningsii Gilg
Croton pseudopulchellus Pax	Monanthotaxis caffra (Sond.) Verdc.	Toddalopsis bremekampi Verdoorn
Croton steemkampianus Gerstner	Monodora junodii Engl. & Diels	Tricalysia junodi (Schinz) Brenan
Dialium schlechteri Harms	Newtonia hildebrandtii (Vatke) Torre	Uvaria caffra E. Mey. Ex Sond.
Drypetes arguta (Muell. Arg.) Hutch	Ptaeroxylon obliquum (Thunb.) Radlk.	Wrightia natalensis Stapf
Grewia microthyrsa K. Schum. Ex Burret	Pteleopsis myrtifolia (Laws.) Engl. & Diels	Zanthoxylum sp.
Haplocoelum gallense (Engl.) Radlk.	Rhus gueinzii Sond.	

doi:10.1371/journal.pone.0017983.t001

Results

In 2005, 12638 individual plants from 95 woody species, and in 2007, 17825 individual trees and 143 woody species were recorded in all treatments. In 2007, the dominant Sand Forest species *S. leptoclada*, *T. junodii*, and *U. caffra* made up 49.9% of all trees, compared to 53.4% in 2005.

The twelve replicates of the experiment were considered to be homogeneous in 2005 as, when only taking the more abundant species (n = 26) into account, there were no significant differences among treatments for the seedling ($F_{0.05(2)2,33} = 0.363$, $P = 0.698$), sapling ($F_{0.05(2)2,33} = 0.944$, $P = 0.399$), and overall (i.e. all size classes combined) tree and stem densities ($F_{0.05(2)2,33} = 0.842$, $P = 0.440$ and $F_{0.05(2)2,33} = 1.905$, $P = 0.165$ respectively). Note that when all species present were included in this analysis, there were still no significant differences for any of these contrasts (seedling: $F_{0.05(2)2,33} = 1.044$, $P = 0.363$; sapling: $F_{0.05(2)2,33} = 0.758$, $P = 0.464$; tree density for all size classes combined: $F_{0.05(2)2,33} = 0.883$, $P = 0.444$; stem density for all size classes combined: $F_{0.05(2)2,33} = 2.734$, $P = 0.080$).

In contrast to this, for the 26 species in 2007 there were significant differences among the treatments in both the overall tree densities ($F_{0.05(2)2,33} = 5.180$, $P = 0.011$) and the overall stem densities ($F_{0.05(2)2,33} = 4.426$, $P = 0.020$), with densities in the full exclosure (−E−N) being significantly greater than in the open access treatment (+E+N) (overall tree density, Tukey: $P = 0.010$; overall stem density, Tukey: $P = 0.027$). The overall abundance of individual trees in the partial exclosure (−E+N), were not significantly different from those in the open access (+E+N) or in the full exclosure (−E−N) treatment. However stem densities were greater in the full exclosure than in the partial exclosure, although this was marginally not significant (Tukey: $P = 0.056$). Pair-wise comparisons between 2005 and 2007 showed a significant increase in the full exclosure for overall tree densities (−E−N: $F_{0.05(2)1,22} = 7.387$, $P = 0.013$). Differences in overall stem densities per treatment between 2005 and 2007 were not significant (open access (+E+N): $F_{0.05(2)1,12} = 0.599$, $P = 0.454$; partial exclosure (−E+N): $F_{0.05(2)1,22} = 0.537$, $P = 0.471$; full exclosure (−E−N): $F_{0.05(2)1,22} = 2.401$, $P = 0.136$). This indicated that recruitment was taking place within the full exclosure (−E−N).

Seedling density of the 26 species differed significantly among treatments in 2007 ($F_{0.05(2)2,33} = 3.582$, $P = 0.039$; Fig. 2). Seedling densities in the full exclosure (−E−N) were significantly higher than in the open access (+E+N) treatment (Tukey: $P = 0.035$), indicating that both nyala and elephant in combination reduced seedling densities. This is concordant with analysing seedling densities by tree diameter class as opposed to height class. Seedling density (0–1 cm diameter class) differed significantly among treatments ($F_{0.05(2)2,33} = 5.104$, $P = 0.012$), with greater seedling densities in the full exclosure (−E−N) than in the open access treatment (+E+N: Tukey: $P = 0.010$; Fig. 3).

For the 26 species, pair-wise comparisons of seedling (≤0.5 m in height) density between 2005 and 2007 was not significantly different within the partial exclosure (−E+N: $F_{0.05(2)1,22} = 3.186$, $P = 0.088$). However, there was a significant increase in seedling densities in the open access treatment (+E+N: $F_{0.05(2)1, 12} = 5.386$, $P = 0.039$) and the full exclosure between 2005 and 2007 (−E−N: $F_{0.05(2)1,22} = 9.755$, $P = 0.005$; Fig. 4).

For the 26 species, sapling densities in 2007 were not significantly different among treatments ($F_{0.05(2)2,33} = 1.421$, $P = 0.256$; Fig. 2), and there were no significant differences in sapling densities within each treatment between the two sampling years ($P > 0.21$). Using stem diameter as opposed to height, there were also no significant differences in densities of saplings (1.01 to 4 cm diameter class) among treatments in 2007 ($F_{0.05(2)2,33} = 0.123$, $P = 0.884$; Fig. 3).
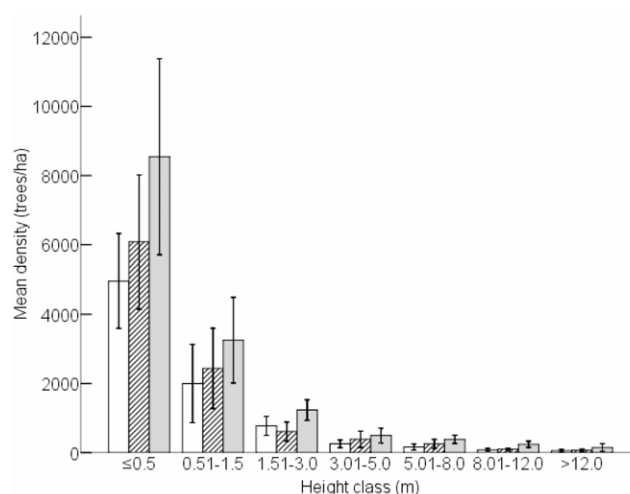

Figure 2. Mean density (trees/ha) per height class (i.e. seedlings: ≤0.5 m; saplings; 0.51–1.5 m) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclosure (−E+N, diagonal hatching) and full exclosure (−E−N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.
doi:10.1371/journal.pone.0017983.g002

Seedling stem densities in 2007 were significantly different among the three treatments ($F_{0.05(2)2,33} = 5.030$, $P = 0.012$; Fig. 5), with seedling stem densities significantly greater in the full exclosure (−E−N) (Tukey: $P = 0.012$) than the open access treatment (+E+N). Sapling stem densities were not significantly different among treatments ($F_{0.05(2)2,33} = 0.146$, $P = 0.865$; Fig. 5). The greater seedling stem densities in the full exclosure also indicate that the differences in the density of individual trees are mostly due to recruitment of individual trees. However, additional stems were added from the recruitment of multi-stemmed trees or from the production of new stems from coppicing as a response to browsing prior to the establishment of the experiment.

Population structures were assessed using diameter size distributions for all species combined. In 2007, diameter size distributions were significantly different among treatments ($G_{12} = 3169$, $P ≤ 0.017$ for all pair-wise comparisons). In all treatments, the highest abundance was found in the smallest size (≤1.0 cm) class (Fig. 3). Population structures approached an inverse J-shaped curve.

Both seedling and sapling densities of each of the six selected focus species did not significantly differ among treatments (seedlings: $P > 0.54$; saplings: $P > 0.33$; Fig. 6a, 7a). However, the population structures of each of these six species had missing diameter size classes (mainly middle size classes). The population structures of *S. leptoclada*, *U. caffra* and *T. junodii* approached the inverse J-shaped curve characteristic of increasing populations, which is supported by the strong negative SCD slopes for these species (Fig. 6b, 7b, Table S1). *D. schlechteri*, *N. hildebrandtii* and *P. myrtifolia* showed a SCD slope closer to zero, indicating a disruptive population structure with little regeneration. However this was not significant for *N. hildebrandtii* (in any of the treatments) and *D. schlechteri* (in the full exclosure (−E−N)).

Discussion

In addition to any effect small herbivores, rodents and invertebrates may have on recruitment [7,22,23], we show that forest regeneration is also impacted by both mega- and
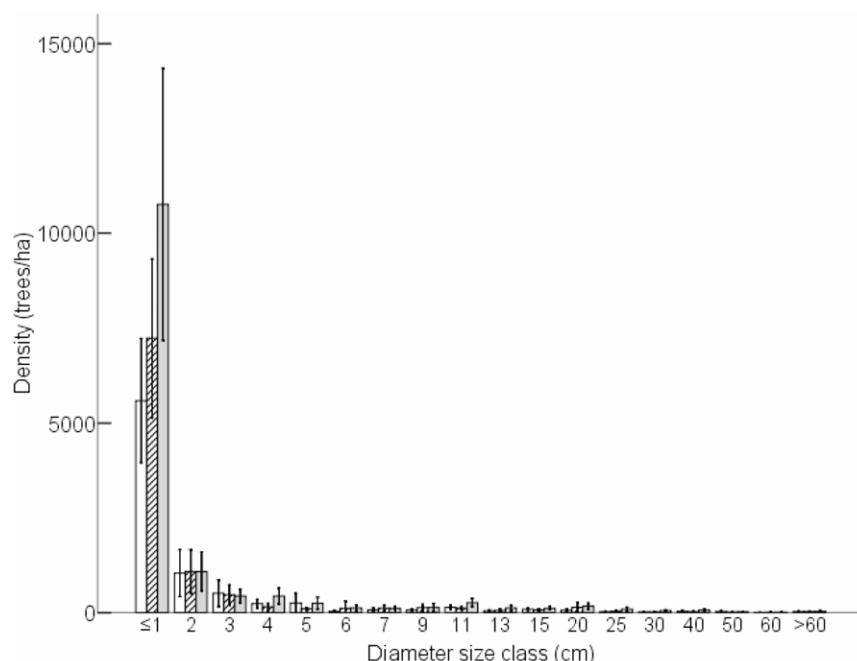
Figure 3. Mean density (trees/ha) per diameter size class (i.e. seedlings: ≤1 cm; saplings; 1–4 cm) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclosure (−E+N, diagonal hatching) and full exclosure (−E−N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.
doi:10.1371/journal.pone.0017983.g003

mesoherbivores as we managed to experimentally separate the browsing effects of elephant and nyala on recruitment. Both elephant and nyala potentially forage on recruiting individuals as the preferred feeding height of elephant falls between 1.0 and 2.0 m [4], and that of nyala between 0.6 and 1.1 m [5].

Neither seedlings nor saplings of the three common and three characteristic focus species showed a significant effect from browsing. Elephants have been found to select for *D. schlechteri*, *N. hildebrandtii*, *P. myrtifolia* and *T. junodii*, and use *S. leptoclada* less selectively in Sand Forest in Tembe Elephant Park (TEP) (*U. caffra* does not occur in TEP) [31]. However, it may well be that elephant in Phinda do prefer the first four species, but do not impact on the seedlings or saplings. To our knowledge, feeding
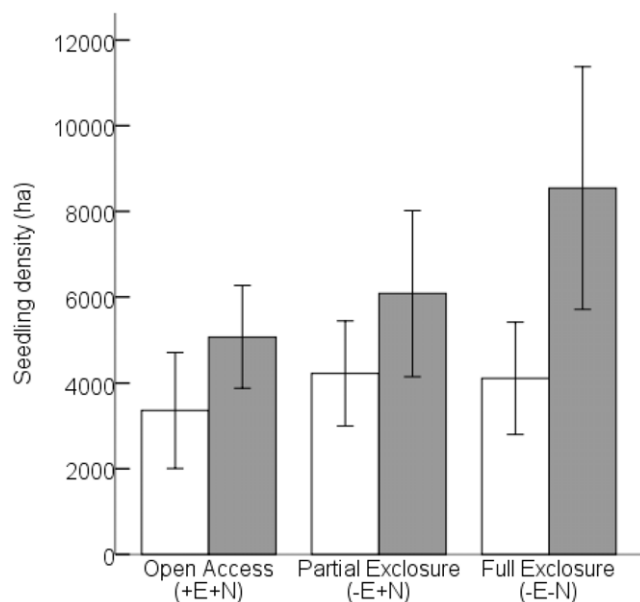

Figure 4. Mean seedling density (trees/ha) for all 26 species combined per treatment per sampling year. Open bars: 2005; grey bars: 2007. The bars indicate 95% confidence intervals of the means. N = 7 replicates for the open access treatment (+E+N) and N = 12 for the partial (−E+N) and full exclosure (−E−N).
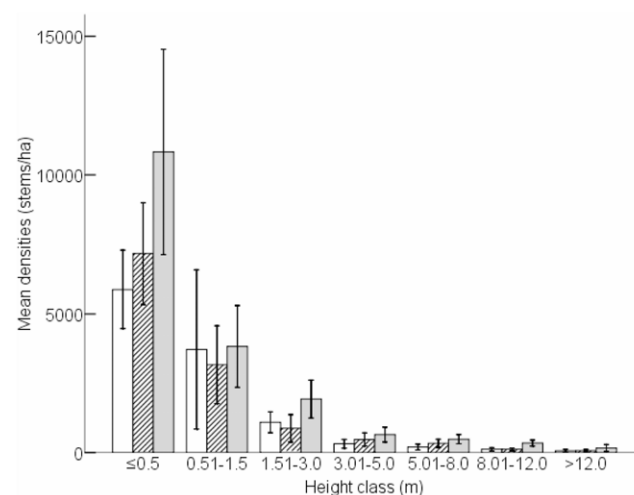doi:10.1371/journal.pone.0017983.g004

Figure 5. Mean stem density (stems/ha) per height class (i.e. seedlings: ≤0.5 m; saplings; 0.51–1.5 m) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclosure (−E+N, diagonal hatching) and full exclosure (−E−N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.
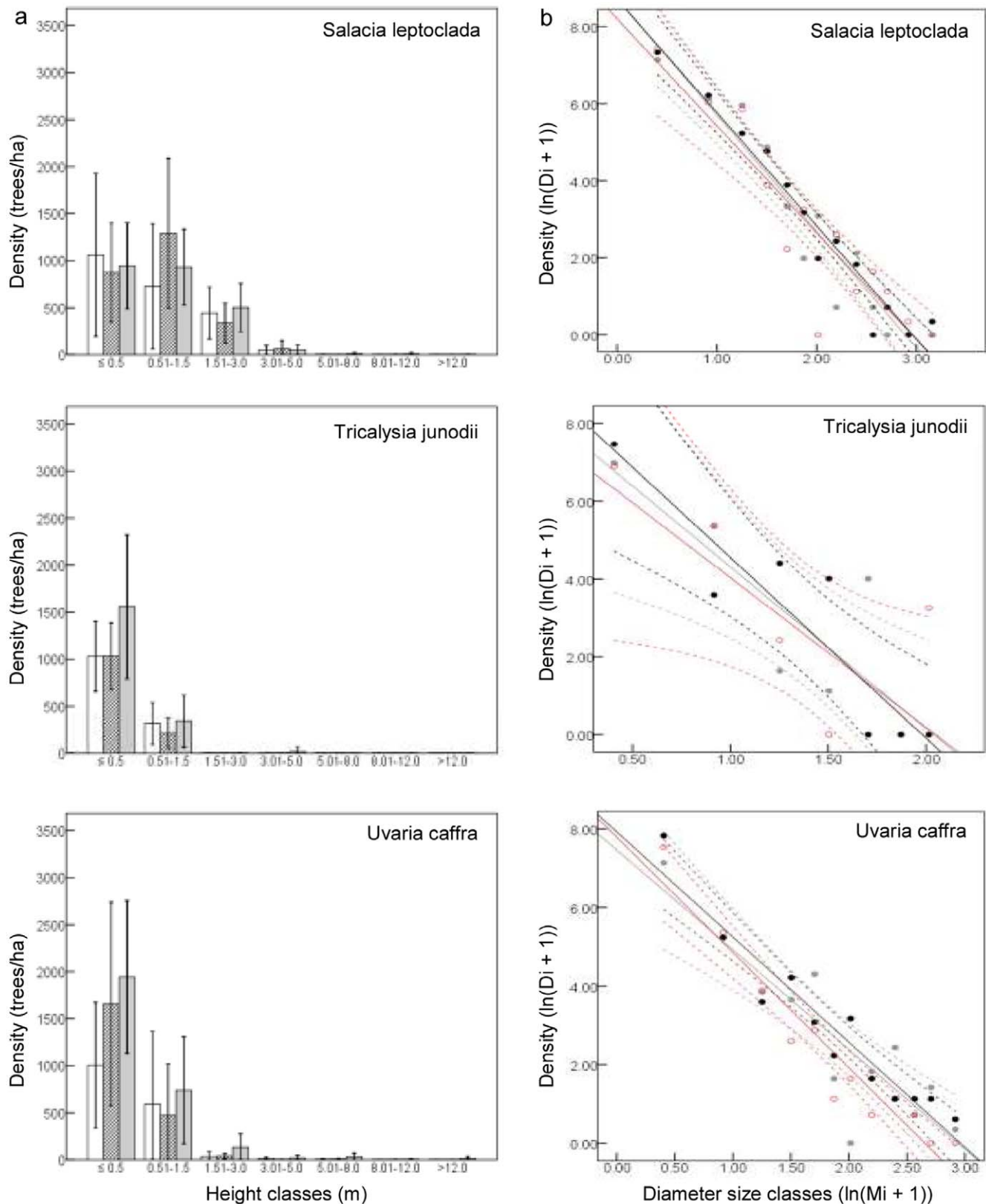doi:10.1371/journal.pone.0017983.g005

Figure 6. Size distribution curves of three common Sand Forest species in the three treatments. a, height class distribution (i.e. seedlings: ≤0.5 m; saplings; 0.51–1.5 m); b, linear regression of diameter class distribution. Open access (+E+N, open bars, grey circles and lines), partial exclosure (−E+N, diagonal hatching, red circles and lines) and full exclosure (−E−N, grey bars, black circles and lines). The bars (a) and dotted lines (b) indicate 95% confidence intervals. N = 12 replicates per treatment.
doi:10.1371/journal.pone.0017983.g006

Figure 7. Size distribution curves of three characteristic Sand Forest species in the three treatments. a, height class distribution (i.e. seedlings: ≤0.5 m; saplings; 0.51–1.5 m); b, linear regression of diameter class distribution. Open access (+E+N, open bars, grey circles and lines), partial exclosure (−E+N, diagonal hatching, red circles and lines) and full exclosure (−E−N, grey bars, black circles and lines). The bars (a) and dotted lines (b) indicate 95% confidence intervals. N = 12 replicates per treatment.
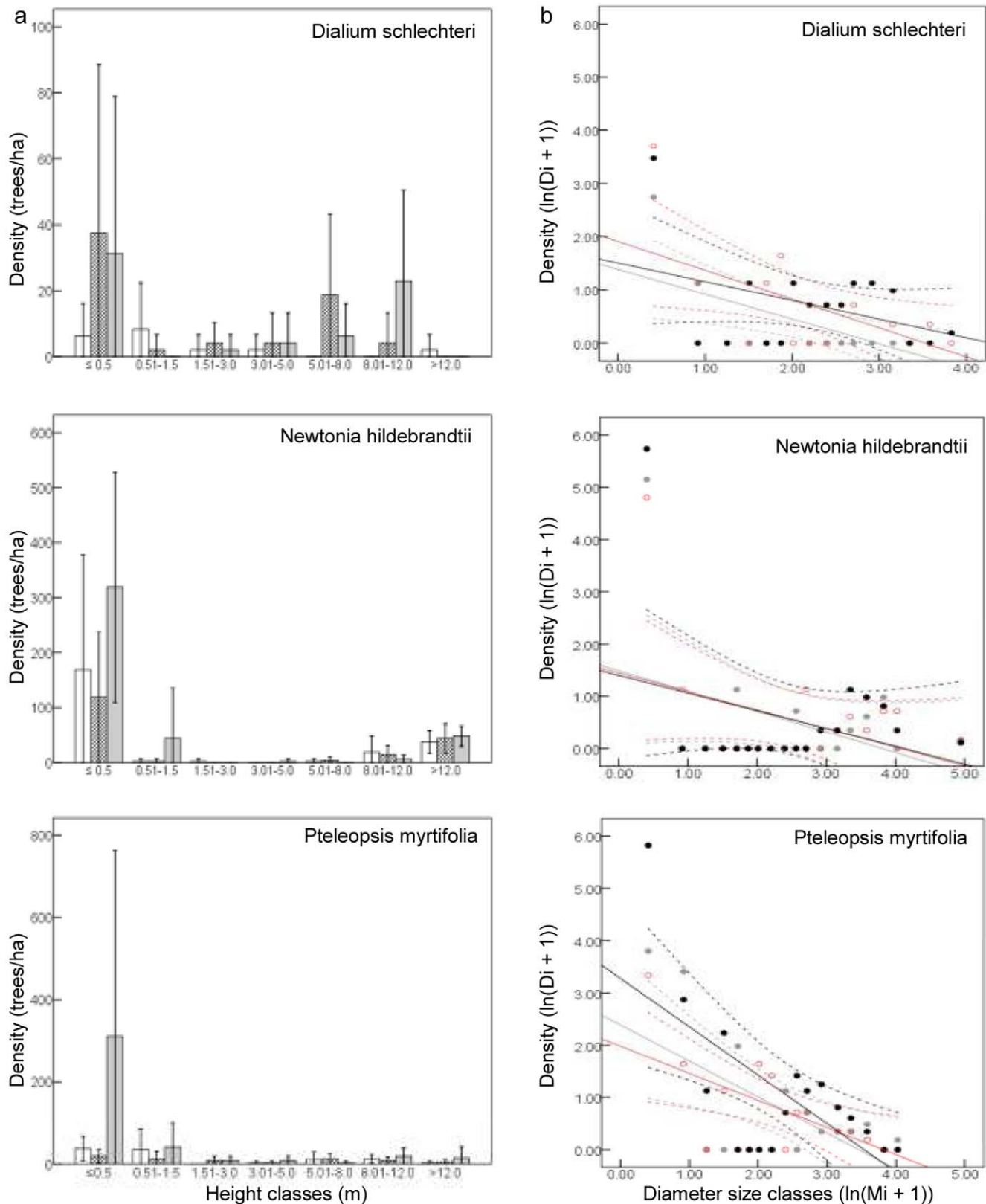doi:10.1371/journal.pone.0017983.g007

preferences of nyala have not yet been published. In addition, Sand Forest soil seed banks have been found to be poor in TEP [32], which is consistent with the low seed bank densities for dry tropical forests [32]. Together with the short time frame of this study, this might explain the absence of a browsing effect on our focus species.

All three large tree species (*D. schlechteri*, *N. hildebrandtii* and *P. myrtifolia*) had size classes missing in the middle size cohorts, which may be explained by previous human utilisation of stems. In the last 25 years, the human population in the region [33,51] has drastically increased with a concurrent intensification of the use of forest products, such as construction timber, fuel wood, wood for curios and medicinal plants [52,53]. Missing size classes may also be a result of poor recruitment in the past; however there is little consensus over the potential causes underlying low recruitment rates in Sand Forest, which range from climatic factors (e.g. drought), periodic recruitment events, to browsing pressure [31,32,54].

Regeneration success, and hence recruitment of woody species into taller height classes, is dependent on a variety of factors. Seedling mortality is size-dependent, with the highest mortality occurring in the height class below 10 cm [55]. This implies that seedlings are most at risk during the establishment phase, when young trees are often most palatable [56]. Therefore, seedlings may need to escape a "browsing trap" (held in a height class making them more vulnerable to browsers) [57] induced by small- and medium-size herbivores [9,10,58], before being able to grow into the sapling phase. Our results support this as we found increased survival of individual trees and stems where both nyala and elephant were excluded, suggesting that browsing pressure may have been a limiting factor for Sand Forest recruitment in the past. This is strengthened by the relatively higher stem density in the full exclosure (−E−N). Trees within the seedling height which were browsed just prior the initiation of the experiment may have coppiced by 2007 after browsing release. This indicates a continued browsing pressure in the other treatments, and an inhibition of recruitment due to browsing. In addition, seedling densities had increased within the open access treatment (+E+N) and the full exclosure (−E−N) between the sampling years, but not in the partial exclosure (−E+N). This could be due to spatial heterogeneity in seed rain between treatments, but is more likely to be caused by increased browsing by nyala in absence of elephant [59] suppressing recruitment in the partial exclosure (−E+N). This effect of nyala is supported by the higher seedling densities found in the full exclosure (−E−N) from which they are excluded, than in the open access treatment (+E+N) where they are present with elephant.

While our research was conducted in one single Sand Forest patch, and we should thus be cautious with the interpretation of our results, we do believe that the mechanisms described here are applicable to other Sand Forest patches and other forest systems. Woodland populations are believed to benefit from a release from browsing pressure by megaherbivores [23,36,60]. Our findings (cf. [10,40]) argue this viewpoint as we show that also the effects of mesoherbivores in combination with megaherbivores on forests dynamics cannot be ignored. This illustrates that while attention is often focussed on the individual herbivore species, the importance of browsing effects by multiple species on vegetation has often been neglected. Therefore effects of both mega- and mesoherbivores need to be taken into account when conserving woodlands

and forests. This is especially important in the context of the 'elephant problem' [39], where conservation managers are concerned with the impacts of increasing elephant population densities on the environment, which may lead to the loss of tall trees and possibly to the conversion of woodland to grassland [36,61]. While elephants can alter the vertical structure of vegetation from top down by impacting on tall trees, we show that both mega-and mesoherbivores in combination and nyala on their own, also have a strong top down effect on seedlings in forests (cf. [40] as a comparison to riparian woodlands for impala only), thereby preventing recruitment into taller height classes.

While two years of exclusion from browsers is a short time scale to observe changes in overall tree population structures (e.g. of individual species or in the larger height classes), this experiment shows that by manipulating disturbance factors (e.g. herbivory), changes in recruitment can be demonstrated within a short time interval (cf. [7]; 3 years). The exclosures as presented in this study are being maintained for long-term monitoring to better understand the effects of herbivores on woody vegetation. Our results suggest that the traditional notion that recruitment of Sand Forest is uncommon [31,54] might be a misconception. We show that recruitment is taking place, at least into the seedling phase, but that further recruitment into taller height classes is prevented by strong browsing pressure. Certainly, the importance of browsing, and especially of multiple browsers, needs to be carefully considered in management planning for conservation areas.

We emphasise here the need to consider all possible factors influencing tree communities, and not only the "obvious" or "political" ones. In the case of Sand Forest, while fencing elephants from the Sand Forest will provide a reduction in damage to larger trees [16,62], it would be critical to also exclude mesoherbivores in order to promote seedling recruitment and thus long-term sustainability of the few remaining Sand Forest patches in Southern Africa.

Since tourism revenues are an important source of income for most parks, the creation of botanical reserves within the protected area can be a lucrative management strategy. This type of management approach could also be applicable to other natural systems.

Supporting Information

Table S1 Regression analyses for tree abundance vs. tree diameter.
(DOC)

Author Contributions

Conceived and designed the experiments: GL BP RS. Performed the experiments: GL. Analyzed the data: GL RM. Wrote the manuscript: GL RM BP RS.

References

1. de Garine-Wichatitsky M, Fritz H, Gordon IJ, Illius AW (2004) Bush selection along foraging pathways by sympatric impala and greater kudu. Oecologia 141: 66–75.

2. Fritz H, Duncan P, Gordon IJ, Illius AW (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. Oecologia 131: 620–625.

3. Owen-Smith RN (1988) Megaherbivores: the influence of very large body size on ecology. Cambridge: Cambridge University Press. 369 p.

4. Lagendijk DDG (2003) Mopane woodlands: a food source for elephants [MSc thesis]. Wageningen: Wageningen University. 57 p.

5. Kirby T, Shannon G, Page B, Slotow R (2008) The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. Acta Zoologica Sinica 54: 561–568.

6. Eckhardt HC, van Wilgen BW, Biggs HC (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. Afr J Ecol 38: 108–115.

7. Augustine DJ, McNaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. J Appl Ecol 41: 45–58.

8. Pickett STA, Cadenasso ML, Benning TL (2003) Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. In: du Toit JT, Rogers KH, Biggs HC, eds. The Kruger Experience: ecology and management of savanna heterogeneity. Washington: Island Press. pp 22–40.

9. Belsky AJ (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. Afr J Ecol 22: 271–279.

10. Prins HHT, van der Jeugd HP (1993) Herbivore Population Crashes and Woodland Structure in East Africa. J Ecol 81: 305–314.

11. Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple states in the Serengeti-Mara woodlands. J Anim Ecol 59: 1147–1164.

12. Ben-Shahar R (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. Plant Ecol 136: 189–194.

13. Hawthorne WD, Parren MPE (2000) How important are forest elephants to the survival of woody plant species in Upper Guinean forests. J Trop Ecol 16: 133–150.

14. Gadd ME (2002) The impact of elephants on the marula tree *Sclerocarya birrea*. Afr J Ecol 40: 328–336.

15. Jacobs OS, Biggs R (2002) The impact of the African elephant on marula trees in the Kruger National Park. S Afr J Wildl Res 32: 13–22.

16. Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R, et al. (2008) The utilization of large savanna trees by elephant in southern Kruger National Park. J Trop Ecol 24: 281–289.

17. Burke A (1997) The impact of large herbivores on floral composition and vegetation structure in the Naukluft Mountains, Namibia. Biodiv Conserv 6: 1203–1217.

18. Bergquist J, Örlander G, Nilsson U (1999) Deer browsing and slash removal affect field vegetation on south Swedish clearcuts. For Ecol Manage 115: 171–182.

19. Cadenasso ML, Pickett STA, Morin PJ (2002) Experimental test of the role of mammalian herbivores on old field succession; community structure and seedling survival. Journal of the Torrey Botanical Society 129: 228–237.

20. Merrill EH, Beyer HL, Jones GP, McDaniel GW (2003) Deciduous woodland conservation under heavy deer browsing on Devils Tower National Monument, USA. J Nat Conserv 10: 221–232.

21. Levick S, Rogers K (2008) Patch and species specific responses of savanna woody vegetation to browser exclusion. Biol Conserv 141: 489–498.

22. Shaw MT, Keesing F, Ostfeld RS (2002) Herbivory on Acacia seedlings in an East African savanna. Oikos 98: 385–392.

23. Goheen JR, Young TP, Keesing F, Palmer TM (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. J Ecol 95: 129–138.

24. Hagenah N (2006) Among rodents and rhinos: interplay between small mammas and large herbivores in a South African savanna [PhD]. Wageningen: Wageningen University. 146 p.

25. Riginos C, Young TP (2007) Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. Oecologia 153: 984–995.

26. Siebert F, Eckhardt HC (2008) The vegetation and floristics of the Nkhuhlu exclosures, Kruger National Park. Koedoe 50: 126–144.

27. Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland; Mucina L, Rutherford MC, eds. Pretoria: South African National Biodiversity Institute.

28. Kirkwood D, Midgley JJ (1999) The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. Bothalia 29: 293–304.

29. Matthews WS, Van Wijk AE, Van Rooyen N, Botha GA (2003) Vegetation of Tembe Elephant Park, Maputaland, South Africa. S Afr J Bot 67: 573–594.

30. Siebert SJ, Fish L, Uiras MM, Izidine SA (2004) Grass assemblages and diversity of conservation areas on the coastal plain south of Maputo Bay, Mozambique. Bothalia 34: 61–71.

31. Matthews WS (2005) Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest [PhD]. Pretoria: University of Pretoria. 254 p.

32. Kellerman MJS, Van Rooyen MW (2007) Seasonal variation in soil seed bank size and species composition of selected habitat types in Maputaland, South Africa. Bothalia 37: 249–258.

33. Moll EJ (1980) Terrestrial plant ecology. In: Bruton MN, Cooper KH, eds. Studies on the ecology of Maputaland: Rhodes University & The Natal Branch of the Wildlife Society of Southern Africa. pp 52–68.

34. Botes A, McGeoch MA, Van Rensburg BJ (2006) Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. Biol Conserv 130: 573–583.

35. Gaugris JY, Van Rooyen MW, Bothma JDP (2008) Growth rate of selected woody species in northern Maputaland, KwaZulu–Natal, South Africa. South African J Bot 74: 85–92.

36. Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D, et al. (2008) Effects of elephants on ecosystems and biodiversity. In: Scholes RJ, Mennell KG, eds. Elephant Management: A Scientific Assessment for South Africa. Johannesburg: Witwatersrand University Press. pp 146–205.

37. Shannon G, Matthews WS, Page BR, Parker GE, Smith RJ (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. Diversity and Distributions 15: 776–783.

38. Repton M (2007) Vegetation utilisation by elephants in the Mkuze and Phinda Game Reserves [MSc]. Durban: University of KwaZulu-Natal.

39. Owen-Smith N, Kerley GIH, Page B, Slotow R, Van Aarde RJ (2006) A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. S Afr J Sc 102: 389–394.

40. Moe SR, Rutina LP, Hytteborn H, Du Toit JT (2009) What controls woodland regeneration after elephants have killed the big trees? J Appl Ecol 46: 223–230.

41. Druce HC, Pretorius K, Druce D, Slotow R (2006) The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. Koedoe 49: 77–84.

42. Druce HC, Pretorius K, Slotow R (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. Biol Conserv 141: 3127–3138.

43. Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth: PRIMER-E. 167 p.

44. Lykke AM (1998) Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. Biodiv Conserv 7: 1261–1275.

45. Obiri JAF, Lawes MJ, Mukolwe M (2002) The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. For Ecol Manage 166: 131–148.

46. Walker BH, Stone L, Hederson L, Vernede M (1986) Size structure analysis of the dominant trees in a South African savanna. S Afr J Bot 52: 397–402.

47. Everard DA, Midgley JJ, Van Wyk GF (1995) Dynamics of some forests in Kwa Zulu-Natal, South Africa, based on ordinations and size-class distributions. S Afr J Bot 61: 283–292.

48. Van Wyk GF, Everard DA, Midgley JJ, Gordon IG (1996) Classification and dynamics of a southern African subtropical coastal lowland forest. S Afr J Bot 62: 133–142.

49. Condit R, Sukumar R, Hubbell SP, Foster RB (1998) Predicting population trends from size distributions: a direct test in a tropical tree community. Am Nat 152: 495–509.

50. Kyle R (2004) Resource use in the indigenous forests of Maputaland: are conservation strategies working? In: Lawes MJ, Eeley HAC, Shackleton CM, Geach BGS, eds. Indigenous Forests and Woodlands in South Africa: Policy, People and Practice. Scottsville: University of KwaZulu-Natal Press. pp 713–736.

51. Lawes MJ, Obiri JAF, Eeley HAC (2004) The uses and value of indigenous forest resources in South Africa. In: Lawes MJ, Eeley HAC, Shackleton CM, Geach BGS, eds. Indigenous Forests and Woodlands in South Africa: Policy, People and Practice. Scottsville: University of KwaZulu-Natal Press. pp 227–234.

52. Gaugris JY, Van Rooyen MW (2007) The structure and harvesting potential of the sand forest in Tshanini Game Reserve, South Africa. South African Journal of Botany 73: 611–622.

53. Midgley JJ, Everard DA, Van Wyk G (1995) Relative lack of regeneration of shade-intolerant canopy species in some South African forests. S Afr J Science 91: 7–8.

54. Turner IM (1990) Tree seedling growth and survival in a Malaysian rain forest. Biotropica 22: 146–154.

55. Fenner M, Thompson K (2005) The ecology of seeds. Cambridge: Cambridge University Press. 250 p.

56. Bond WJ, Archibald S (2003) Confronting complexity: fire policy choices in South African savanna parks. International Journal of Wildland Fire 12: 381–389.

57. Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. Ecology 85: 1555–1561.

58. Smallie JJ, O'Connor TG (2000) Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. Afr J Ecol 38: 352–359.

59. Lagendijk G, Page BR, Slotow R (2011) Short-term effects of single species browsing release by different-size herbivores on Sand Forest vegetation community. South Africa Biotropica, In press.

60. Biggs HC, Slotow R, Scholes RJ, Carruthers J, Van Aarde RJ, et al. (2008) Towards integrated decision making for elephant management. In: Scholes RJ, Mennell KG, eds. Elephant Management: A Scientific Assessment for South Africa. Johannesburg: Witwatersrand University Press. pp 537–586.

61. Caughley G (1976) The elephant problem - an alternative hypothesis. E Afr Wildl J 14: 265–283.

62. Grant CC, Bengis R, Balfour D, Peel M, Davies-Mostert HT, et al. (2008) Controlling the distribution of elephants. In: Scholes RJ, Mennell KG, eds. Elephant Management: A Scientific Assessment for South Africa. Johannesburg: Witwatersrand University Press. pp 329–369.