DOES HARVESTING UNDERSTOREY TREES AFFECT THE MAINTENANCE OF TREE DIVERSITY?

S. Boudreau and M.J. Lawes
Forest Biodiversity Research Unit, School of Biological and Conservation Sciences
University of KwaZulu-Natal, Pietermaritzburg

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Abstract

Understorey gaps are common in subtropical forests where pole-size trees are harvested for building materials. The creation of artificial understorey gaps potentially affects tree regeneration and the maintenance of forest tree diversity by locally increasing resource availability (light, nutrients, moisture). Understorey tree gaps had significantly lower foliage density in the 3-10 m stratum and higher soil moisture. However, fine root biomass and nutrient availability (N, P, K, C_{org}) were not different to controls under intact understorey. Light intensity at the forest floor was a function of the age of the understorey gap, being greater in recent gaps but did not differ between older gaps and controls. The early regeneration community in gaps differed in composition from intact understorey. Understorey gaps promoted the regeneration of understorey species (density and species richness) probably by increasing community-wide seedling establishment of understorey species. However, understorey gaps had no effect on the early regeneration of canopy species. We argue that under low harvesting intensity (11.6 % of the available pole-size stems) understorey gaps have a neutral role in the long-term maintenance of understorey species diversity and no apparent role in the long-term maintenance of canopy tree species diversity. Our findings suggest that low levels of subsistence harvesting of understorey species will not detrimentally affect the overall species composition of scarp forest.

1. Introduction

Although canopy gaps are important for the maintenance of forest tree diversity (Connell, 1978; 1989) the ecological processes by which this occurs are still unclear. Gap dynamics theory suggests that differences in shade tolerance abilities influence the spatial and temporal patterns of tree species recruitment (Brokaw, 1985; Connell, 1978; Sheil & Burslem, 2003; Whitmore, 1989). Typically, pioneer shade-intolerant and light-demanding species recruit into large gaps while shade-tolerant species establish under the forest canopy or in smaller gaps (Brown & Jennings, 1998; Denslow, 1987; Whitmore, 1989) and this can result in a highly predictable succession of gap-filling species (Brokaw, 1985; Connell, 1978). However, recent studies suggest that canopy gaps play a neutral role in maintaining species richness, promoting whatever diversity and mix of tree species are locally present in a given forest for reasons other than the local disturbance regime, such as recruitment limitation (Brokaw & Busing, 2000; Hubbell *et al*. 1999; Obiri & Lawes 2004; Schnitzer & Carson, 2001; Webb & Peart, 2000; Wright, 2002).

By definition, gaps in the horizontal structure of forest create local sites where additional resources, both above- and below-ground, become available due to the absence of a tree or part of a tree. In most forest types, canopy gaps are relatively rare, occupying <10% of the forest area (Connell *et al.,* 1997; Hart & Hart, 1989; Midgley *et al*., 1995; Obiri & Lawes, 2004; Parker, 1995; Uhl & Murphy, 1981). In contrast, understorey gaps, defined as an opening in the understorey and/or subcanopy stratum beneath an intact canopy are relatively common, occupying ca. 50% of a forest's area (Connell *et al*., 1997).

There is growing evidence that the selection (species establishment) that takes place beneath a closed canopy has an important influence on the pool of species available to take advantage of the short burst of resources in newly-created gaps (Connell, 1989). From the perspective of understorey dynamics, the canopy gap versus non-gap paradigm overlooks the continuum of light levels beneath the closed canopy in tropical forests (Clark *et al.,* 1996; Lieberman *et al*., 1989; Montgomery & Chazdon, 2001; Nicotra *et al*.,1999). In addition, increases in the availability of water and nutrients associated with a decrease in root competition in all types of gaps may also have an important effect on recruitment (Connell, 1971; Fox, 1973). Subtle changes in magnitude and spatial distribution of light, water and nutrients beneath closed canopies may influence seedling establishment and long-term survivorship of new recruits of tree species (Caldwell & Pearcy, 1994; Chazdon, 1988; Denslow 1987; Montgomery & Chazdon, 2002). Thus, gaps in the understorey, unlike many canopy gaps, may provide suitable conditions for, and promote the establishment of, shade-tolerant species, thereby contributing to the maintenance of forest tree diversity (Connell *et al.,* 1997).

Understorey gaps are very common in most of the small indigenous forest patches in Africa where pole-size trees are harvested for building material. Harvesting intensity varies between forest patches but on average is approximately 10% of the available stems (Burgess *et al*., 2000; Luoga *et al.*, 2002; Obiri *et al.*, 2002). These artificial understorey gaps are in addition to natural understorey gaps and thus have the potential to further influence tree regeneration and diversity. Here we investigate this proposition in the Ongoye Forest Reserve, South Africa. Our specific objectives are to examine (1) changes in resource availability (light, nutrients, water) associated with the creation of understorey gaps by subsistence harvesters, and (2) the potential effect of these small gaps on tree stem density, tree species richness and species assemblage in a subtropical forest.

2. Methods

Understorey gaps were sampled in the Ongoye Forest Reserve (OFR; 28° 50'S, 31° 42'E; 3900 ha). The reserve is located on the Ongoye range of hills (altitude: 305 m - 490 m), 12 km inland from the coast. A species-rich coastal scarp forest (2611 ha) is set in a mosaic of coastal grassland and rocky granitic outcrops (1277 ha, Figure. 1). Scarp forest physiognomy is characterized by a poorly developed herb layer, a well-developed seedling and sapling stratum, an open understorey and a medium to high canopy (von Maltitz *et al*., 2003). The mean number of understorey and canopy trees per ha is 718 and 246 respectively, and the mean canopy tree species richness per 0.0625 ha plot is 9 (Krüger & Lawes, 1997). Currently, the forest is subject to low levels of subsistence harvesting by local communities, with 11.6% of the available pole-size stems being harvested (102 harvested stems ha^{-1}, 8 cm < DBH < 15 cm; Boudreau *et al.,* 2005).

The influence of subsistence harvesting on the regeneration of woody species was investigated using a matched-pairs sampling design in which seedling and sapling density and species richness was compared between artificial understorey gaps, created by the removal by harvesters of one pole-size *Englerophytum natalense* tree (*n* = 26; the most commonly used species at OFR), and the intact understorey nearby. To control for edaphic, slope and/or drainage differences, the distance between the paired understorey gap and intact understorey control plot at a site did not exceed 25 m, but was far enough apart to ensure that the control plot was not affected by the understorey gap. Sample sites were located >100 m apart to ensure sample independence. Based on the condition of the stumps we sampled only old understorey tree gaps that were created >3 years prior to our study.

Seedlings and saplings were measured in 25 m^2 circular plots (radius of 2.82 m) centred on the bole (8cm < DBH < 10cm) of the stump of an understorey *E. natalense* tree in the gap and a live stem in the control plot. In each plot, all seedlings and saplings taller than 10 cm were identified and their height and diameter were measured. Foliage height density in the immediate area of the plots (cylinder of 10 m diameter) was evaluated in seven height strata (0-0.5 m, 0.5-1 m, 1-3 m, 3-5 m, 5-10 m, 10-15 m, 15-20 m; Krüger and Lawes, 1997) and was ranked on the Walker scale of 0-7 (Walker, 1976).

Harvesting of pole-size trees is believed to lead to a decrease in root competition, a subsequent increase of soil nutrient availability and an increase in the light intensity reaching the forest floor. To quantify nutrient availability, soil samples were systematically collected inside each plot (12 subsamples per plot) from two depths (0-10 cm; 10-20 cm) using a beta-auger with a diameter of 25 mm (in 21 of the 26 matched-pairs plots used to describe the seedling and sapling stratum). Following standard soil sampling methods all the subsamples from the same depth interval in a plot were combined (Carter, 1993). The composite sample was air-dried, sieved (2 mm) and analysed for total nitrogen (ammonium, standard Kjeldahl method), phosphorus (Hunter method), potassium (Hunter's extract) and organic carbon.

Light and water availability and fine-root biomass in understorey gaps and intact understorey was compared using a separate set of matched-pairs understorey gaps and control plots. Separate plots were used because of the destructive nature of the fine-root biomass sampling, the need to examine the latter in newly created plots (see below), and so that we could resample the original plots later on. In separate plots, photosynthetically active radiation (PAR) reaching the forest floor was measured from sunrise to sunset in five newly created gaps (two months old) and in six older gaps (>3 years old) and their respective control plots. We used Apogee Light Bar Sensors (six quantum sensors per bar) which average PAR over 50 cm. Sensors were connected to a Campbell Scientific data-logger (CR200). Incoming direct PAR radiation was recorded simultaneously in adjacent open grassland and percent PAR reaching the forest floor is given relative to this standard.

We examined soil moisture and fine-root biomass in 25 separate matched-pairs plots (see above). Only understorey gaps created less than two months prior to the study were sampled to minimise the contribution of regenerative stems to the fine-root biomass. Four soil cores, 70 mm in diameter and 150 mm deep were collected from each new understorey gap and control plot. Samples were placed in hermetic plastic bags to prevent water loss. The composite samples were weighed, dried at 70°C for 96 hours and weighed again to evaluate soil moisture. Samples were then sieved using 2 mm mesh filters and the roots hand-picked from the remaining organic debris. The roots were then cleaned and weighed.

Regenerative individuals were classified into two height-classes (10-100 cm, 100-400 cm). Woody species were classified as canopy, understorey and vine species. Based on their light requirements, canopy species were subdivided into shade-intolerant (pioneer) and shade-tolerant species (Table 1). To avoid Type I errors induced by testing the same null hypothesis many times, we simultaneously tested for differences in the independent habitat variables (stem density and species richness before and after rarefaction analysis, foliage height density, fine root biomass and soil moisture, soil nutrients, light intensity) between the understorey gaps and the control plots using MANOVA (SPSS 1999). To preserve the matched-pairs design of the experiment the data were blocked by sample pair. The Wilks lambda test statistic (likelihood ratio criterion) varies between 0 and 1 and tests the overall significance of the effects of the treatments on the dependant variables. Should this test be significant, the univariate F-tests are then consulted to ascertain which of the factors causes the overall significant effects. Rarefaction analyses were performed in BioDiversity Professional (McAleece *et al.,* 1997) and used to verify if the differences in species richness between understorey gaps and control plots were due to differences in stem density (Chazdon *et al.,* 1999). Rarefaction uses probability theory to estimate species richness for a sample of a given size (Magurran, 2003). Sample plots (a given understorey gap and its adjacent control plot) were rarefied down to a common seedling abundance level. The rarefied species richness was included as a variable in the MANOVA.

Differences in community composition of the early regeneration between gaps and intact understorey were tested using a Blocked Multi-response Permutation Procedures (MRBP) test, a nonparametric permutation procedure for testing the hypothesis of no difference between pre-defined groups (Biondini *et al.*, 1988; McCune *et al.,* 2002). Similarly, the predictability of the species composition in gaps relative to the composition in control plots, and whether there was a distinct regeneration niche-guild in understorey gaps, were tested with Multi-response Permutation Procedures (MRPP). Both analyses were conducted using PC-Ord for Windows version 4 (McCune & Mefford,1999). The test statistic, *T*, describes the separation between groups. The more negative *T* is, the stronger the separation. The effect size is provided by the chance-corrected within-group agreement (*A*). *A* describes within-group homogeneity, compared to the random expectation. $A = 1$ when all items are identical within groups (delta = 0); $A = 0$ when heterogeneity within groups equals expectation by chance; $A < 0$ with more heterogeneity within groups than expected by chance. *P* = probability of smaller or equal delta.

In addition, we tested for species priority effects (SPE) in understorey gap colonisation. If SPE were important, we predicted that locally present species (i.e. those in the control plots) would have a higher probability of colonising a gap than species not locally present. Under SPE the average Euclidian distance between the species composition of an understorey gap and its associated control plot should be smaller than the distance between the control plots of different sites. We tested for SPE using Resampling Statistics for Excel (Blank *et al*., 2001) as one can test specific hypotheses that cannot be tested using MRPP in PC-Ord. We used euclidian distances calculated in Multi-Variate Statistical Package (MVSP, Kovach, 1999) as our distance measure in the resampling routines.

3. Results

3.1 Foliage height density and fine root biomass

The harvesting of a single pole-size tree creates a gap in the understorey so that foliage density in the 3-5 m and 5-10 m strata was significantly less in old (> 3 yr) understorey gaps than in control plots (Table 2). In contrast, foliage height density below 3 m was greater in understorey gaps because of higher stem densities than beneath intact understorey (see below). Foliage height density in the canopy stratum (> 10 m) did not differ between gap and control. Fine-root biomass was slightly, but not significantly less in understorey gaps (Table 3) and there was no apparent below-ground gap associated with the removal of understorey trees.

3.2 Understorey gaps and resource availability

The moisture content (w/w) of superficial soils (0-15 cm) in understorey gaps was significantly higher than in adjacent control sites (Table 3) even though fine root biomass was slightly lower in gaps. Major nutrient concentrations (N, P and K) and the percent organic carbon did not differ between understorey gaps and control plots (Table 4). However, nutrient concentrations were consistently higher overall in the superficial soil layer (0-10 cm) than in deeper soils (10-20 cm). The low levels of soil nitrogen (< 1 mg.kg^{-1}) are comparable to those found in tropical forests (Powers *et al*., 2005).

With less foliage in understorey gaps and the associated subcanopy, we expected more light to penetrate gaps. PAR reaching the forest floor under intact understorey strata was very low with daily values averaging less than 5 µmol m^{-2} s^{-1} and 99% of PAR was intercepted by forest foliage. In understorey gaps, the percent incoming PAR reaching the forest floor was a function of gap age, being significantly higher in newly created gaps (ca. 5%) but no different to control plots in older gaps (ca. 1%; age*treatment, $F_{1,18}$ = 21.279, P < 0.001). This may be due to the higher density of newly established regenerative stems in older gaps (Table 5).

3.3 Do understorey gaps contribute to the maintenance of tree species diversity?

Stem density of seedlings and saplings (height classes: 10-100 cm, 100-400 cm) of understorey species was significantly higher in understorey gaps than in control plots (Table 6). Although not significant, the mean stem density of young individuals of canopy species (10-100 cm) was nearly twice as high in understorey gaps than in the control plots. However, the stem density of canopy species in the 100-400 cm size range, did not differ significantly between gap and control plots. Vines or climber species were less abundant in gaps than in control plots.

Overall, the species composition of the tree seedling and sapling community differed significantly between gaps and intact understorey (Table 7). At the site scale, the species richness of understorey species (both height classes) was higher in gaps than under intact understorey, while there was no significant difference for canopy species (Table 6). The species richness of gaps was linked to greater stem density in understorey gaps (rarefied species richness; $F_{1,51}$ = 0.674, P = 0.419).

Species composition in gaps was much more variable than in adjacent control plots and more variable than among control plots from different sites (MRPP analysis, P < 0.001), indicating little gap-to-gap predictability of species composition or no gap regeneration guild (Table 7). In fact, more species were recorded in understorey gaps (73) than in the control plots (62). Species priority effects were not evident in the colonisation of understorey gaps as the average Euclidian distance between the species composition of an understorey gap and its associated control plot was significantly larger than the distance between the control plots of different sites (the opposite of what we would expect if species priority effects were important).

4. Discussion

The notion that understorey gaps are important for the maintenance of tree diversity arises from the relative rarity of canopy gaps compared to natural understorey and/or subcanopy gaps (Connell *et al.,* 1997; Hart & Hart, 1989; Midgley *et al*., 1995; Obiri & Lawes, 2004; Parker, 1995; Uhl & Murphy, 1981). Most seedlings, saplings and small understorey adults, which determine the future species composition of a forest, spend most of their lives in subcanopy or understorey gaps beneath a closed canopy (Connell *et al*., 1997). Thus, alteration of the natural spatio-temporal frequency of understorey gaps, for instance by subsistence harvesting of pole-size trees (Burgess *et al*., 2000; Cawe & McKenzie, 1989; Luoga *et al*., 2002; Muir, 1990; Obiri *et al*., 2002), has the potential to affect the regeneration dynamics and composition of woody species in a forest.

The creation of understorey gaps at OFR significantly increases the light intensity reaching the forest floor, which in turn increases seedling establishment in the months following gap creation. Increased light availability has been shown to positively affect seedling growth and survival under an intact canopy (Kobe, 1999; Montgomery & Chazdon, 2002). However, our results suggest that in the first year or two after gap creation, the beneficial effects to new recruits of leaf removal in the 3-10 m stratum was counterbalanced by an increase in regeneration density in the lower stratum, resulting in similar light intensity at the forest floor in both older gaps (i.e., beneath dense early regeneration) and under an intact understorey. A similar phenomenon has been described in large canopy gaps where the growth of existing and newly established shrubs, lianas and herbs rapidly reduced light availability at the forest floor (Denslow *et al.,* 1998). Nonetheless, lower foliage density in the 3-10 m stratum in old understorey gaps in this study implies that light availability was still higher at the sapling level than in control plots. The combination of an initial increase in density of seedlings and higher light availability in strata above the seedling stratum as the gap ages, may explain high sapling density (100-400 cm) in understorey gaps in this study. Furthermore, rarefaction analysis showed that the greater species richness in understorey gaps than beneath the intact understorey was a function of this higher stem density in understorey gaps. Thus, it appears that conditions inside understorey gaps (greater light availability and moisture) promote the establishment and maintenance of many tree species, particularly from the pool of understorey species.

In contrast, understorey gaps did not significantly alter the likelihood of canopy tree species establishment and survival (pioneer as well as shade-tolerant species). As expected, the almost complete absence of pioneer (light-demanding) species in our plots (Table 1) corroborates the results of many studies, that light demanding species regenerate only in canopy gaps where light intensity is high (Brokaw, 1987; Dalling *et al.,* 1998; Lawton & Putz, 1988; Popma *et al*., 1988; Schnitzer & Carson, 2001). Pioneer species accounted for <1.5% of the regenerative stems of canopy species.

We expected to encounter more shade-tolerant canopy species in understorey gaps (Brown & Jennings, 1998; Denslow, 1980, 1987; Whitmore, 1989). However, we recorded only seven shade-tolerant canopy species in our plots. Of these, three species accounted for 97% of the regenerative stems of canopy species. Although slight increases in light availability are known to increase the growth of canopy species under a closed canopy (Kobe, 1999; Montgomery & Chazdon, 2002), shade-tolerant canopy species did not appear to be sensitive to such increases (from ca. 1% to ca. 4%) in our study. Overall, no difference in stem density and species richness of saplings (100-400 cm) of canopy species between understorey gaps and intact understorey lead us to conclude that, even though canopy species seedlings establish beneath a closed canopy, their survival and growth is poor in the first years following their establishment. Considering the high diversity of the canopy stratum at Ongoye (> 50 species can reach the canopy), the above suggests that: (1) recruitment of most shade-tolerant canopy species is low under an intact canopy and understorey, but (2) the survival of canopy species in the advanced regeneration (> 400 cm) is high, and (3) the turnover of canopy individuals is low relative to the temporal scale of natural disturbances in the understorey.

4.1 Conservation implications

Although we did not identify an understorey gap-filling guild (species composition in gaps was much more variable than under intact understorey), the diversity of understorey species was greater in understorey gaps than in controls. These data suggest that understorey gaps have the potential to contribute significantly to the maintenance of tree diversity in the understorey stratum, by increasing community-wide seedling establishment. However, low gap-to-gap predictability of tree species composition and the absence of a species priority effect indicate that understorey gaps promote whatever diversity and mix of understorey tree species that happens to be locally present (i.e., play a neutral role in maintaining species richness; *sensu* Hubbell *et al*., 1999). On the other hand, understorey gaps have no effect on canopy species diversity. Therefore, current low levels of subsistence harvesting of understorey species (Boudreau *et al*. in press) are unlikely to alter species composition of this scarp forest, especially as understorey gaps favour the species that are commonly harvested (understorey species) and that occur at high density. However, because our conclusions are based on a static pattern from a relatively small spatial scale, they should not be used to affirm that pole-size tree harvesting has no impact on forest dynamics. We examined the effect of the removal of only a single pole-size tree (small understorey gaps) on the regeneration of woody species. The effect of larger harvesting gaps on the regeneration of woody species should be investigated. In addition, harvesting pole-sized stems from canopy species would result in very different patterns and possibly arrest succession in these forests and cause dominance by understorey species. Therefore, it is important to manage the selective harvesting of woody stems at OFR to prevent significantly altering forest dynamics and species composition.

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Addendum

Table 1. The abundance and shade tolerance of canopy species recorded in the plots (understorey gaps and control)

Species	**10-100 cm**	**100-400 cm**
Shade-intolerant (pioneer)		
Albizia adianthifolia	26	0
Macaranga capensis	2	0
Shade-tolerant		
Chrysophyllum viridifolium	17	6
Drypetes gerrardii	165	38
Garcinia gerrardii	81	31
Milletia sutherlandii	1571	32
Podocarpus latifolius	1	1
Trichilia emetica	0	3
Zanthoxylum davyi	1	0

Table 2. Differences in percent foliage height density between understorey gaps and control plots (*n* = 17; MANOVA: Wilks' lambda = 0.276, $F_{7,10}$= 3.74, *P* = 0.03)

Foliage height	**Understorey gap (%) Mean ± *SE***	**Control (%) Mean ± *SE***	***F*-value *d.f.* = 1,16**	***P*-value**
0-0.5 m	15.5 ± 1.7	6.5 ± 1.0	17.2	0.001
>0.5-1.0 m	16.7 ± 2.6	8.4 ± 1.5	6.4	0.022
>1.0-3.0 m	24.8 ± 1.9	17.3 ± 2.2	6.9	0.018
>3.0-5.0 m	24.6 ± 4.5	46.7 ± 5.4	9.1	0.008
>5.0-10.0 m	54.7 ± 6.9	76.3 ± 4.5	12.3	0.003
>10.0-15.0 m	43.4 ± 6.9	51.4 ± 6.3	1.3	0.265
>15.0-20.0 m	34.9 ± 5.1	32.4 ± 5.2	0.1	0.710

Table 3. **Differences in fine root biomass and soil moisture between newly created understorey gaps and control plots (n = 25; MANOVA: Wilks' lambda = 0.725, $F_{2,23}$= 3.74, P = 0.025)**

Variable	Understorey gap Mean ± *SE*	Control Mean ± *SE*	*F*-value *d.f.* = 1,24	*P*-value
Fine root biomass (g)	18.3 ± 1.4	21.6 ± 1.3	3.0	0.095
Soil moisture (%)	19.8 ± 0.6	18.4 ± 0.5	6.4	0.043

Table 4. **Summary statistics for nitrogen, phosphorous, potassium and organic carbon. No parameter differed significantly between understorey gap and control plots (n = 21; MANOVA: Wilks' lambda = 0.885, $F_{3,3}$= 1.86, P = 0.130)**

Depth	Variable	Understorey gap Mean ± *SE*	Control Mean ± *SE*
0-10 cm	N (mg/kg)	0.17 ± 0.02	0.19 ± 0.01
	P (mg/kg)	12.7 ± 2.4	14.8 ± 2.0
	K (mg/kg)	112.2 ± 6.2	121.1 ± 7.0
	Organic C (%)	6.5 ± 0.5	7.2 ± 0.6
10-20 cm	N (mg/kg)	0.11 ± 0.01	0.12 ± 0.01
	P (mg/kg)	8.4 ± 1.5	8.9 ± 1.3
	K (mg/kg)	93.4 ± 5.5	105.1 ± 11.6
	Organic C (%)	4.2 ± 0.3	4.7 ± 0.3

Table 5. **Percentage of the PAR daily photon flux reaching the forest floor in understorey gaps and under intact understorey (control)**

Gap age	Understorey gap (% of incoming PAR) Mean ± *SE*	Control (% of incoming PAR) Mean ± *SE*
Young	4.6 ± 0.7	1.1 ± 0.2
Old	0.8 ± 0.2	0.5 ± 0.1

Table 6. Differences in the numbers of regenerative stems and their species richness between understorey gaps and control plots (*n* = 26; MANOVA: Wilks' lambda = 0.234, $F_{10,16} = 5.235$, *P* = 0.002)

Variable	Understorey gap Mean ± *SE*	Control Mean ± *SE*	*F*-value *d.f.* = 1, 25	*P*-value
Stem density				
Understorey 10-100 cm	103.7± 11.7	47.2 ± 6.7	29.8	< 0.001
Understorey 100-400 cm	14.0 ± 1.5	6.9 ± 0.8	29.0	< 0.001
Canopy 10-100 cm	45.2 ± 11.1	26.5 ± 5.7	3.1	n.s.
Canopy 100-400 cm	2.5 ± 0.5	1.8 ± 0.6	0.9	n.s.
Vine	15.0 ± 2.6	10.2 ± 1.2	4.1	n.s.
Species richness				
Understorey 10-100 cm	10.6 ± 0.6	8.0 ± 0.5	26.9	< 0.001
Understorey 100-400 cm	5.5 ± 0.5	3.5 ± 0.3	21.3	< 0.001
Canopy 10-100 cm	2.9 ± 0.2	2.3 ± 0.2	4.1	n.s.
Canopy 100-400 cm	1.2 ± 0.2	0.9 ± 0.2	1.6	n.s.
Rarefied species richness	12.0 ± 0.8	11.5 ± 0.7	0.7	n.s.

Table 7. Summary statistics for MRBP and MRPP analyses

Hypothesis	*T*	*P* - value	*A*
Do understorey gaps and control plots differ in species composition?	-6.66	< 0.001	0.08
Is species composition more predictable in understorey gaps than in control?	-5.38	0.001	0.04
Is species priority effect important for the colonisation of understorey gaps?	-*	< 0.001**	-*

* Resampling statistics in excel does not provide T and A values

** The average Euclidian distance between the species composition of an understorey gap and its associated control plot was significantly larger than the distance between the control plots of different sites, the opposite of what we would expect if species priority effects were important.

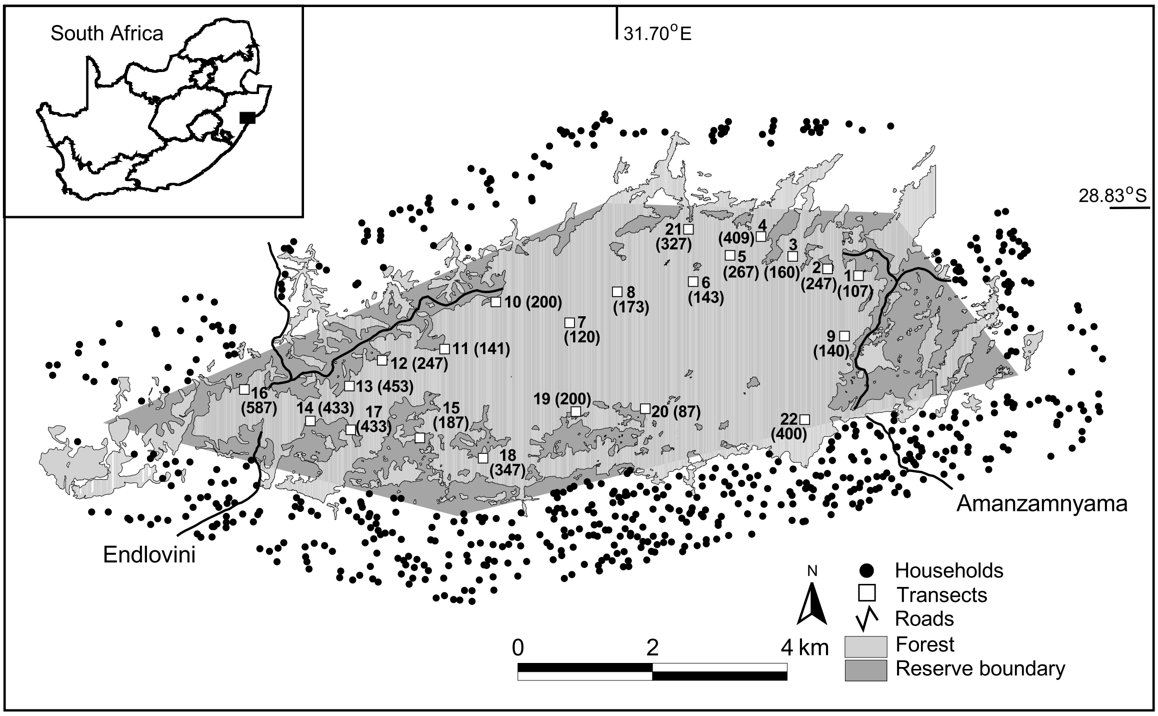

Figure 1. Location of the Ongoye Forest reserve, KwaZulu-Natal, South Africa.