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Forest product harvesting in the Eastern Cape, South Africa: Impacts on habitat structure

The Eastern Cape Province harbours 46% of South Africa's remaining indigenous forest cover, and is one of the country's poorest and least developed provinces. Forest resources thus represent a vital component of rural livelihoods in this region. Consequently, forest management policies aim to balance the needs of resource users with the ecological integrity of forest ecosystems. In a recent study, forest bird ranges were shown to have declined in the Eastern Cape over the past 20 years, despite increases in forest cover over the same time period, indicating that habitat degradation may be driving forest bird losses. Given that harvesting of forest products represents the primary human disturbance in forests in the Eastern Cape today, insight is needed regarding the link between resource use and habitat modification. We report on effects of harvesting of three key forest products – poles, timber and medicinal bark – on habitat structure at the ground, understorey and canopy layers in indigenous forests in the province. Harvest activities had considerable impacts on habitat structure, depending on the nature and extent of harvesting. Bark and timber harvesting resulted in canopy gaps, whereas pole harvesting reduced tree density, resulting in understorey gaps. Overall, harvest activities increased the frequency of canopy disturbance, and density of understorey layer foliage. Unsustainable bark harvesting practices increased the mortality rate of canopy trees, thereby increasing dead wood availability. By providing insight into human-mediated habitat modification in forests of the Eastern Cape, this study contributes to the development of ecologically informed sustainable resource management policies.

Significance:

- Unregulated harvesting of forest products in state-managed indigenous forests of the Eastern Cape results in habitat modification.
- The nature and extent of habitat modification is dependent on the type and intensity of resource use, indicating that resource use may be sustainably managed.
- Timber and medicinal bark harvesting activities result in canopy disturbances, thereby altering natural canopy gap dynamics, with concomitant impacts on understorey habitat structure.
- Changes in forest habitat structure associated with high levels of resource use are likely to have ramifying effects on forest biodiversity.

Introduction

Habitat loss and modification are currently the primary drivers of forest biodiversity loss globally.¹ Unlike many parts of Africa, forest cover in the Eastern Cape, which harbours close to half (46%) of South Africa's remaining indigenous forest cover, has increased over the past 20 years² – an increase which is attributed to the revegetation of previously cultivated fields in response to increasing trends of de-agrarianisation in rural areas³, together with carbon fertilisation⁴. Thus, while habitat loss appears not to be a major threat to forest biodiversity, degradation has been identified as a major concern.⁵⁻⁹ While much forest degradation in South Africa is attributed to extensive historical logging¹⁰, commercial-scale logging has not occurred in indigenous forests in the Eastern Cape for the past 80 years, after being outlawed in 1939 in all but one forest complex, where limited commercial harvesting was re-introduced in 1975⁹. Consequently, informal harvesting of forest products now comprises the primary anthropogenic disturbance in forest habitats in the region⁵⁻⁹ and is largely related to poor socio-economic conditions in the province¹¹. Thus, although forests comprise a mere 2.2% of provincial land cover¹², their socio-economic value is significant, with thousands of rural households dependent on forest resources for subsistence and commercial use¹³. While forest policies in South Africa aim to develop forests for sustainable use, several studies have reported unsustainable harvest rates occurring across the region^{7,8,12,14}, largely attributed to a decline in the capacity of institutional and traditional structures to regulate resource use^{15,16}. A *de facto* open-access system thus governs forest resource use in South Africa today, leading to increasing concern that unregulated resource use is degrading forest habitats and compromising the conservation of forest biodiversity.

Long-term harvesting of forest products has significant effects on temperate forest habitats, driving changes in habitat structure and tree species composition, even when occurring at relatively low levels.^{8,17} Moreover, the ecological impact of resource use depends on the plant part harvested and intensity of use.¹⁸ Thus, while grazing of livestock in forests may affect soil quality¹⁹ and increase exotic cover²⁰, timber harvesting affects canopy closure, mean tree size and understorey density^{21,22}. The extent to which a resource has been commercialised is also of consequence, as resources used to generate income, particularly in the context of *de facto* open-access systems, are often harvested more intensely, and frequently unsustainably, and thereby have more profound ecological impacts.^{12,14,23}

Human activities that modify habitat structure, in turn, may influence faunal community assemblage in forests. For example, habitat features at the local scale relate to the occurrence of specific functional traits and community

structure in avifaunal populations.²⁴ Consequently, studies have shown forest faunal populations, including amphibians, bats, birds and reptiles, to be sensitive to human-mediated changes in habitat structure, with species specialised in their foraging or microhabitat requirement being particularly sensitive.²⁵⁻³⁰ Given the critical ecosystem functions provided by forest fauna – including seed dispersal, pest control and pollination³¹ – human activities that modify habitat structure may have ramifying effects on forest ecosystem functioning.

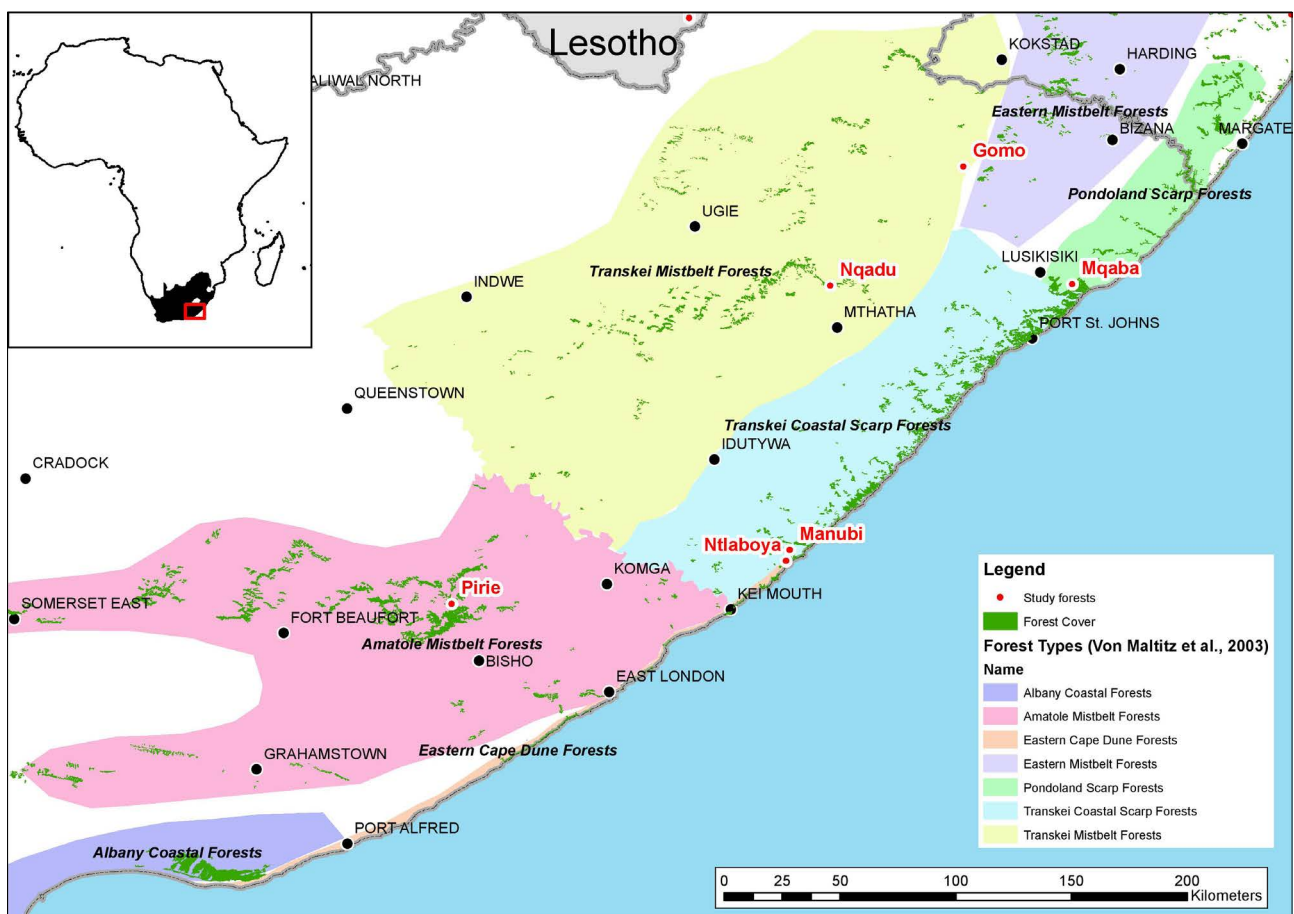
In a recent study, half of South Africa’s forest-dependent bird species were shown to have experienced range declines in the past 20 years, with declines most notable in the Eastern Cape, despite forest cover increases in this region over the same time period.² This finding suggests that habitat-scale disturbances rather than landscape-scale habitat loss may be driving bird declines in the region. We thus aimed to assess the effects of harvest activities on habitat structure (defined as the composition and arrangement of physical matter at a location³²) at the forest scale. Specifically, we examined how different harvest activities modify habitat structure at the canopy, understorey and ground level in six forests, representative of five national forest types, across the Eastern Cape region. Resource use focused on extraction of live biomass from forests, namely understorey trees for poles, canopy trees for timber and crafts, and bark for medicinal purposes, as these represent key resource use types in the region.⁸

Methods

Study site

The study was conducted in the Eastern Cape Province of South Africa between April and July 2016. Forest cover in this region is discontinuous and highly fragmented (Figure 1).⁹ Within the study area, six forests were

sampled, including five national forest types in the two main zones of forest, i.e. the lowland coastal and scarp forests of the subtropical coastal zone, and the warm-temperate mistbelt forests found on the south to southeastern aspect of inland mountain ranges (Figure 1).⁹ Specifically, the following forests were sampled: Mqaba (Pondoland Scarp Forest), Manubi (Transkei Coastal Forest) and Ntlaboya (Eastern Cape Dune Forest) of the lowland zone; and Gomo, Nqadu (Transkei Mistbelt Forest) and Pirie (Amathole Mistbelt Forest) of the montane zone (Figure 1). Within the Transkei mistbelt region, forests located within matrixes of timber plantations leased by the state to private companies are often deemed to be better protected than those which are not, so a forest in each category was sampled, with Nqadu associated with privately managed plantations while Gomo was associated with plantations managed by the South African Department of Environment, Forestry and Fisheries (DEFF). Study forests were selected based on their size, protected status, and the proximity of surrounding human settlements. Specifically, selected forests were greater than 150 ha, and unfenced; managed by DEFF; and had rural settlements within 4 km of the forest boundary. While most forest patches in the Eastern Cape are smaller than 150 ha, and prone to negative effects of fragmentation,^{5,9} study forests were selected to represent larger, more ‘intact’ forest patches within the region. This is because these forests have larger core areas (i.e. portion of forests unaffected by edge effects) and are thus of high biodiversity value, such that insight into anthropogenic pressures within these forests is of conservation priority.⁵ Furthermore, given that 70% of forests in the Eastern Cape region are managed by DEFF, and are often associated with communities in close proximity,⁵ study forests are representative of the current socio-political context within which larger, ‘intact’ forests in the region occur. Lastly, study forests have endured colonial logging,¹⁰ followed by subsistence harvesting in recent times, such that they are representative of the history of human impacts.



Source: Forest types after Von Maltitz et al.⁹

Figure 1: Location of the six study forests in the Eastern Cape Province, South Africa.

Study design

A total of 89 circular plots of 0.04 ha (radius 11.3 m) were sampled, with an average of 15 plots sampled per forest. Points for sampling plots in each forest were selected to represent varying levels of disturbance from resource use, based on detailed discussion and guided walks in each forest with DEFF staff (forest managers and/or forest guards), and local community members, in addition to visual assessment by J.L. of human use in each forest, conducted over two reconnaissance trips prior to sampling. Plot locations were selected to represent the continuum of harvesting disturbances present at each forest, from heavily harvested sites to those with little or no harvesting present. Heavily harvested plots were defined as those where >20% of available stems were harvested for poles, timber or bark. Where 10–20% of available stems were harvested, plots were described as intermediately harvested, while low levels of harvesting were defined as harvest levels of <5% of any resource at the plot level. This non-random sampling approach aimed to provide an objective overview of resource use within each forest, as well as samples from the full range of harvest activities and intensities, against which to investigate habitat changes and, in a linked study, avifaunal responses to resource use.²⁴ Based on this categorisation, 6% ($n=8$) of plots overall had no harvesting, while 27%, 30% and 34% had low, intermediate and high levels of harvesting, respectively. A minimum distance of 150 m was maintained between selected plots, and 50 m between plots and the forest edge (i.e. all survey sites were within the forest interior), while distance into the forest interior ranged from 50 m to 900 m.

Data collection

At each plot, microhabitat structure and foliage profile were recorded within three nested circular plots of 0.2 ha (radius of 25.2 m), 0.04 ha (radius of 11.3 m), and 0.01 ha (radius of 5.6 m), respectively. In the 0.2 ha plot, all standing dead trees (henceforth, snags) were recorded by diameter (cm) at 1.3 m above the ground, i.e. diameter at breast height (DBH), and cause of death, i.e. natural or due to bark harvesting. Natural snags include standing trees that have died due to factors other than harvesting, such as wind effects, senescence or disease. In the 0.04-ha plot, the following variables were recorded: DBH of all living stems (>5 cm DBH); percentage canopy cover; mean canopy height; percentage coverage of bare ground, leaf litter, grass cover and herbaceous cover; and foliage density at 0–0.5 m; 0.5–1 m; 1–2 m; 2–5 m; 5–10 m and 10–20 m. Foliage density at each height class was estimated using a 8-m-long telescoping pole and marked at each height interval. The pole was sequentially set up at eight evenly spaced points 11.3 m from the plot centre (i.e. along the 0.04-ha circular plot boundary) and visual estimates of foliage density (as a percentage) at each height class were made from the plot centre. Foliage density scores were further converted into a foliage height diversity index (FHDI) using the Shannon–Weiner Diversity Index formula, as follows:

$$H = - \sum_{i=1}^s p_i \ln(p_i)$$

where p_i is the proportion of the total foliage which lies in the i th layer of the chosen horizontal layers. This index thus provided a measure of the vertical heterogeneity at each plot.

A rangefinder was used to assist with estimates of foliage density beyond the length of the telescoping pole, as well as to estimate mean canopy height at each plot. Abundance of coarse woody debris was measured based on the number of grounded dead logs (diameter > 10 cm; length > 1.5 m). Harvest activities were also measured in the 0.04-ha plot: stumps, i.e. trees harvested for poles or timber, were counted and diameter measured. Based on diameter, stumps were categorised as pole (5–19.9 cm diameter) or timber (>20 cm diameter) harvesting, after Obiri et al.⁹ Trees harvested for medicinal bark were recorded using

DBH and extent of bark removal on individual trees up to 3 m on the tree stem (scored 1 – 6 based on percentage of bark removed, where 1 = 1–10%; 2 = 11–25%; 3 = 26–50%; 4 = 51–75%; 5 = ringbarked to any extent %; 6 = total ringbark, where ringbarked stems are those where bark has been removed from around the full circumference of the stem, after Cunningham³³). In 0.01-ha plots, sapling (stem diameter 1–5 cm) abundance was recorded.

Data analyses

Pole and timber harvest intensities were calculated per plot for each size class based on the accumulated harvestable stems (stumps plus standing stems) as follows:

$$\text{Tree harvest index}_j = \text{number stumps}_j / (\text{number stumps}_j + \text{number stems}_j),$$

where j represents the size class being assessed.

Bark harvest intensity was assessed based on a bark harvest index derived from summed bark removal scores assigned to individual bark-harvested trees, calculated at each plot, as follows:

$$\text{Bark harvest index} = \text{summed bark removal score} / \text{no. individuals bark harvested}$$

Harvest effects on forest structure were investigated using (1) linear mixed models for habitat variables measured on a continuous scale; (2) generalised linear mixed models for habitat variables measured as counts, and (3) beta regression for habitat variables measured as per cent cover. A mixed-modelling approach was used in all cases to account for the nested study design, with sample forests included as a random effect throughout the analysis to account for plots being nested within study forests. Separate models were used to assess the response of each habitat feature to harvesting, with pole, timber and bark harvest indices included as the explanatory variables in addition to, and in all possible combinations of two-way interactions with one another. The two-way interaction between timber and bark was not included, as bark and timber harvesting were seldom recorded within a single plot. Spearman's rank correlation test was used to test for significant correlations between harvest variables, to avoid issues related to multicollinearity. The test showed the harvesting variables to be uncorrelated ($-0.4 < r < 0.4$). Habitat variables measured as counts (tree, snag, sapling and grounded log abundance) were modelled using generalised linear mixed models, with a Poisson distribution and log-link. Response variables measured as per cent cover were converted to proportions and modelled using a beta regression. Model assumptions were verified by plotting residuals versus fitted values, and versus each covariate in the model. Where interaction terms did not improve model strength based on Akaike information criterion (AIC) values, they were removed from the final model. Data from Pirie were not included in these analyses as minimal harvesting was recorded in this forest, and these analyses aimed to assess effects in disturbed forests.

Results

Of the 18 measured structural variables, 12 were significantly impacted by harvesting activities, with responses dependent on the type and intensity of resource use (Figures 2–5; Table 1). Furthermore, the two-way interaction between pole and timber harvesting was shown to affect structural habitat heterogeneity (Figure 5; Table 1). Five habitat features were unaffected by harvest activities: canopy height; mean DBH; lower-understorey (0.5–1 m) foliage density; mid-storey (2–5 m) foliage density; and canopy layer (5–10 m) foliage density (Table 1).



Table 1: Response of structural habitat variables to pole harvesting intensity (Pole), timber harvesting intensity (Timber) and bark harvesting intensity (Bark) derived from linear mixed models; *p*-values in bold indicate statistical significance (*p*<0.05)

Response	Fixed effect	Estimate	s.e.	t-value	<i>p</i> -value
Foliage height diversity index	Intercept	1.87	0.04	45.87	0.00
	Pole	0.24	0.13	1.85	0.07
	Timber	0.47	0.24	1.97	0.05
	Bark	-0.01	0.04	-0.32	0.75
	Pole*Timber	-3.20	1.41	-2.26	0.03
Canopy height (m)	Intercept	12.56	0.91	13.87	0.00
	Pole	-0.14	1.85	-0.08	0.93
	Timber	0.25	3.27	0.08	0.94
	Bark	0.27	0.79	0.33	0.74
Mean diameter at breast height (DBH) (log-transformed)	Intercept	1.25	0.04	31.13	0.00
	Pole	0.06	0.10	0.64	0.52
	Timber	-0.20	0.18	-1.13	0.26
	Bark	-0.02	0.04	-0.51	0.61
Mean basal area per ha (log)	Intercept	1.79	0.06	28.99	0.00
	Pole	-0.42	0.13	-3.22	<0.01
	Timber	-0.02	0.23	-0.09	0.93
	Bark	-0.02	0.06	-0.43	0.67
Coarse woody debris	Intercept	1.78	1.17	10.68	0.00
	Pole	-0.82	0.43	-1.88	0.06
	Timber	1.42	0.73	1.94	0.05
	Bark	0.50	0.17	3.02	<0.01
Tree abundance (>5 cm DBH)	Intercept	4.16	0.11	39.32	0.00
	Pole	-0.91	0.16	-5.83	<0.01
	Timber	0.18	0.26	0.68	0.50
	Bark	-0.03	0.07	-0.43	0.68
Sapling abundance (<5 cm DBH)	Intercept	3.63	0.20	18.46	0.00
	Pole	-1.29	0.19	-6.73	<0.01
	Timber	0.81	0.27	3.06	<0.01
	Bark	-0.34	0.07	-4.49	<0.01
Snag abundance (DBH > 10 cm)	Intercept	2.16	0.17	12.93	0.00
	Pole	-0.65	0.38	-1.70	0.09
	Timber	-0.62	0.65	-0.95	0.34
	Bark	0.08	0.14	5.87	<0.01
Canopy cover (%)	Intercept	1.06	0.06	17.55	0.00
	Pole	-0.64	0.36	-1.81	0.07
	Timber	-1.41	0.57	-2.45	<0.05
	Bark	-0.72	0.14	-5.10	<0.01
Herb cover (%)	Intercept	-1.41	0.46	-3.05	0.00
	Pole	2.49	0.81	3.08	<0.01
	Timber	-2.22	1.72	-1.30	0.20
	Bark	0.13	0.36	0.35	0.73
Leaf litter cover (%)	Intercept	-0.52	0.30	-1.75	0.00
	Pole	-2.95	0.77	-3.79	<0.01
	Timber	-1.45	1.13	-1.28	0.20
Bare ground cover (%)	Intercept	-3.17	0.27	-11.87	0.00
	Pole	0.22	0.86	0.26	0.80
	Timber	3.43	1.21	2.84	<0.01
Herb layer foliage density (0–0.5 m)	Intercept	-0.003	0.48	-0.007	0.99
	Pole	1.72	0.85	2.02	<0.05
	Timber	0.36	1.27	0.28	0.77
Lower-understorey foliage density (0.5–1 m)	Intercept	-0.61	0.22	-2.76	0.00
	Pole	0.99	0.78	1.27	0.21
	Timber	1.73	1.37	1.26	0.21
Upper-understorey foliage density (1–2 m)	Intercept	-1.10	0.23	-4.76	0.00
	Pole	0.81	0.82	0.99	0.32
	Timber	3.41	1.37	2.48	<0.05
Understorey foliage density (0–2 m)	Intercept	-0.53	0.14	-3.68	0.00
	Pole	0.96	0.54	1.76	0.08
	Timber	1.65	0.94	1.75	0.08
Mid-storey foliage density (2–5 m)	Intercept	-0.90	0.22	-4.17	0.00
	Pole	-0.22	0.65	-0.34	0.74
	Timber	0.10	1.12	0.09	0.93
Canopy layer foliage density (5–10 m)	Intercept	0.001	0.30	0.00	1.00
	Intercept	-0.12	0.18	-0.66	0.51
	Pole	0.78	0.47	1.66	0.10
Canopy layer foliage density (5–10 m)	Timber	-0.92	0.84	-1.10	0.27
	Bark	-0.24	0.20	-1.19	0.23

Bark harvesting

Increasing bark harvesting intensity negatively affected canopy cover and sapling abundance (<5 cm DBH), while herb layer (0–0.5 m) foliage density, overall understorey (0–2 m) foliage density, number of grounded logs and snag abundance (i.e. standing dead trees; >10 cm DBH) increased with bark harvesting intensity (Figure 2; Table 1).

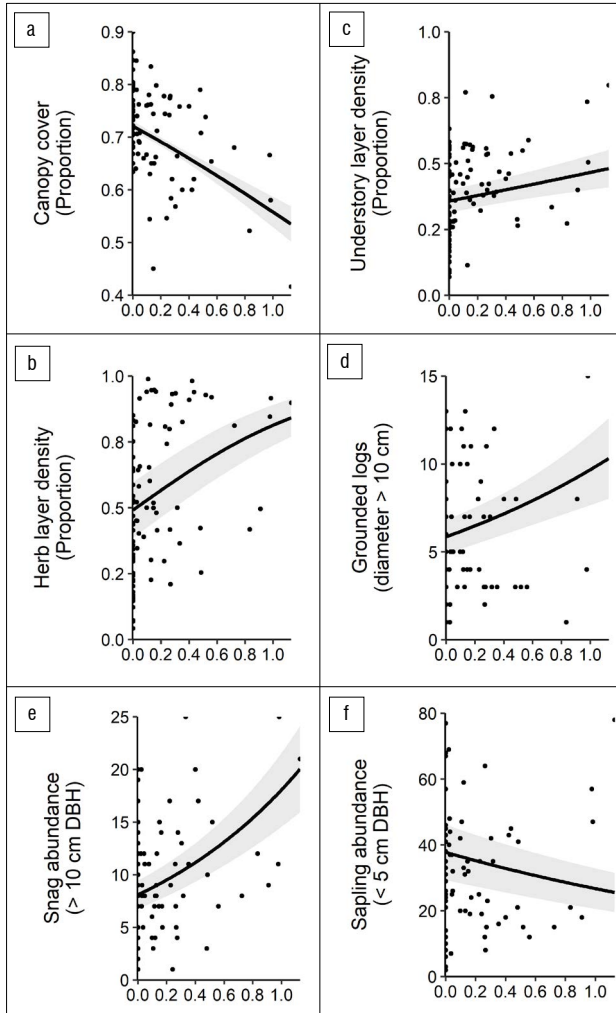


Figure 2: Effect of bark harvesting intensity, measured as the summed score of bark removal from individual bark-harvested trees per plot, based on Cunningham³³ on (a) canopy cover, (b) herb layer (0–0.5 m) foliage density, (c) understorey (0–2 m) foliage density, (d) number of ground logs, (e) snag abundance and (f) sapling abundance (<5 cm diameter at breast height). Relationships shown are derived from mixed models with forest included as a random effect (Table 1); however, graphic representations depict population-level predictions (i.e. excluding random effects).

Pole harvesting

Increasing pole harvesting intensity resulted in declines in tree abundance, sapling abundance, basal area per hectare and leaf litter cover. Conversely, herb layer (0–0.5 m) foliage density and herb cover increased with increasing pole harvesting intensity (Figure 3; Table 1).

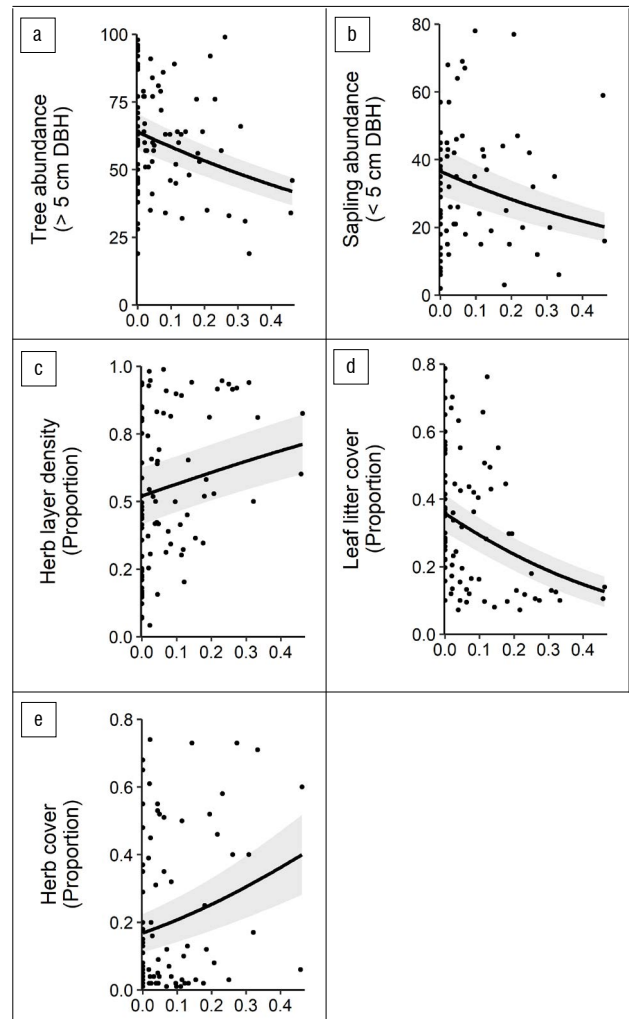


Figure 3: Effect of pole harvesting intensity, measured as the proportion of available stems (5–19.9 cm diameter at breast height/DBH) harvested, on (a) tree abundance (>5 cm DBH), (b) sapling abundance (<5 cm DBH), (c) herb layer (0–0.5 m) foliage density, (d) leaf litter cover and (e) herb cover. Relationships shown are derived from mixed models with forest included as a random effect (Table 1); however, graphic representations depict population-level predictions (i.e. excluding random effects).

Timber harvesting

Increasing timber harvesting intensity resulted in a decline in canopy cover, while a positive relationship was found between the extent of timber harvesting and upper-understorey layer (1–2 m) foliage density, number of grounded logs, bare ground cover, and sapling abundance (Figure 4; Table 1).

Interacting harvest effects

Foliage height diversity index (FHD) was negatively affected by the interaction between timber and pole harvesting. Specifically, FHD increased in response to increasing timber harvest intensities where pole harvest levels were low (i.e. 5% of available stems), but declined in response to increasing timber harvest levels where pole harvest intensities were high (i.e. 20% of available stems; Figure 5; Table 1).

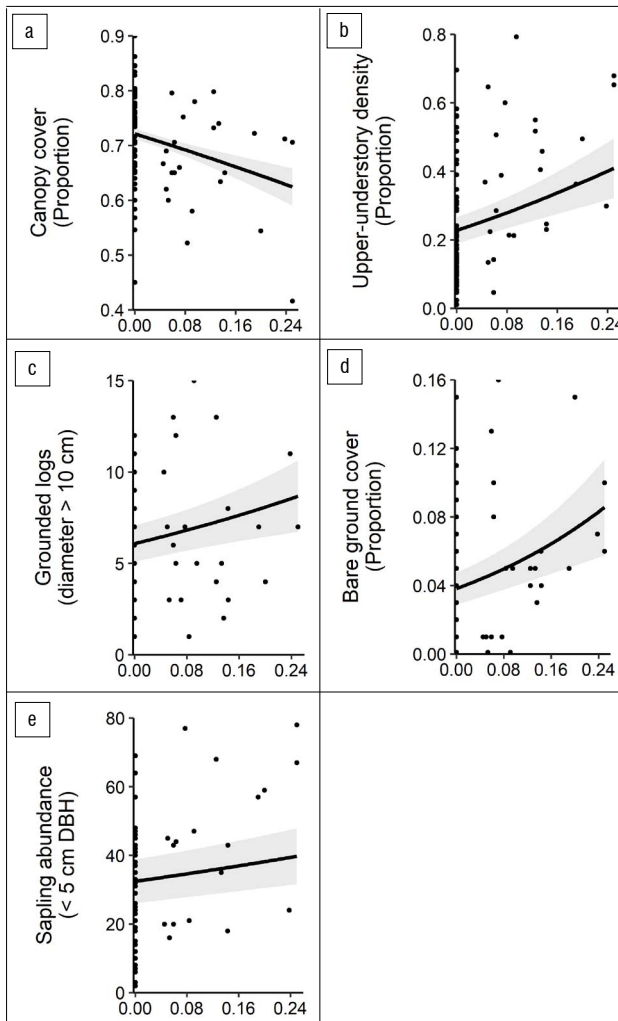


Figure 4: Effect of timber harvesting intensity, measured as the proportion of available stems (> 20 cm diameter at breast height/DBH) harvested, on (a) canopy cover, (b) upper-understorey layer (1–2 m) foliage density, (c) number of grounded logs, (d) bare ground cover and (e) sapling abundance. Relationships shown are derived from mixed models with forest included as a random effect (Table 1); however, graphic representations depict population-level predictions (i.e. excluding random effects).

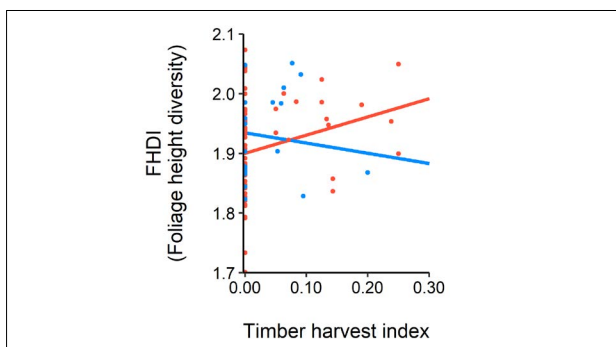


Figure 5: Effect of the two-way interaction between pole and timber harvesting on the foliage height diversity index (FHD). The two lines represent variation in FHD response to timber harvest intensity in the presence of low (i.e. 5%; red) and high (i.e. 20%; blue) intensities of pole harvesting, respectively. Relationships shown are derived from mixed models with forest included as a random effect (Table 1); however, graphic representations depict population-level predictions (i.e. excluding random effects).

Discussion

The findings of this study show that unregulated harvesting of medicinal bark, poles and timber results in multiple structural modifications to forest habitats in state forests of the Eastern Cape. Specifically, bark and timber harvesting created canopy gaps, while pole harvesting created understorey gaps, with variable implications for ground and understorey layer microhabitat structure, respectively. Our findings are thus in agreement with those of previous studies which have shown significant impacts of resource use on forest habitat structure in South Africa.^{7,17,34} While the long-term ecological effects of harvest-mediated habitat modification are largely unknown³⁴, they represent changes to the natural disturbance regime, and are thus likely to have ramifying effects on forest patterns and processes³⁵, and faunal populations²⁶. However, results of this study show that the extent of habitat modification is dependent on the nature and intensity of harvesting, and that different harvest activities, where occurring together at a fine spatial scale, may have interactive effects on habitat structure.

Bark harvesting

While several studies have examined the ecological implications of bark harvesting at individual and population levels^{36–39}, concurrent impacts on habitat structure have been relatively under-studied. Increasing bark harvesting intensities resulted in a decline in canopy cover and sapling abundance, and an increase in herb layer (0–0.5 m) and understorey layer (0–2 m) foliage density, grounded logs, and snag density (i.e. standing dead trees). These habitat modifications are the result of excessive bark removal from tree stem circumferences, preventing the transport of photosynthetic products to tree roots, leading to root loss or death, thereby driving declines in canopy health and potential tree mortality.^{39,40} This creates gaps in the forest canopy, thereby increasing light availability to the forest floor such that ground and understorey layer foliage density increases. Over time, bark-harvested trees die and become snags which then decay, and dead branches drop to the ground, increasing the amount of grounded dead wood.

The substantial habitat-scale impacts of bark harvesting are perhaps best demonstrated by the close to 50% mean increase in snag abundance recorded across the four forests which experienced the highest levels of bark harvesting (Gomo, Manubi, Nqadu and Ntlaboya; Table 2), and associated increases in the number of grounded logs. While the ecological implications of the collection of dead wood for fuelwood from indigenous forests in South Africa have been cause for concern^{6,41}, with negative effects on cavity-nesting mammals and birds⁴², few studies have highlighted the creation of dead wood in forests due to bark harvesting. The important ecological role of dead wood has long been recognised by ecologists.⁴³ However, the value to forest taxa of harvest-mediated dead wood creation, at the cost of living canopy trees of a select few species and canopy cover, is currently unknown but likely to be multifaceted and taxon dependent.

Pole harvesting

Unlike bark and timber harvesting, pole harvesting did not affect the forest canopy, but resulted in a decline in basal area and stem density of trees and saplings. This finding reflects the nature of pole harvesting wherein multiple understorey trees are harvested at a fine spatial scale, thereby creating gaps in the understorey, as shown by Boudreau and Lawes¹⁷. Despite the lack of any major canopy disturbances, as pole harvesting intensity increased, multiple understorey layer features were affected: foliage density at the herb layer (0–0.5 m) and herb cover increased, while leaf litter cover declined. Thus, while declines in basal area, tree and sapling density were a direct effect of harvesting, altered understorey and ground layer conditions are likely to be an indirect response driven by increases in light availability and soil moisture content due to a reduction in tree density.^{17,44}

Although beyond the scope of this study, increased herb cover in understorey gaps caused by pole harvesting may suppress seedling establishment.⁴⁴ Thus pole harvesting has the potential to alter not only structural habitat features, but also seedling recruitment, and therefore the maintenance of forest tree diversity. As indicated, changes

Table 2: Extent of harvesting activities recorded at each study forest, showing means (\pm s.e.) within each forest, with superscript letters indicating significant differences between forests

Harvest type	Lowland forests			Montane forests			Test statistic and p -value
	Manubi	Mqaba	Ntlaboya	Gomo	Nqadu	Pirie	
Bark harvest index	0.25 \pm 0.08 ^{ab}	0.03 \pm 0.01 ^{bc}	0.28 \pm 0.11 ^{abc}	0.31 \pm 0.07 ^a	0.16 \pm 0.05 ^{abc}	0.01 \pm 0.01 ^c	$\chi^2 = 27.02$, d.f. = 5, $p < 0.01$
Proportion of pole-sized trees harvested per plot	0.10 \pm 0.03 ^a	0.07 \pm 0.02 ^a	0.05 \pm 0.03 ^{ab}	0.14 \pm 0.04 ^a	0.08 \pm 0.03 ^{ab}	0.00 \pm 0.00 ^b	$\chi^2 = 28.45$, d.f. = 5, $p < 0.01$
Proportion of timber-sized trees harvested	0.07 \pm 0.02 ^a	0.07 \pm 0.02 ^a	0.02 \pm 0.02 ^{ab}	0.02 \pm 0.01 ^{ab}	0.00 \pm 0.00 ^b	0.00 \pm 0.00 ^b	$\chi^2 = 21.72$, d.f. = 5, $p < 0.01$

in understorey conditions are dependent on the harvest intensity. Similarly, changes in seedling recruitment caused by pole harvesting are determined by understorey gap size,⁴⁴ with larger gaps causing a potential successional shift in seedling recruitment. However, Boudreau and Lawes¹⁷ showed that under low harvesting intensity (11.6% of available pole-sized stems), pole harvesting did not negatively affect the long-term maintenance of tree diversity, suggesting that rates of pole harvesting measured in the current study (regional average of 7% of available pole-sized stems; Table 2) may not adversely affect tree species composition. However, modifications to understorey layer conditions may affect forest fauna. For example, leaf litter cover is a critical habitat for many forest invertebrates.⁴⁵

Timber harvesting

At the habitat scale, timber harvesting resulted in canopy gaps through the selective extraction of canopy trees, driving an increase in upper-understorey (1–2 m) foliage density, sapling abundance, and bare ground cover. Furthermore, timber harvesting increased the number of grounded logs as a result of the large portions of harvested trees that are left in the forest after only the main stem of the harvested tree is removed. Furthermore, increases in dead wood may be associated with incidental tree damage associated with canopy-tree felling. Similar structural responses to selective timber harvesting have been shown by studies in tropical forests.^{21,22,46} The creation of canopy gaps in forest systems represents a vital component of natural forest disturbance regimes, given their important role in promoting regeneration, tree diversity and habitat heterogeneity.^{22,47–50} The gap phase represents a time of rapid plant growth⁴⁹, attributed to increased resource availability and/or decreased resource competition⁵¹, demonstrated in the current study by the increased foliage density in the understorey. Furthermore, habitat conditions in canopy gaps compared to those in intact forest have been shown to differ significantly with respect to microclimate^{51,52}, detritus²⁷, productivity⁵³, and plant species composition^{47,49}. Consequently, multiple forest taxa, including birds, reptiles and invertebrates, have been shown to distinguish between canopy gap and intact habitats.^{22,46,50,54,55} This finding suggests that timber harvest activities, and concomitant habitat modifications, are likely to have ramifying effects on forest biodiversity.

The degree to which timber harvest activities affect forest biodiversity, beyond direct population-level impacts on target species, is likely to be dependent on the frequency of the disturbance, and the extent of incidental habitat damage. With regard to the former, selective harvesting practices in the Eastern Cape are likely to be less destructive than mechanised selective logging operations, which cause considerable damage through clearing for roads and log storage sites.⁴⁶ Informal timber harvesting in the Eastern Cape is generally un-mechanised, with felled timber split in the forest, and carried out on foot along narrow footpaths (J.L. personal observation). The frequency of disturbance is thus likely to be more cause for concern, as the harvest-driven increase in the proportion of forest-under-gap conditions is likely to have implications for ecosystem functioning.³⁵

Interacting harvest effects

The positive relationship between foliage height diversity and biodiversity has been well established, and is based on niche theory which predicts that a greater diversity of habitats supports a greater diversity of species.⁵⁶ The decline in foliage height diversity in response to the interaction between pole and timber harvesting activities shown in this study indicates that, where these harvest types occur together at high rates, structural habitat complexity is reduced, and likely to negatively affect biodiversity at the habitat scale. This finding suggests that management strategies should limit the extent to which pole and timber harvesting activities occur together, and reduce the damage/lopping of smaller, non-target trees often associated with timber harvesting activities (J.L. personal observation), so as to maintain habitat heterogeneity in harvested areas.

Conclusion

The findings of this study indicate that resource use from state forests in the Eastern Cape has a significant impact on forest structure, although the nature and extent of the impact is dependent on the type and intensity of resource use. These results should be viewed within the context of forests that have a long history of human exploitation, from extensive colonial era logging to current subsistence and informal commercial harvesting of multiple forest products. However, the effects of long-term human exploitation are likely to have affected the current condition of all sampled forests, such that the findings of this study are indicative of habitat responses to more recent resource use disturbances. Similarly, while habitat structure is modified by random natural disturbances, such as windfalls, lightning or fire-spotting, which are vital components of natural disturbance–recovery regimes that maintain forest dynamics, resource use represents disturbances that occur in addition to these natural disturbances under which forest species have adapted, and thus may affect ecosystem persistence and resilience. Further research is needed to determine specific levels of resource use that can be sustained without negatively affecting forest biodiversity. Specifically, research regarding the impact of resource use on forest taxa at multiple trophic levels is needed to provide insight into ecosystem-wide implications of harvest-mediated habitat modification, and to contribute to the development of ecologically informed forest management policies.

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Competing interests

We declare that there are no competing interests.

Data availability

The data sets generated and/or analysed during the current study are available from the corresponding author on request.

Authors' contributions

J.L. designed the study methodology, conducted data collection and data analysis, and wrote the initial draft of the manuscript. M.I.C. conceptualised the study, acquired funding, and contributed extensively to the writing of the manuscript revision.

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