

Regeneration failure and the potential importance of human disturbance in a subtropical forest

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Abstract. A lack of regeneration of shade-intolerant canopy species has been reported in several subtropical South African forests. The subtropical forest of Hluhluwe-Umfolozi Park, KwaZulu-Natal, was examined in order to determine the extent of regeneration, the forest grain, dynamics and conservation value. Field sampling took the form of recording DBH for all woody species in 29 0.04-ha circular plots, walking 5-m wide transects in mature and marginal forest to record size classes of important species and analysis of 20 gaps. A community analysis was performed using the multivariate program TWINSPLAN. Size-class distributions indicate a lack of regeneration and suggest a prevalence of shade-intolerant species in the canopy. The composition of the canopy and subcanopy are distinct from one another and the forest is coarse-grained. Conservation of the present species composition could be aided by encouraging patch-scale disturbance. It is hypothesized that swidden agriculture may have favoured the formation of the present forest canopy structure.

Keywords: Canopy composition; Coastal scarp forest; Gap; Grain; Large-scale disturbance; Multivariate analysis; Size class; South Africa.

Introduction

Modern forest ecosystem characteristics are often determined by the legacies of past land use (e.g. Binford et al. 1987; Williams 1990; Gómez-Pompa & Kaus 1992; Watkins 1993; Whitney 1994; Northrop & Horn 1996; Noble & Dirzo 1997; Ogden et al. 1998; Lindbladh & Bradshaw 1998; Foster et al. 1999). It is even becoming accepted that many assumptions regarding the relative importance of natural processes in controlling these forests may need to be reviewed (Foster et al. 1999). 'Natural' disturbance regimes of forest ecosystems include both small-scale, autogenic processes such as tree- and branch-fall (Brokaw 1985, 1989; Uhl et al. 1988; van Wyk et al. 1996) and large-scale, allogenic processes such as earthquakes, volcanism, hurricanes and fires (Veblen et al. 1992; Okitsu et al. 1995; Akashi & Mueller-Dombois 1995; Batista et al. 1998; Carlton & Bazzaz 1998). To this list, human disturbances, generally in the form of large-scale clearance for cultivation or selective removal through logging, must now be added.

Grain

The disturbance regime has profound impacts on the composition of the forest. The balance between shade-tolerant and intolerant species occurring in a forest is largely controlled by the degree of large and small-scale disturbances. Simplistically, one would expect shade-tolerant species to exhibit advanced regeneration under closed canopies, which could then take advantage of small light gaps to reach the canopy, whereas shade-intolerant species would require large light gaps in order to regenerate and reach the canopy (Midgley et al. 1995).

These factors and the scale over which they occur can be concisely expressed by the concept of 'grain' (see Midgley et al. 1990; Everard et al. 1995). In a fine-grained forest, the composition of the canopy is similar to the subcanopy and consists of predominantly shade-tolerant species. Small-scale disturbance is sufficient to allow regeneration, which occurs primarily by advanced regeneration from a sapling bank. In a coarse-grained forest, the canopy and subcanopy are markedly different and consist of both shade-tolerant and shade-intolerant species. Both small- and large-scale disturbances occur and the latter enable the regeneration of shade-intolerant species, but not near their adults. All southern African forests can be seen as fitting along a continuum between fine- and coarse-grain extremes (Everard et al. 1995; van Wyk et al. 1996). Grain is a useful classificatory measure especially for forest conservation, as forests of similar grain would have similar dynamics and can thus be managed in the same manner (Everard et al. 1995).

Lack of regeneration in KwaZulu-Natal forests

The issues of naturalness and human legacy are critical to our management of the remaining forest patches of KwaZulu-Natal, South Africa. These diminishing forest patches now comprise approximately 100 000 ha, or 1.05 % of the vegetation cover in KwaZulu-Natal (Cooper 1985). As with the protection of other natural resources, the conservation of these forests has involved

their incorporation into reserves. This simple act of protection is presumed to restore a 'natural' disturbance regime, exclusive of human activity. However, researchers have reported a lack of regeneration of the canopy dominants occurring in many of these forests (Midgley et al. 1995). It would seem that the 'natural' gap-phase disturbance regime is not presently conducive to regeneration of the current canopy dominants, a situation that needs to be addressed if these forest reserves are to remain sustainable functional units.

This paper focuses on the Hluhluwe Forest in KwaZulu-Natal, South Africa, and examines the current forest structure and regeneration patterns in an attempt to understand the conditions required for the regeneration of the canopy dominants and to assess the extent of their recruitment failure. We discuss the potential importance of past human disturbance in influencing the current ecosystem characteristics. This paper centres around three lines of inquiry. Firstly, is present regeneration in gaps, in terms of species and density, sufficient to explain present canopy composition and size class distributions? Secondly, is the scale of vegetation patchiness greater than that determined by tree-fall gaps? Thirdly, is there evidence for large-scale cohorted regeneration rather than continuous replacement?

Study area

The Hluhluwe-Umfolozi Park ($28^{\circ} 00' S$ and $28^{\circ} 26' S$; $31^{\circ} 43' E$ and $32^{\circ} 09' E$) (Watson & Macdonald 1983) is situated in KwaZulu-Natal, South Africa (Fig. 1). It covers 900 km^2 with an altitude ranging from 60 m to 750 m above sea level (Whately & Porter 1983). The Hluhluwe Game Reserve, where this study was based, occupies the northeastern 225 km^2 of this complex (Whately & Porter 1983). Forest communities are restricted to the high rainfall hillsides or to riverine belts (Brooks & Macdonald 1983). Here the rain falls mainly between October and March with a mean annual rainfall of 990 mm (50 yr) and a 27.4% coefficient of variation (Brooks & Macdonald 1983). Although there is great edaphic heterogeneity in the Hluhluwe-Umfolozi Park (Whately & Porter 1983), the forests occur mainly on basalt outcrops which are found in the northwest and eastern part of the Hluhluwe Game Reserve (Whately & Porter 1983).

Methods

Vegetation sampling methods

Plot and transect sampling

We sampled woody vegetation in the mature forest and on the forest margins in order to examine the composition and dynamics of the forest. These data were recorded using 19 0.04-ha circular plots (radius 11.28 m) randomly located in stands of mature forest. A further 10 plots were sampled at the forest margins. A comparison between plots in the mature forest and at the margins provided an indication of forest expansion or decline. In all the plots, the total height or stem diameters at breast height (DBH) for all woody species were categorized. Categories used were seedlings 25 cm in height; understorey (> 25 cm but < 2 m high); subcanopy (> 2 m but clearly not reaching canopy) and canopy (> 2 m and in the canopy). The criterion for canopy status was for a tree to be over two-thirds the mean plot height and have access to unimpeded light from above. In terms of sampling seedlings, one quadrant (0.01 ha) was used as

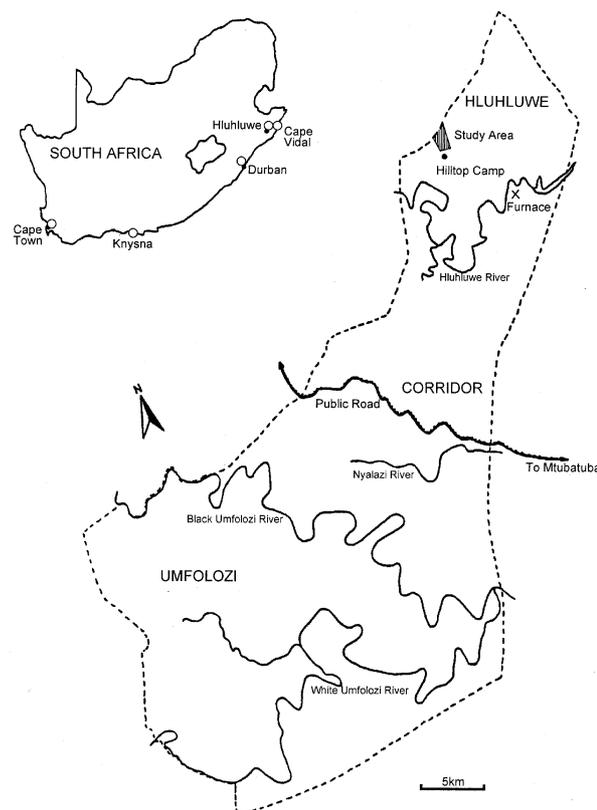


Fig. 1. Map of the Hluhluwe-Umfolozi Game Reserve showing the position of the Hluhluwe Forest study area and the location of an Iron-Age furnace.

a subsample of the entire plot, excepting in areas of high seedling density where five 1-m² subsamples were used per 100 m². At each of these plots a site description was made, including aspect, slope, mean canopy height and estimated distance from forest margin.

5-m wide transects were also sampled through the mature forest in order to supplement the plot data for species size class frequency distributions. The direction of these transects was chosen randomly and then strictly maintained in order to prevent biasing the data towards larger, more visible individuals. A similar procedure was used for transects along the forest margins. However here the forest edge served to delimit the course of the transect. Size classes were created for the 11 most common species and analysed by creating a ratio of small stems (< 10 cm DBH) to large stems (> 10 cm DBH) and determining stem density in both the margins and in the mature forest. Size class analyses are an interpretation of static data and should be interpreted with caution.

Tree-fall gap sampling

20 tree-fall gaps were sampled in the mature forest. Tree-fall gaps were defined as any current light gap, within continuous forest, that was caused by the standing death or fall of a tree. We attempted to ascertain the gap-maker and potential gap-taker whenever possible. Small branch-fall gaps were ignored and thus our sampling was biased towards larger gap sizes. Data collected included the area of gap, the number and species of seedlings present and the size (DBH) of all woody species.

Large-scale recruitment ('patch') sampling

Due to observations indicating low recruitment in shaded areas and tree-fall gaps, we searched for evidence of previous recruitment in large-scale disturbances in old fields ('patches'). We reasoned that documentation of three elements associated with these patches would constitute evidence for the existence of regeneration in large-scale disturbances: These elements were, firstly, the existence of patches of closed forest with a higher than normal abundance of an apparently shade-intolerant canopy species. Secondly, these patches should have a small range in DBH as a result of establishing as a cohort after large gap formation. Thirdly, the area of these patches should be significantly larger than that of forest tree-fall gaps.

All patches had to meet the criteria of containing individuals that were smaller than the maximum sizes recorded for those specific species. This criterion was established in order to eliminate the potential problem of recording trees that had converged on the same maximum size and thus falsely appeared as a uniform

cohort. In each patch, species and DBH were recorded of all canopy trees > 20 cm DBH. Sampling stopped after either recording tree species other than the dominant canopy species of that patch, or individuals noticeably larger than the mean DBH of the patch. The areas of these patches were noted for comparison to tree-fall gap sizes that were sampled in the forest. Five such patches within the mature forest community were sampled.

Multivariate analysis

A multivariate analysis was used to examine the relationship between forest canopy and subcanopy and the forest margins. In this analysis, similar overstorey and understorey composition implies shade tolerant regeneration. The plot data were classified using the hierarchical classification program TWINSpan (Hill 1979). TWINSpan is a polythetic divisive method and plots are separated on the basis of total species composition (Kent & Coker 1992). Thus, the dendrogram produced by TWINSpan provides an indication of which plots are similar in species composition to one another. The program was run with defaults and the numbers of stems per species per plot were used as the importance values. Only woody plants were used, as data were not complete for creepers and herbs. The analysis was run for all species and then again with the dominant understorey species removed. Removing the understorey species from the analysis allowed for a closer examination of patterns of the canopy species without the swamping effect of a few ubiquitous understorey species.

The sample plots were separated into a canopy subplot and a subcanopy subplot. This created four plot categories, namely Forest Canopy (fc), Forest Subcanopy (fs), Margin Canopy (mc) and Margin Subcanopy (ms). By examining how the analysis separated the plots we could interpret both grain and succession.

Size-class analysis

Frequency distributions of the dominant tree species were created by grouping plot and transect data into size classes. Size class distribution curves were then analysed by creating a ratio of small stems (< 10 cm DBH) to large stems (> 10 cm DBH). One would expect small stem: large stem ratios to be > 1 for species that are successfully recruiting. Ratios of << 1 would indicate species with low recruitment and hence low representation in juvenile size classes. In mature forest with a low level of disturbance, such as Hluhluwe Forest, size-class distributions help to indicate whether or not a species is recruiting under the canopy. Under these conditions, species with large numbers of individuals in the

Table 1. Ratio of small stems (< 10 cm DBH) to large stems (> 10 cm DBH) and density of stems (per ha) for various species in Mature Forest and Forest Margins. Ratios > 1 implying recruitment under current conditions are marked in bold type.

Species	Mature forest stems		Forest margin stems	
	small / large	density	small / large	density
<i>Celtis africana</i>	0.22	53.9	0.32	112
<i>Chaetacme aristata</i>	0.51	42.1	1.11	20.0
<i>Chrysophyllum viridifolium</i>	0.26	13.1	-	-
<i>Combretum kraussii</i>	0.13	2.63	1.00	0.00
<i>Drypetes gerrardii</i>	0.93	101	1.50	12.5
<i>Ekebergia capensis</i>	4.05	31.5	5.17	20.0
<i>Harpephyllum caffrum</i>	0.00	13.1	0.00	7.50
<i>Protorhus longifolia</i>	0.00	19.7	0.00	40.0
<i>Vepris lanceolata</i>	0.12	9.21	0.00	10.0

Subcanopy (fs), Margin Canopy (mc) and Margin Subcanopy (ms). The first division divided samples into subcanopy plots and canopy plots. Within the 30 subcanopy plots of the first group there were five misclassified canopy plots. Within the 26 canopy plots of the second group there were two misclassified subcanopy plots. These strong groupings are evidence of a significant difference in composition between the canopy and subcanopy layers.

Demography

The size-class distributions of the nine most common canopy species are shown in Fig. 3. Other species were too rare to create meaningful size-class distributions. The ratios of small stem to large stems (< 10 cm DBH / > 10 cm DBH) and stem density are shown for these nine species in mature forest and in forest margins (Table 1). The stem density indicates relative abundance in margins and forest.

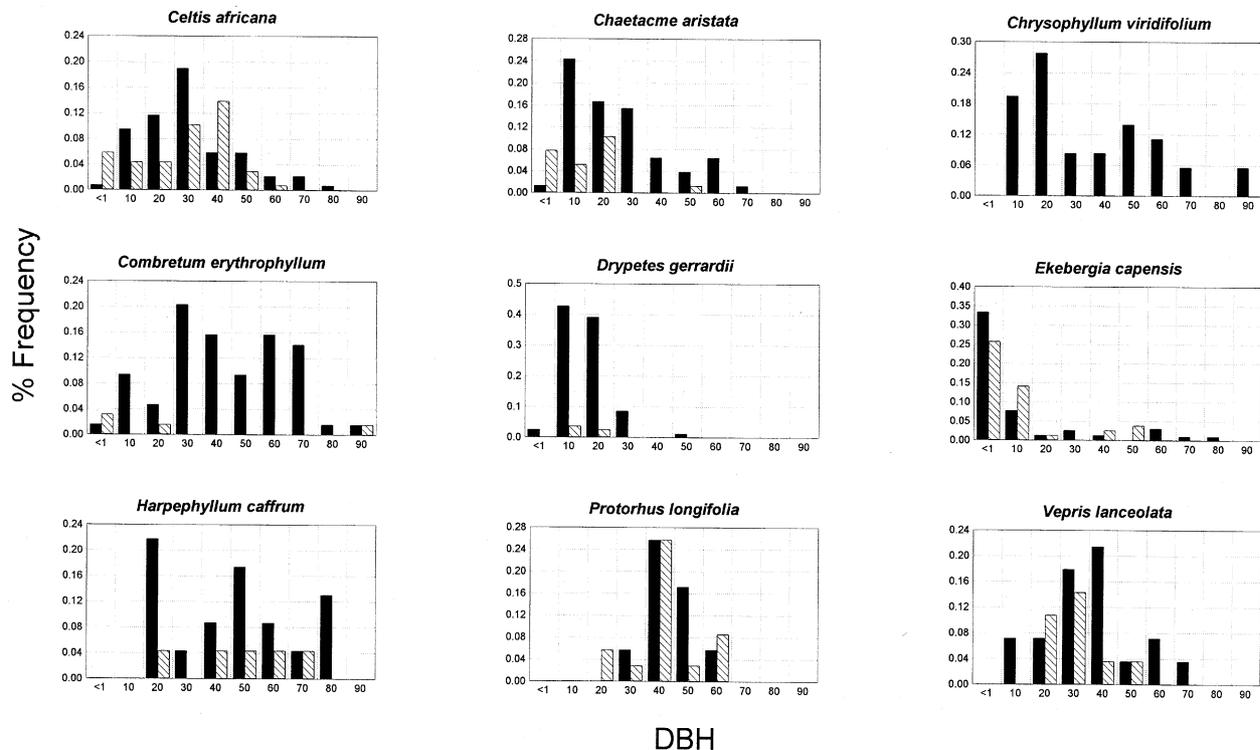


Fig. 3. Size-class distributions of the nine most common tree species in Hluhluwe Forest in closed forest and forest margins (Solid bars = Forest; bars with diagonal hatching = Margins).

Table 2. Differences between numbers and densities ($/m^2$) of *Celtis africana* seedlings (< 25 cm tall) and recruits (> 25 cm but < 2 m tall) under canopy (non-gaps) and in gaps.

	Sample	area (m^2)	No. of stems	density	χ^2 ($/m^2$)	$p <$
Seedlings	Plots	8400	4	0.0005	14.70	0.0001
	Gaps	4838	15	0.0031	(d.f. = 1)	
Recruits	Plots	8400	5060	0.6024	2264.68	0.0000
	Gaps	4838	100	0.0207	(d.f. = 1)	

Only one species, *Ekebergia capensis*, has a ratio of > 1 in the mature forest and shows a true negative exponential curve indicative of shade-tolerance and successful, subcanopy regeneration (Table 1, Fig. 3). *Chrysophyllum viridifolium*, *Drypetes gerrardii* and *Chaetacme aristata* have distributions that approximate a negative exponential curve, but they lack regeneration in the first size class (Fig. 3). All the other species examined here have ratios of < 1 in the forest and exhibit unimodal or bimodal shaped curves with very low levels of recruitment (Table 1, Fig. 3). Three species, *Chaetacme aristata*, *Drypetes gerrardii* and *Ekebergia capensis*, have ratios > 1 in the forest margins (Table 1). However, species like *Chrysophyllum viridifolium*, *Harpephyllum caffrum*, *Vepris lanceolata* and *Protorhus longifolia*, a common component of margins, do not seem to be recruiting at all in the margins (Table 1).

Table 3. Relative abundance of the dominant species in each patch (putative large disturbance) versus all forest plot data. The frequency of each species (%) is shown, with number of stems sampled in parentheses. The null hypothesis that tree species frequency was equal in patches and forest was tested for by χ^2 .

Patch	Species	% of patch (n)	% of forest (n)	χ^2	$p <$
1	<i>Protorhus longifolia</i>	63% (24)	4.0% (261)	32.62	0.0000
2	<i>Calodendrum capense</i>	32% (19)	0.0% (261)	63.98	0.0000
3	<i>Protorhus longifolia</i>	62% (13)	4.0% (261)	39.88	0.0000
4	<i>Harpephyllum caffrum</i>	16% (19)	1.0% (261)	15.45	0.0001
	<i>Protorhus longifolia</i>	47% (19)	4.0% (261)	34.53	0.0000
5	<i>Margaritaria discoidea</i>	25% (16)	11% (261)	27.52	0.0000

Tree-fall gap dynamics

In the 20 tree-fall gaps sampled, five species were identified as gap makers. *Combretum kraussii* occurred as a gap maker in five gaps, and was the only species occurring more than once in this role. There were 19 species of potential gap-takers recorded. Of potential canopy species, the most frequently occurring gap-takers, *Chrysophyllum viridifolium*, *Combretum kraussii* and *Chaetacme aristata*, appeared three times each. Advanced regeneration from subcanopy species, such as *Englerophytum natalense*, often filled tree-fall gaps. No

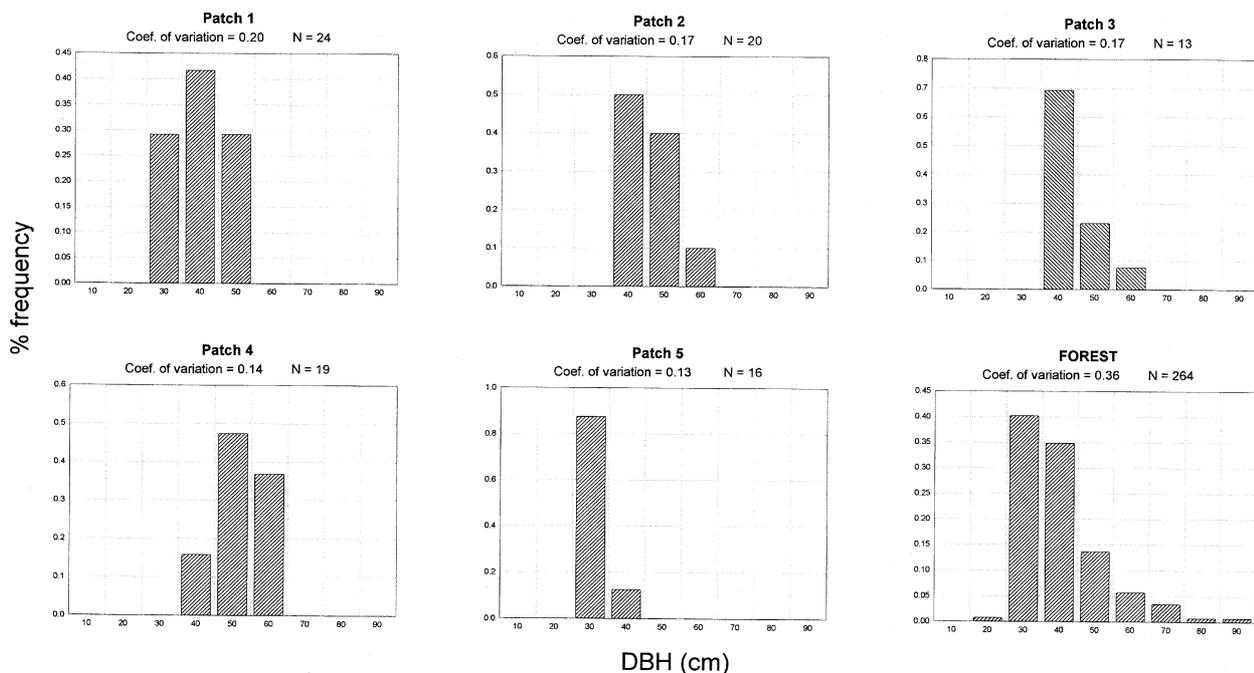


Fig. 4. Frequency distribution of DBH of all canopy trees over 20 cm DBH sampled in Patches (putative large disturbances) and in Forest plots.

specific replacement patterns were observed. In general, recruitment in tree-fall gaps was extremely poor and did not differ substantially from the closed canopy forest. The largest gap sampled was 800 m², with the average size being 240 m².

Due to the low levels of recruitment occurring in the forest and the gaps, only one species, namely *Celtis africana*, was found in sufficient numbers to allow a comparison of recruitment between the forest and tree-fall gaps. This comparison, of density of seedlings (< 25 cm high) and understorey recruits (between 25 cm and 2 m high) in gaps and non-gaps, shows that the density of seedlings was much lower, while the density of understorey recruits was much higher, in gaps than in non-gaps (Table 2). Thus, we infer for *Celtis africana* that survivorship of seedlings in gaps is higher than in the forest as a greater proportion of seedlings grow into the recruit class from gaps.

Patchiness and Large-scale disturbance

The relative abundance of the dominant species in all patches is significantly greater than the average abundance in the forest (Table 3). The frequency distributions of the DBH of trees in patches have lower coefficients of variation than that found for canopy trees over 20 cm DBH in the forest (Fig. 4). The areas of the patches are significantly ($p < 0.0093$) larger than that of the gaps (Table 4).

Discussion

Grain

The TWINSpan classification shows canopy and subcanopy components of individual plots to be distinct from one another. This is indicative of a coarse-grained forest (Midgley et al. 1990) and reflects the situation of light-demanding canopy species and shade-tolerant understorey species. In a fine-grained forest, canopy and subcanopy composition are generally similar (Midgley et al. 1990).

Size-class distributions

In forests in which gaps comprise a small part of the forest area, such as Hluhluwe Forest, shade-tolerant species should exhibit negative exponential curves (Everard et al. 1995). This negative exponential curve reflects the situation of many small individuals and few large individuals. A forest species with this type of frequency distribution would appear to be successfully regenerating under the canopy, awaiting a gap for

Table 4. Comparison of median area between patches (hypothesised to be created by large disturbances) and tree-fall gaps. Means tested for significant difference by Kruskal-Wallis.

	Median (m ²)	n	χ^2	p <
Patches	2100	5	6.77	0.0093
Gaps	200	20	(d.f. = 1)	

advancement into the canopy. In shade-intolerant species, recruits cannot develop under the canopy and regeneration is limited to sprouting and gap recruitment. This type of species would typically have a greater number of large than small individuals, and would thus exhibit a much flatter, or even bell-shaped, curve (Everard et al. 1995) under conditions of infrequent gap disturbance.

The size-class distributions are typical of a coarse-grained forest. Most canopy species display low ratios of small:large stems, indicating a lack of regeneration in the smaller size classes. Species with this demography would seem to be persisting in the form of a few large individuals until large-scale disturbance enables them to recruit once again.

Species that do have higher small:large stem ratios generally lack recruits in the first class (< 1 cm DBH) and are not visibly recruiting under the canopy. This could well be due to the effects of browsing by *Tragelaphus angasii* (Nyala) and *Cephalophus natalensis* (Red duiker) in this forest. Certainly regeneration failures due to grazing impact have been documented in other forests (Tilghman 1989) and this is an avenue for future research. For *Protorhus longifolia* a lack of individuals < 10 cm (DBH) suggests an absence of, rather than intermittent, recruitment.

In the forest margins, recruitment levels are not uniformly different from the closed forest (Table 1). This suggests that expansion of currently dominant canopy species is not occurring through their regeneration in the margins. In fact, the TWINSpan classification does not distinguish between margin and forest plots.

Tree-fall gap dynamics

It is apparent that unless the disturbance has created a sufficiently large gap, the canopy will be filled by advanced regeneration from shade-tolerant subcanopy species, or by lateral infill from surrounding trees. This was seen on numerous occasions and further supports the coarse-grain designation for this forest, as coarse-grained forests typically require large-scale disturbances in order to maintain species diversity.

Tree-fall gaps positively influence the reproduc-

tive success of certain species. For *Celtis africana* there is an increase in understorey sized plants in gaps compared with non-gaps. There is also far lower density of seedlings in these gaps. The numerous seedlings produced under intact forest canopy, presumably below con-specific adults, rarely attain a size of > 5 cm (pers. obs.). This implies that survival and growth to the following size class of the seedlings is greatly enhanced in gaps.

Despite this, gaps seem to be relatively unimportant in terms of regeneration success in the Hluhluwe forest. Most of the dominant canopy trees of this forest are apparently shade-intolerant species incapable of advanced regeneration and many species do not seem to be recruiting at all. These species are not able to establish in the small gaps created by standing tree death or branch fall. Much larger gaps, such as those caused by multiple tree fall or fire, might allow regeneration of these species. However, no direct evidence of large-scale disturbance was seen in the forest under the current disturbance regime. Nevertheless, by employing indirect methods, old areas of large-scale disturbance could be detected.

Patchiness and large-scale disturbance

Three lines of evidence support the previous existence of large-scale gaps currently filled by patches of even-aged canopy species. Firstly, the abundances of the dominant shade-intolerant species were significantly higher in patches than in forest. Secondly, these patches had a median area of 2100 m², which is significantly larger than normal forest gaps. Thirdly, there was a small range in DBH sizes of canopy trees in the patches compared with the rest of the forest.

In addition to the evidence above, a carbon isotope study was performed on trees cored in these patches. This isotope study was aimed at creating a technique with which to examine past regeneration environments (West 1999; West et al. in press). In this study, it was demonstrated that the ratio of ¹³C/¹²C in tree cores could be used to differentiate between trees that grew up under a canopy or in small gaps and those that recruited in open areas or large gaps. The results showed that the isotopic ratios of trees from the Hluhluwe patches differed significantly from trees in the closed forest (and hence small gaps), indicating that they recruited as a cohort in a large clearing (West et al. in press).

Thus it appears as if large-scale disturbance played a part in the establishment of the current shade-intolerant canopy communities of Hluhluwe Forest. Establishing the potential cause of this disturbance is a very interesting problem.

Hypothesis on the origins of coarse-grained forest in Hluhluwe

The forest of Hluhluwe-Umfolozi Park does not seem to undergo any major disturbance at present. Human impacts are minimal, consisting mainly of small-scale poaching of medicinal plants and trees. Lightning induced fires are rare in the forest although in time of drought they may occur. Hurricanes occur extremely infrequently and do not create blow-down disturbance in South African forests (Midgley et al. 1997). Multiple tree-fall gaps were not observed in this study. There does not seem to be any evidence for extremely intensive grazing occurring, nor is there historical evidence of elephants occurring in this forest (Brooks & Macdonald 1983). Thus, the question arises of how patches of light-demanding canopy species originated and still exist. It would seem that disturbance was more prevalent in the past than at present, and the most probable cause for this would be anthropogenic impacts.

The KwaZulu-Natal area has been utilised by indigenous peoples for swidden agriculture and iron-smelting for roughly 1700 yr (Hall 1981; Deacon 1992; Scholes & Walker 1993). This iron-age lifestyle required a large timber supply and has been identified as a potentially landscape transforming epoch (Feely 1980; Hall 1984a, b). We hypothesise that such a lengthy period of low-density swidden agriculture and associated iron-age practices induced a patchy forest composed of fast-growing, shade-intolerant species. When the reserve was proclaimed in 1895 (Brooks & Macdonald 1983), the anthropogenic impacts were phased out. This allowed the maturation of these species into the closed canopy community seen today.

Additional archaeological evidence and isotopic techniques could test this hypothesis. The analysis of soil carbon isotopes has been used to show vegetation change (Ambrose & Sikes 1991; Bond et al. 1994; Pessenda et al. 1996; Desjardins et al. 1996; Connin et al. 1997). The possibility for application of this technique to human generated disturbances and old agricultural lands is an exciting point for further research (West 1999). This hypothesis could apply to other coarse-grained forests on the Eastern seaboard of South Africa. Forests where present disturbance is minimal and where there is a history of human settlement would be ideal for further investigation.

Conservation implications

It seems likely that forests such as Hluhluwe Forest have been impacted by humans in the past to such an extent that the forest composition was substantially altered and the legacy of this continues today (Foster et al. 1999). The trees now dominating the canopy, having recruited during times of patch-scale disturbance, are now unable to recruit under a so-called 'natural' treefall disturbance regime in the forest reserves. It is important for conservation authorities to realise the processes involved in the creation of current vegetation compositions and to factor this into their targets and strategies for conservation. It would seem that a review of the relative importance of natural disturbance in controlling these systems is called for.

The incorporation of human utilisation into forest management and conservation is an idea slowly gaining momentum (Noble & Dirzo 1997; Dejong 1997; Foster et al. 1999). In forests such as Hluhluwe Forest, judicious harvesting by local communities could be mutually beneficial to the reserve and the local people. The key problem is to regulate the harvesting in a manner compatible with management goals, traditional land use and the ecology of the species. Thus, in any management plan of this nature there is a need for (a) a clear statement of management goals, (b) clear communication with the local communities, and (c) monitoring, enforcement and follow-up. The recognition that adaptive management is needed is important, since an episodic, extreme disturbance might not have been observed in this study.

In Hluhluwe, the harvesting of shade-tolerant species, based on a sound forest model and management plan focusing on certain patches and controlling for soil damage etc., may well aid the recruitment of shade-intolerant species by imposing a more appropriate disturbance regime for the maintenance of forest diversity. If this strategy can be proven in this and other areas, there should be significant implications for Southern African conservation.

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