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Dynamics of the forest vegetation of the Umtiza Nature Reserve, East London

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Keywords: dynamics, eastern Cape, forests, grain, size-class distribution

ABSTRACT

The forest community at the Umtiza Nature Reserve near East London was surveyed using 24 plots (0.04 ha) in which all woody stems >0.5 m tall were enumerated. Based on a classification using numbers of stems of canopy species, it was assumed that basically only one forest community was sampled. Further multivariate analyses suggest that this forest is fine-grained. Sample plots were similarly placed in ordination space irrespective of whether woody species occurrence was used as importance value or if species occurrence per size class was used separately [seedlings (0.5–1.0 m), saplings (1–5 m) or canopy individuals (>5 m)]. An analysis of size-class distributions of the most common canopy species indicated that the majority of species exhibited inverse J-shaped size-class distributions. This is the expected pattern for a fine-grained forest. In these measures of dynamics, this forest is not fundamentally different to the more temperate Afromontane forests.

UITTREKSEL

'n Opname is gemaak van die woudgemeenskap in die Umtiza-natuurreservaat naby Oos-Londen; alle houtagtige stamme >0.5 m hoog is in aanmerking geneem. Gebaseer op 'n klassifikasie waarin aantal stamme van blaredakspesies gebruik word, is daar aangeneem dat basies slegs een woudgemeenskap ingesluit is. Verdere veelvoudige variantanalises dui daarop dat hierdie woud fyn gegrein is. Monsterpersele is eenders in ordinasieruimte geplaas ongeag of voorkoms van houtagtige spesies as belangrikheidswaarde gebruik is en of voorkoms van spesies per grootteklas afsonderlik gebruik is [saailinge (0.5–1.0 m), jong bome (1–5 m) of blaredak-individue (>5 m)]. Ontleding van grootteklas-verspreidings van die mees algemene blaredakspesies het getoon dat die meeste spesies omgekeerde J-vormige grootteklas-verspreidings vertoon het. Dit is die verwagte patroon vir 'n fyngrein-woud. In hierdie metings van dinamika, verskil hierdie woud nie fundamenteel van die meer gematigde Afromontaanse woude nie.

INTRODUCTION

In brief, forest dynamics is the complex product of interactions between disturbance regime (e.g. type of disturbance, turnover rate), life histories of constituent species along a shade-tolerant to shade-intolerant continuum and particulars of the regeneration arena (e.g. regeneration bottlenecks due to biotic or abiotic events). As such the study of dynamics needs several inputs. In this preliminary study we concentrated on aspects of the grain and life history components of dynamics. By life histories we mean whether a species is relatively shade-tolerant 'climax' or shade-intolerant 'pioneer' and this we have inferred from size-class distributions.

By grain we mean 'the mosaic of structural phases' (Whitmore 1989); or the spatial patterns of seedlings/saplings and canopy individuals of the different species. Coarse-grained forests tend to have at least some (recently disturbed) areas which are dominated by shade-intolerant species. When plotted in ordination space, coarse-grained forests should show clear separation of plots according to whether pioneers or climax species are present, especially when their sizes are considered. In fine-grained forests most species can regenerate close to adults and therefore there are no great differences in species composition or size-class distributions amongst plots. In other words the successional process occurs on a small spatial scale in fine-grained forests.

Recent work has shown that in many different forests at any one time gaps occupy about 1–2% of the area (Barden 1989; Connell 1989). In forests not subject to catastrophes these values suggest that stems in the small size classes of shade-intolerant species should be rare in comparison to the large bank of advance regeneration of shade-tolerant species. Thus the size-class distributions of shade-intolerant species should be flatter than those of shade-tolerant species. A forest comprised of many species with relatively flat size-class distributions should thus be a relatively coarse-grained forest.

Very little has been published on the dynamics of South African forests. At the moment there is therefore no model to predict the grain of a South African forest either for a given environment (e.g. climate and soils) or for forest structure (e.g. whether there is a preponderance of large or small-sized individuals). Midgley *et al.* (1990) indicated that the southern Cape forests [part of White's (1983) Afromontane Forest type] were extremely fine-grained. At the scale of 0.04 ha plots, most species were able to recruit continuously and most canopy species were shade-tolerant. This was interpreted as being due to the unproductive environment (cool climate, poor soils) and conservative disturbance regime (few large gaps) which has favoured shade-tolerant species and restrained both woody and herbaceous shade-intolerant species.

In contrast to the southern Cape forests, our working hypothesis for tropical and subtropical gap-phase forests,

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such as are found at our study site, is that they can be expected to have a greater component of shade-intolerant species, of both herbaceous and woody types. This is due to their situation in a more productive environment (higher temperatures, summer rainfall) which increases the opportunities for regeneration of fast-growing pioneer species. Such forests should therefore be more coarse-grained due to intermittent recruitment of shade-intolerant canopy dominants leading to spatially segregated size classes. Thus an ordination or classification of sample plots using the occurrence of a species in the seedling, sapling or canopy size classes, should reveal spatially distinct groups in a coarse-grained forest. In a fine-grained forest, where species are able to regenerate close to their own adults, data of species occurrence by size class should have little influence on classifications or ordinations.

Our survey was done in a coastal forest of the eastern Cape. According to Acock's (1988) classification these forests appear to fall between the Coastal Tropical Forest Type (Veld Type No. 1) and Valley Bushveld (Veld Type No. 23). White (1983) mapped these forests as the Tongaland-Pondoland Forest type and most recently they have been mapped as Dune Thicket (Lubke, Tinley & Cowling 1988). Information on forest dynamics in the eastern Cape is conspicuous by its absence in the overview of vegetation in the eastern Cape by Lubke, Tinley & Cowling (1988) and in Everard (1987).

Our objectives were to use information from plots to: 1, briefly describe the vegetation; 2, compare ordinations of plots using information on presence/absence of potential canopy species in the seedling, sapling or canopy layers, to infer grain; and 3, analyse the size-class distributions of the important species to infer their life histories.

STUDY AREA

The study area is situated in the Umtiza Nature Reserve (33°02'S; 27°47'E) which is located on a northeast-facing slope of the Buffalo River Valley, about 10 kilometres from East London. Thicket/forest vegetation covers about 550 ha of the reserve. One of the aims of this reserve is to afford high conservation status to two forest tree species: *Umtiza listeriana* Sim, belonging to a monotypic genus of the Fabaceae, and *Buxus macowanii* Oliv., the box-wood much exploited in the eastern Cape in the past.

Maximum altitude in the reserve is 180 m and many streams dissect the area giving it a variety of aspects. The geology of the area has been mapped as Beaufort Group (Rust 1988) and the soils are mapped as weakly developed soils on rock with black to brown clays and clay loams (Hartmann 1988).

At East London, annual precipitation is 919.2 mm which falls mainly in summer. Mean maximum and minimum temperatures are 22.7°C and 14.0°C respectively. East London is extremely windy (mean wind speed of 4.7 ms^{-1}) as opposed to Cape Town (4.0 ms^{-1}) and George (2.5 ms^{-1}). (Climate information from Weather Bureau, Pretoria.)

METHODS

Sampling

The broad vegetation communities of the Umtiza Nature Reserve were mapped from aerial photographs and essen-

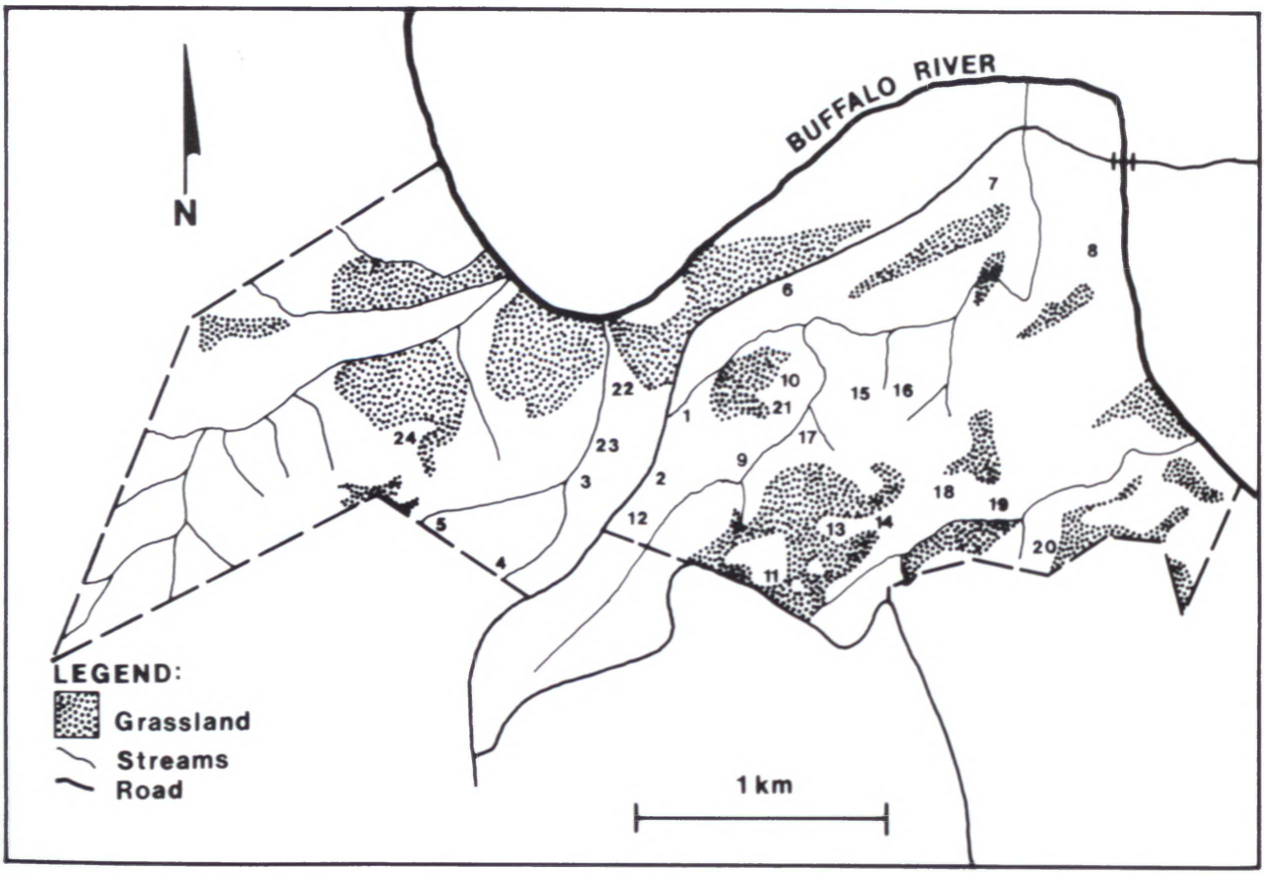

FIGURE 1.—The location of the 24 sample plots at the Umtiza Nature Reserve in the eastern Cape. The shaded-in areas represent *Acacia karroo* grassland and the clear areas forest.

TABLE 1.—A species list, based on 24 sample plots, of the forest vegetation of the Umtiza Nature Reserve

	Numbers of plots		
	Seedlings (0.5–1 m)	Saplings (1–5 m)	Canopy individuals (>5 m)
Acacia karroo	–	–	1
Acalypha glabrata	–	–	1
Acokanthera oppositifolia	1	2	1
Allophylus decipiens	11	6	7
Apodytes dimidiata	–	–	2
Brachylaena discolor	7	2	2
B. elliptica	8	5	4
Buxus macowanii	13	12	16
Calodendrum capense	–	–	1
Canthium inerme	4	5	–
Carissa bispinosa	6	8	1
Cassine aethiopica	2	1	2
C. crocea	–	1	5
C. tetragona	2	2	5
Celtis africana	1	1	1
Chaetacme aristata	7	6	12
Clausena anisata	1	1	–
Coddia rudis	2	7	2
Commiphora harveyi	–	1	–
Croton gratissimus	1	1	–
Cussonia spicata	8	12	9
Dalbergia obovata	1	–	4
Diospyros simii	1	1	–
D. dichrophylla	3	2	2
D. whyteana	5	4	4
Dovyalis caffra	2	1	–
D. rhamnoides	–	1	–
D. zeyheri	1	1	–
Ehretia rigida	–	1	–
Ekebergia capensis	1	–	–
Erythrina caffra	1	2	1
Encephalartos altensteinii	–	1	–
Euclea natalensis	10	6	9
E. schimperi	1	1	2
Eugenia capensis	2	2	3
Euphorbia triangularis	1	2	1
Grewia occidentalis	3	2	1
Halleria lucida	–	1	–
Harpephyllum caffrum	4	1	16
Hippobromus pauciflorus	5	2	1
Hyperacanthus amoenus	8	3	3
Ilex mitis	4	3	–
Kiggelaria africana	–	–	1
Maerua racemulosa	12	9	1
Maytenus heterophylla	6	5	7
M. peduncularis	2	2	4
Mimusops obovata	1	1	3
Monanthotaxis caffra	2	3	1
Nuxia congesta	2	–	1
Olea capensis	9	7	5
O. europaea subsp. *africana*	–	1	1
O. woodiana	10	5	18
Olinia ventosa	1	–	–
Pavetta lucida	–	1	–
Pittosporum viridiflorum	1	1	1
Pleurostylia capensis	8	2	4
Podocarpus falcatus	–	–	1
Psychotria capensis	–	1	–
Ptaeroxylon obliquum	11	2	17
Rhus chirindensis	2	2	6
R. natalensis	1	1	–
R. undulata	1	–	–
Schotia latifolia	3	–	6
Scolopia mundii	4	3	1
S. zeyheri	6	7	8
Scutia myrtina	4	1	9
Sideroxylon inerme	–	–	1
Strychnos henningsii	–	1	3
Suregada africana	2	3	7
Trichocladus ellipticus	1	1	2
Trimeria grandiflora	–	1	1
Triumfetta pilosa var. *effusa*	1	–	–
Umtiza listeriana	6	4	11
Vepris undulata	13	3	8
Zanthoxylum capense	11	4	3
Z. davyi	5	3	1

tially two types were found to occur; an *Acacia karroo*/grassland and a thicket/forest type. A grid was placed over a 1:10 000 map of the reserve and 24 sites were selected at random in the forest communities (Figure 1). At each site a square plot of 20 × 20 m was laid out and all woody plants >0.5 m tall were enumerated. These plots were demarcated permanently for further studies on disturbance, mortality and growth. At each sample plot each stem was allocated to one of three size classes: seedlings (0.5–1.0 m in height), saplings (<5 m in height) and canopy (>5 m). Stem diameter at breast height (dbh) was measured for stems >5 m. Identifications were made in the Albany Herbarium, Grahamstown. Nomenclature follows Gibbs Russell *et al.* (1987). The forest canopy ranged from 5–8 m in height with an occasional emergent up to 15 m. At each plot, slope and aspect were noted and two soil samples were taken for standard chemical analyses by the Agricultural Research Institute at Dohne.

Analysis

Initially we classified the forest vegetation using the multivariate package TWINSPAN (Hill 1979a), with numbers of stems as the importance values and the default settings of the package. In total about 60 species occurred in the canopy (>5 m in height; Table 1) in our 24 plots. By using species occurrence in seedling, sapling or canopy levels as separate species, we could increase the apparent number of 'species' to about 150 and the apparent number of 'plots' to 72.

In the second part of this study we used multivariate techniques to represent grain or succession in space. Multivariate techniques have long been used for discerning successional trends, e.g. Fox (1990) used community trajectories in multivariate space to study mammal succession over time. We made comparisons between classifications and ordinations of plots but using the two data sets (i.e. 60 spp. versus 150 'spp.' and 24 versus 72 'plots'). The eigenvalues produced by an ordination/classification give an indication of the variance explained by an axis [low eigenvalue (<0.5) = poor separation of samples]. The breadth of an ordination axis gives an indication of the homogeneity amongst samples, with a value of 400 (4 s.d.) indicating that species occurring at one end of an axis are almost completely absent at the other end (Hill 1979b). At this stage there are no rigorous tests for comparing ordinations, although some progress has been made (Grossman, Nickerson & Freeman 1991). We merely visually inspected the package outputs for differences in eigenvalues and breadth of axes, for the various classifications/ordinations we performed.

We also calculated the position of centroids for ordinations of plots using presence/absence of canopy species in seedlings, saplings and canopy size classes separately. A meaningful successional trajectory would be indicated by significant directional trend in ordination space as defined by information from each size class.

Our expectations were that in a coarse-grained forest, significantly different eigenvalues or breadth of axes would result when data from each size class were used separately, rather than when information about the canopy layer only, was used. We expected centroids to be widely separated in ordination space when species by size-class information was incorporated.

For the second part of the study, the DECORANA (DCA-option)/TWINSPAN packages (Hill 1979a, b) were again used. Presence/absence (due to the great discrepancies in numbers of stems amongst size classes) was used as the importance value, and again we used the default settings of the package.

RESULTS

Environmental data

Soil colours recorded included very dark brown, dark red-brown, dark brown and brown-black, and soil texture was sandy clay loam. The soils also had a relatively high pH and calcium content (Table 2). Slopes were mostly gentle and aspect was predominantly between 90° and 270°.

Vegetation description

Very little phytosociological data have been published on the eastern Cape forests and thickets. Furthermore, vegetation patterns are complex (see Acocks 1988). For this reason we have appended an annotated species list (Table 1). The maximum number of stems observed per 0.04 ha sample for the canopy size class was 74, for seedlings it was 454 and for saplings 25. The maximum number of seedlings per sample plot was high for the following species: *Ptaeroxylon obliquum* (421), *Buxus macowanii* (189) and *Ilex mitis* (256). Species richness per 0.04 ha of woody plants ranged from 13–36.

The separation of the forest into types, based on abundance of canopy individuals, was weak (eigenvector = 0.376). Furthermore, axis 1 was only a maximum of 2.5 s.d. units broad and axis 2 only 2.3 s.d. units. This probably reflects the overlapping distribution of the common species and many rare species (Table 1). Down-weighting for rare species made a negligible difference in eigenvalues. We have taken this weak separation of types and small spread in ordination space of the forest to indicate that only one vegetation community was present. Most of the canopy species are well represented in the seedling and sapling (Table 1) size classes. Essentially the forest is dominated by *Ptaeroxylon obliquum, Harpephyllum caffrum, Olea woodiana, Chaetacme aristata, Umtiza listeriana* and *Buxus macowanii* (see Table 1).

TABLE 2.—Environmental information pertaining to the study area. For slope and aspect classes, numbers represent numbers of plots. Values in brackets indicate the variance

Slope classes			
0–10°	10–20°	20–30°	
13	7	4	
Aspect classes			
0–90°	91–180°	181–270°	271–360°
2	8	8	6
Soil chemistry (means)			
pH	%C	Na (ppm)	Ca (ppm)
5.5 (0.3)	195 (0.3)	0.9 (0.2)	14.2 (46.7)

TABLE 3.—Sample plots belonging to first two groups, and associated eigenvalues, produced by TWINSPAN using presence/absence data for canopy species (60 spp.) and canopy species in three size classes separately (about 150 spp.)

Only canopy species	Canopy species per size class
(eigenvalue = 0.26)	(eigenvalues = 0.29)
group 1 (sample plots) 17, 9, 21, 19, 24, 11, 18, 22, 23, 14, 20, 13, 15, 16	group 1 (sample plots) 13, 15, 16, 17, 14, 22, 18, 24, 11, 20, 23, 19, 9, 21
group 2 (sample plots) 3, 2, 4, 6, 12, 1, 5, 10, 7, 8	group 2 (sample plots) 3, 7, 8, 4, 6, 12, 1, 2, 5, 10

Vegetation dynamics

The groupings of samples produced at the first division using 60 species (i.e. only canopy species) versus 150 species (i.e. canopy species per size class separately), whilst having different orderings, were identical (Table 3) and both had similar and small eigenvalues (0.26 compared to 0.29). This indicates that species by size-class data do not produce a different classification or a different separation of samples.

The ordination using 72 'plots' and the 60 canopy species shows considerable overlap of the three size-class groups (Figure 2A, B, C). This is clearly depicted by the similarity of position of each centroid and their relatively close proximity to the origin. There is no suggestion of orderly directional trend of movement of centroids. This could indicate that there is no consistent difference in successional status amongst plots. The spread along the first ordination axis is narrow (about 3 s.d.) and the eigenvector was also small (0.279).

Size-class distribution

Most of the common canopy species have typical inverse J-shaped size-class distributions (Table 4). To this group could be added many of the less common species we encountered but which had similar size-class distributions. This includes species such as *Maytenus heterophylla, M. peduncularis, Cussonia spicata, Euclea natalensis, Brachylaena elliptica* and *Olea capensis* subsp. *capensis*.

DISCUSSION

We interpret the multivariate analysis to indicate that this subtropical forest is fine-grained. This forest is there-

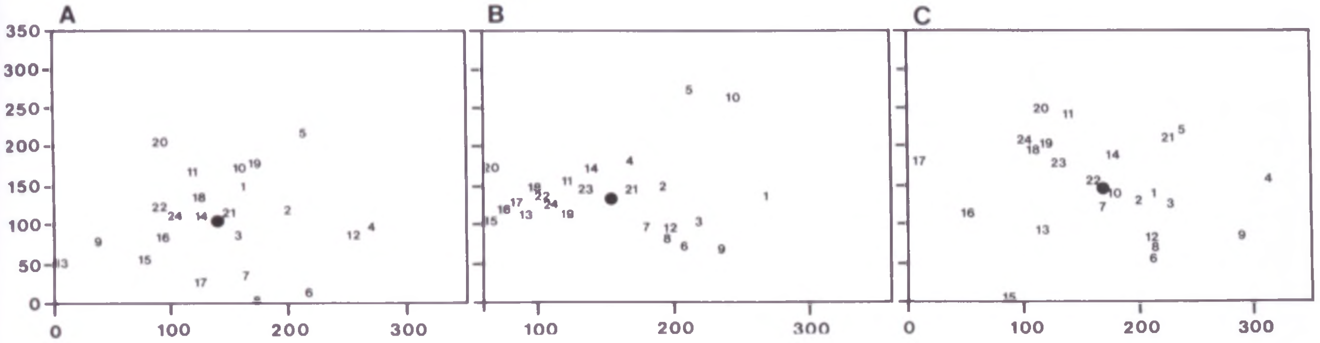

FIGURE 2.—Ordination diagrams using woody species in size classes: A, canopy; B, seedling; C, sapling. All 72 plots were ordinated together but represented separately for clarity. The dots indicate the centroids. In A, samples 22 and 23 are superimposed.

TABLE 4.—Numbers of individuals per size class of the most common canopy species encountered in the Umtiza Nature Reserve

Species	Height (m)		dbh (cm)						
	0.6–0.99	1–5	<10	<15	<20	<25	<30	<35	>35
Buxus macowanii	1 045	279	305	63	13	2	–	–	–
Olea woodiana	123	29	44	26	16	14	12	10	8
Ptaeroxylon obliquum	947	4	16	16	16	11	3	–	2
Umtiza listeriana	46	25	32	15	9	7	1	4	2
Vepris undulata	221	58	8	3	4	–		2	2
Scolopia zeyheri	38	18	11	3	2	–	1	–	–
Harpephyllum caffrum	18	2	9	4	3	4	2	4	9
All stems	3 867	1 229	679	206	100	66	36	27	42

fore fairly similar to the more temperate southern Cape forests (Midgley *et al.* 1990). Both have an abundance of species with inverse J-shaped size-class distributions and co-occurrence of different size classes within a species. These results indicate that large-scale disturbances are not important in determining community composition of both these forest types.

From a conservation perspective, because the shifting mosaic of structural phases (sensu Whitmore 1989) is fine-grained (or stationary) at Umtiza, relatively small patches of forest may be viable because most species can regenerate on a small spatial scale. Obviously, other factors need to be taken into account (edge effects, visits by dispersers) to complete the picture. We predict that the disturbance regime at Umtiza will be conservative (preponderance of small gaps) and that advance regeneration will inherit most gaps.

Finally, it is clear from this survey that *Umtiza listeriana* and *Buxus macowanii*, the two species of special conservation importance, are both abundant and apparently regenerating adequately. They appear to be well conserved in the Umtiza Reserve.

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