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ANNEXURE 1

Fourie, A.B., Matthews, W.S. & Hattingh, R.P. 2002. Vegetation induced variability of hydraulic characteristics of Aeolian sand. Proc. 3rd International Conference on Unsaturated Soils, Recife, Brazil, March 2002, Vol.1, pp. 411–415.

Vegetation induced variability of hydraulic characteristics of an aeolian sand

A.B. Fourie
School of Civil and Environmental Engineering, University of Witwatersrand, South Africa

W.S. Mathews
KwaZulu-Natal Department of Nature Conservation, South Africa

R.P. Hattingh
PHD Consulting, Johannesburg, South Africa

ABSTRACT: There is a growing tendency to derive certain hydraulic characteristics of a soil, such as the water retention curve and saturated hydraulic conductivity, using empirical correlations with the particle size distribution. Useful as these relationships may be, the importance of other factors is recognised as influencing these empirical correlations, eg compaction density. This paper presents results that highlight another, somewhat neglected factor that may have a profound influence on the hydraulic characteristics of an aeolian sand. This is the impact of organic secretions or exudes produced by certain vegetation as a counter to the encroachment of other species. Based on field measurements presented in the paper, it appears as though these organic materials may significantly alter the water repellency of the sand, its water retention characteristics and its hydraulic conductivity. Although the findings should be considered preliminary at this stage, it highlights an area that requires further study.

1. INTRODUCTION

The Tembe Elephant Park in northern Kwazulu-Natal province of South Africa, in addition to having an extremely valuable elephant population, forms a central part of the IUCN International center of plant diversity. Southern Mozambique and the northern part of KwaZulu-Natal are recognised as a Centre of Plant Endemism, namely the Maputaland Centre [MC]. Sand Forest, also known as Licuati Forest in Mozambique, is more or less confined to the broad coastal plain between St Lucia in northern KwaZulu-Natal, South Africa, and Maputo in southern Mozambique—a region known as Maputaland. Forest stands occur as isolated patches mainly associated with ancient north-south trending inland sand dunes. A significant number of the endemics/near-endemics are associated with Sand Forest areas, making this perhaps the most remarkable plant community in the MC .

Field observations have shown that after extensive bushfires have occurred in these forests, the forest vegetation does not re-establish, but rather encroachment of grassland and woodland species takes place and the sand forest retreats. An extensive study was carried out using a neutron probe instrument to measure profiles of water content with depth over a period of over a year at a number of locations within the Park. Sites included healthy sand forest, recently burned forest, grassland and the indigenous woodland habitats. Although the soil conditions are extremely homogeneous in terms of particle size distribution across the study area, being aeolian in origin, the neutron probe profiles at some time after a particular rainfall event were very different.

2. CHARACTERISTICS OF SITE

The area is an extensive level plain of sandy soils, covered by open and closed woodland with patches of short and tall sand forest usually bordered by grassland. A noticeable feature of the sand forest in Tembe is its very sharp boundaries, which in most cases is defined by narrow zones of sparse vegetated to bare sand areas directly adjacent to the sand forest. These zones of bare sand are in most cases followed by grassland communities, with a general appearance reminiscent of pioneer areas. These strips bordering the sand forests were thought to be due to the trampling effect of game and were the subject of an investigation by Mathews et al (2001).

The continuing loss of valuable sand forest areas, particularly their inability to re-establish after bush fires, led to the above investigation, one of the aims of which was to investigate the potential of allelopathic interference amongst competing plant species somehow contributing to the loss of sand forest. A plant may interfere directly with the growth of its neighbours through either resource competition or chemical inhibition. This may take the form of what is known as allelopathic phenomena, whereby a plant may release toxic organic compounds into the environment. Under appropriate conditions, these chemicals are released in sufficient quantities to affect the growth and development of individuals of the same or other species. The substances are released into the environment through leaching of living plants, root exudates, volatilisation, residue decomposition and microbial activity.

It is not this potential allelopathic effect that is important in this study, but how these organic compounds may affect the hydraulic characteristics of a sand. Coupled with the effect of these organic compounds is how they alter (and thus further affect the hydraulic properties of a sand) upon burning. In the work by Mathews et al (2001), samples of sand from various locations were leached with methanol and a trace of the organic compounds present in the leachate obtained on a gas chromatograph. The most striking feature was that there were organic compounds (unidentified) present in the sand forest samples that were present in lesser quantities at the edge of the sand forest and not present at all in the grassland or woodland species. This observation should be borne in mind when considering the permeability and field moisture profiles described later in the paper.

A further complication that seems to arise at Tembe is that bush fires appear to alter the dynamics of the competition between various plant species. Current thinking is that the fires may alter the allelopathic organic compounds, thus changing the ability of one species to resist invasion by another species. Evidence of the effects that bush fires can have on soil characteristics is described below.

3. EVIDENCE FOR CHANGES IN PROPERTIES DUE TO WILDFIRES

In the fields of soil science and agriculture, the concepts of soil water repellency and the effect this may have on hydraulic characteristics is well-documented, eg Doerr et al (2000). It is generally associated with coarse-textured, sandy soils and as shown by De Bano (1991) is most likely to develop in soils with less than 10% clay content.

De Bano et al (1970) and Savage (1974) proposed a mechanism in which heated hydrophobic organic substances in the ground litter and topsoil volatise during burning and a proportion may travel downward into the soil, following a temperature gradient until they condense in a concentrated form, often forming a coating to the soil grains. This movement is easier in permeable, sandy soils. Aside from redistributing and concentrating these hydrophobic substances in the soil, Savage et al (1972) suggested that the heat generated during a fire improved the bonding of these substances to soil particles. It is also interesting to note that the extreme heat generated at the ground surface tends to destroy these substances, with the consequence that water repellent soil may be concentrated at some (usually relatively shallow) depth below the surface (Doerr et al, 2000). This was clearly shown by Scott and van Wyk (1990) who found that under unburnt pine plantations water repellent soils were very infrequent, although they did occur at all depths. In areas where high fuel load fires had taken place, strongly repellent soils were developed below the surface to depths of up to 15cm.

Changes to a soil which make it water repellent are also likely to alter other characteristics of the soil. Dekker and Ritsema (1994) found that an increase in the water repellency of a sandy soil decreased the water retention capacity of the soil, as would be expected.

4. SOME PROPERTIES OF THE TEMBE SAND

The cover sands of the Maputaland region are mainly aeolian in origin and consist of thin veneers of sandy topsoil. X-ray diffraction tests showed the percentage of silica oxide was not less than 94% in the samples tested, indicating that these cover soils consist mainly of sand. A typical grading curve is shown in Figure 1 and very little variation from this curve was obtained. The upper metre, if not more, can be assumed to be extremely similar across the four sites discussed later in the paper, at least as regards particle size distribution.

4.1 In-situ permeabilities

Tests were carried out at six different locations within the southern area of the reserve to determine the in-situ permeability of the aeolian sand and obtain some indication of its variability. The sites were chosen to provide a complete spread of the vegetation zones at Tembe and thus included sand forests and neighbouring grassland and woodland habitats as well as a relatively newly burnt section of sand forest. The tests were carried out using a Guelph permeameter (Reynolds and Elrick, 1985) and two tests at different depths were carried out at each location tested.

Table 1. Hydraulic conductivity measurements at Tembe

Site	Depth (cm)	Hydraulic conductivity (cm/sec)
Grassland	30	10^{-2}
	50	$2x\ 10^{-2}$
Forest edge	20	$7x10^{-3}$
	50	$3x\ 10^{-2}$
Sand forest	20	10^{-3}
	50	$5x\ 10^{-3}$
Deep sand forest	26	$3x\ 10^{-3}$
	51	$5x\ 10^{-3}$
Woodland	20	10^{-3}
	48	10^{-2}
Burnt forest	20	$4x\ 10^{-3}$
	59	10^{-2}

The results are summarized in Table 1 and the value given for permeability is effectively the field-saturated value. Given the extremely homogeneous nature of the sand, the variation in permeability is very pronounced. In particular, the grassland and woodland areas had noticeably higher permeabilities than did the sand forest. The recently burnt forest area also tended to have higher permeabilities than the unburnt forest soils. Of note at this site is the high permeability at a depth of 59cm, which is discussed later in terms of wettability tests.

Although there clearly seems to be significant differences in the measured permeabilities, with variations of one order of magnitude over short distances, one needs to be mindful of the inherent difficulties of carrying out permeability tests accurately.

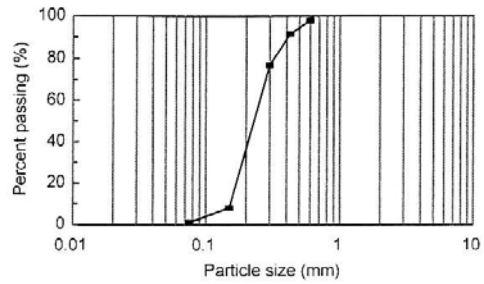

Figure 1. Typical particle size distribution curve for aeolian sand at Tembe

Further testing to determine whether the noted variation is statistically significant or not will be carried out in the near future and at present it is only possible to remark on the apparent variation, which appears to correlate with differences in prevailing vegetation. Although speculative at this time, it may be that if a sand forest area experiences a particularly high fuel-load fire, the organic material produced by the sand forest vegetation (as part of its allelopathic tendencies) is either volatised or fluidised and migrates vertically downwards into the sand, re-condensing at some lower depth to form a particularly hydrophobic layer. This removal of the hydrophobic organic material could explain the increase in permeability that is evident for the newly burnt forest as well as the area on the edge of the forest. More permeable soil may mean that establishment of new sand forest vegetation is more difficult and hence it is out-competed by the grassland vegetation, which then successfully encroaches into newly burnt areas. As indicated above, this is still speculative and a great deal more field testing is necessary.

Further evidence of the significant differences in hydraulic characteristics between adjacent areas that are similar except for the prevailing vegetation type is given in the following section which describes the measured profiles of soil moisture during one month of the rainy season at Tembe.

5 PROFILES OF WATER CONTENT MEASURED IN-SITU

The reported profiles of moisture content were obtained using a nuclear density probe, with the vertical access tubes installed some three months prior to the period for which results are reported here. The calibration of the instrument was checked by measuring the water content of constant-volume samples recovered during excavation for the access tubes and comparing these measurements with the instrument readings.

The two months preceding the time during which the reported measurements were taken were very dry, with a total of only 19mm rainfall. Rainfall during the month studied (October, which is the start of the rainy season) prior to the 22nd of the month totalled only 2½mm. On the 22nd and 23rd there was 22 and 32mm respectively, with very little further rain until the 30th.

The measured profiles of water content are shown in Figure 2, in terms of volumetric water content versus depth below ground surface. Although almost daily results were available, results are only shown for five particular days in order to highlight differences in response at the various sites. Results are shown for a site that was deep within a sand forest, a nearby recently burnt forest area (which had been subjected to a 'deep' burn), a grassland area adjacent to the sand forest and a woodland area.

At the start of the month (ie after the dry winter period) the profiles are relatively uniform, with water contents of only about 2 to 3%. These remained virtually unchanged until the start of the heavy rain on the 22nd of the month. These profiles can thus be considered to be the effective equilibrium profiles and, as shown later, are consistent with the form of the water retention curve reported later in the paper. The first set of readings obtained after the start of the rain was on the 24th of the month and there are striking differences in the response of the various sites to what was the same rainfall event. Firstly, penetration of water into the sand forest soil seemed to occur to a greater depth during the two days after the start of the rain than in the other profiles. It also appeared to get wetter, with values in excess of 12% being reached at 60cm depth. In the woodland area on the other hand, the water content did not rise above 10% and increases in water content were confined to a horizon above a depth of about 70cm, with virtually no penetration of water occurring below this depth. At first glance this appears to be contradicting the measured field permeabilities, since the woodland values were typically about an order of magnitude higher than the forest soil values and one may therefore expect the water to penetrate to greater depth in the woodland

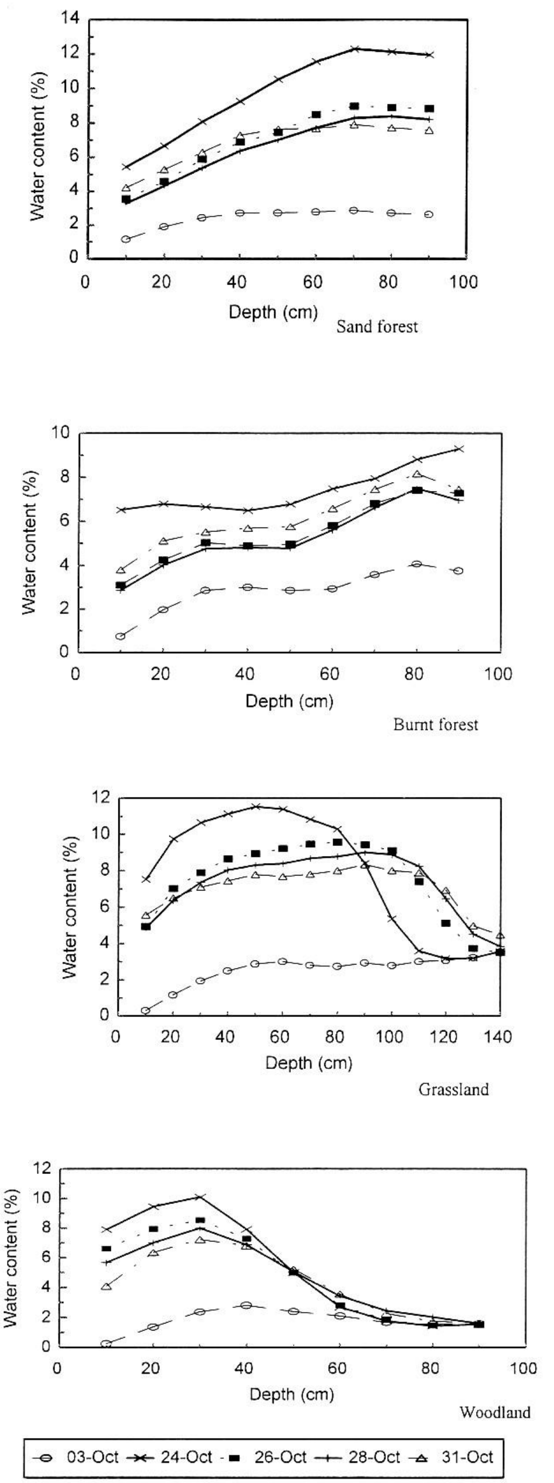

Figure 2. Profiles of water content at four sites in Tembe

area than in the forest area. However, the rate of precipitation was significantly less than the infiltration capacity of any of the soils, at about $2x10^{-4}$ cm/sec if averaged over the 24 hour period. This means that the rainfall was able to enter the soil without saturating it and percolation occurred under partially saturated conditions. The unsaturated coefficient of hydraulic conductivity, which is a function of water content, would have controlled the rate of percolation into the soil profiles. The effects of hydrophobicity could become particularly important in this instance, with the soil's water retention capacity and effectively its unsaturated hydraulic conductivity having a major effect on the downward movement of water after a rainfall event. A water retention test was carried out on a specimen of soil from a depth of 20cm at the burnt forest site. The resulting curve is shown in Figure 3 and as can be seen, the sand had a very low air-entry value and exhibited an extremely rapid loss of moisture upon application of suctions greater than about 4kPa.

In an attempt to determine whether there was any obvious difference in the water repellency of the various profiles, small specimens from each of the test locations and depths at which permeabilities were measured in the field (ie analogous to Table 1) were subjected to a simple wettability test as outlined by Dekker and Ritsema (1994). The test consists of dripping a few drops of distilled water via a standard medicinal dropper onto a level surface of the soil. The

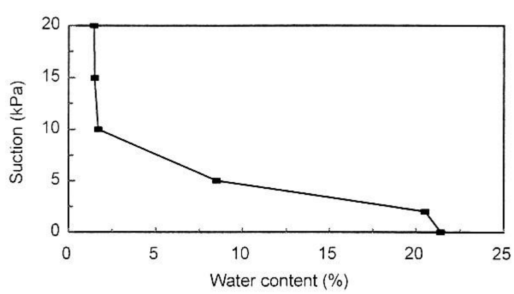

Figure 3: Water retention curve for sample of aeolian sand

time taken for the water drops to penetrate into the soil is measured. If this time is less than 5 seconds the soil is considered easily wettable. If the time is greater than 60 seconds it is strongly repellent. With only one exception, the time taken for the droplet to be absorbed was less than 2 seconds and all the sands were thus highly wettable, with the one exception. This was the specimen from a depth of 59cm in the burnt forest area. The droplet absorbance time was about 20 seconds, indicating a relatively high degree of water repellency.

6 SIGNIFICANCE OF FINDINGS

There is insufficient data at this time to make categorical conclusions as to the effect of vegetation on the hydraulic characteristics of the sandy soil studied. It is desirable to carry out a much larger number of in-situ permeability tests, soil wettability tests and water retention tests, all on the same batch of specimens. In this way some of the apparent anomalies in the measured water content profiles during rainfall periods at various locations within the Tembe reserve may be resolved.

Changes in hydraulic characteristics of the soils at Tembe that result in changes to the vegetation distribution and density are extremely important to the ecological and conservation managers. However, as engineers it is perhaps the reverse that is of most interest, ie how vegetation may change the hydraulic characteristics of a particular soil. From the data presented in this paper, it is very clear that assuming that a number of sand specimens will all have the same water retention and hydraulic characteristics simply because they have a common origin and almost exactly similar particle size distribution curves is erroneous. At the Tembe site, as may occur at many sites where certain vegetation types are prevalent, the vegetation (and the burning of this vegetation which may occur frequently) does appear to have very significant impacts on the hydraulic characteristics of the near-surface soil.

It is clear from the literature that certain vegetation types exude organic substances, usually in an effort to discourage growth of other species. These substances have often been shown to alter the water repellency of the soil that comes into contact with the organic material, perhaps ultimately rendering it highly hydrophobic. Subsequent burning of the vegetation may have the effect of removing these coatings very close to the surface but also causing the organic material to penetrate deeper into the soil profile, often condensing in a localised layer which may be highly hydrophobic. These effects appear to be particularly pronounced in permeable, cohesionless soils, where penetration of the organic substances to relatively significant depths is perhaps easier than in clayey soils.

Although this effect might be considered relatively subtle and of little interest to engineers, it is suggested that in certain circumstances it may in fact override all other considerations regarding appropriate testing and soil characterisation. Changes in field-saturated permeabilities were found to differ by over one order of magnitude (with only 12 tests being done) and it is likely that differences in unsaturated hydraulic conductivity (which would be closely linked to the water retention characteristics of the soil) might be even more pronounced.

Thus although the present study cannot lay claim to providing definitive quantification of the changes to hydraulic characteristics that occur as a consequence of vegetation 'activity', it has highlighted an area of investigation that has perhaps been ignored by geoenvironmental engineers.

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ANNEXURE 2

Van Rensburg, J.B, McGeoch, M.A., Matthews, W., Chown, S.L. & van Jaarsveld, A.S. 2000. Testing generalities in the shape of patch occupancy frequency distributions. *Ecology* 81: 3163–177.

Ecology, 81(11), 2000, pp. 3163–3177

TESTING GENERALITIES IN THE SHAPE OF PATCH OCCUPANCY FREQUENCY DISTRIBUTIONS

BERNDT J. VAN RENSBURG,[1] MELODIE A. MCGEOCH,[1,4] WAYNE MATTHEWS,[2] STEVEN L. CHOWN,[1] AND ALBERT S. VAN JAARSVELD[1,3]

[1]*Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa*
[2]*Tembe Elephant Park, KwaZulu-Natal Department of Nature Conservation, Private Bag X356, KwaNgwanase, 3973, South Africa*
[3]*Centre for Environmental Studies, University of Pretoria, Pretoria 0002, South Africa*

Abstract. Bimodal patch occupancy frequency distributions regularly appear in studies of a variety of taxa at a variety of spatial scales. Metapopulation models associated with the core–satellite hypothesis and a strong rescue effect predict the occurrence of this bimodality. However, there have been numerous other explanations, both artifactual and biological, of bimodality in patch occupancy frequency distributions. One approach to a better understanding of the phenomenon is to conduct studies on a variety of taxa and spatial scales. Here we examine patterns of patch occupancy frequency distributions for plants, dung beetles, and birds at four spatial scales in sand forest and mixed woodland in Tembe Elephant Park and Sileza Nature Reserve in South Africa. We then examine the predictions of each alternative mechanism proposed to explain bimodality with respect to the patterns found in this study. The incidence of bimodality was high. Little evidence was found for any of the artifactual or nonmetapopulation-based explanations of bimodality. Although there were no between-taxon differences in the shape of occupancy distributions, there was a clear trend of decreasing frequency of bimodality with an increase in the size of the area examined. The general shape of range-size frequency distributions in combination with an area effect is suggested as a mechanism underlying this pattern. Metapopulation dynamics associated with a strong rescue effect could also not be excluded as a possible mechanism playing a role in generating the bimodality found at the patch scale.

Key words: area effect; bimodality; community structure; core–satellite hypothesis; metapopulations; range size; rescue effect; South Africa.

INTRODUCTION

Hanski's (1982) core–satellite hypothesis focused much attention on the incidence of bimodality in the distribution of patch occupancy frequency distributions (occupancy distributions). The dynamic metapopulation models developed by Hanski (1982) and Hanski and Gyllenberg (1993) predict bimodal occupancy distributions. In other words, if the extent of occurrence (or range) of species in these distributions is divided into 10% occupancy classes, species occupying >90% of sites are termed core species, and species occupying <10% of sites are termed satellite species, and bimodal distributions with modes in these two classes are termed core–satellite distributions. The key mechanism underlying metapopulation models that predict core–satellite distributions is that these distributions are associated with a strong rescue effect (Hanski and Gyllenberg 1993). The bimodality thus arises as a result of two processes, i.e., an increase in the immigration rate with an increasing proportion of occupied sites and a decrease in the extinction rate with an increasing immigration rate (Hanski and Gyllenberg 1993). Hanski and Gyllenberg (1993) showed that over the long term, the distribution of occupancy frequencies resulting from these colonization–extinction properties of the rescue effect, and from interspecific variation in these extinction–colonization ratios, is bimodal. Therefore, when core–satellite distributions appear in empirical data for particular species assemblages, Hanski's (1982) and Hanski and Gyllenberg's (1993) interpretations suggest a metapopulation structure and the presence of a strong rescue effect in those assemblages.

There have, however, been many other, nonmetapopulation-based interpretations of core–satellite, or bimodal, patch occupancy frequency distributions (see also response to some of these by Hanski [1991]): (1) Bimodality is an artifact because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950). (2) Bimodality may arise from sampling biases when rare species are less likely to be observed or sampled (Nee et al. 1991). Problems associated with sampling rare species therefore result in an inflation of the satellite species mode. (3) The larger the number of sample sites, the greater the proportion of satellite species and the smaller the proportion of core species (Williams 1950, 1964). Therefore, the smaller the sample number used to generate the occupancy distribution, the greater the probability of find-

Manuscript received 22 February 1999; revised 4 October 1999; accepted 19 October 1999.
[4] Address correspondence to this author.

ing bimodality. (4) The presence or absence of bimodality is sensitive to the spatial scale of observation (Williams 1964, Brown 1984). This phenomenon has also been termed "distance scaling" by Collins and Glenn (1997) and was first demonstrated by Williams (1950, 1964). Using maximum sample areas of 1.0 m^2 and plant data, he showed that as the size of the area sampled increases the percentages of satellite species decrease and core species increase. In contrast, Collins and Glenn (1997), at much larger scales of >10 km^2, show an increase in percentage of satellite and a decrease in percentage of core species with an increase in the size of the area sampled (see also Brown 1984). Collins and Glenn (1997) predicted that given an increase in environmental heterogeneity with increasing spatial scale, patterns of local species distribution will change accordingly with an increase in regionally rare species and a decrease in regionally abundant species with an increase in the size of an area sampled. (5) Bimodality is a direct consequence of underlying lognormal or logarithmic rank abundance curves (Preston 1948, Papp 1997). (6) Bimodal occupancy distributions result because species are either specialists or generalists and thus occupy either a few or most habitat patches (Brown 1984). (7) Occupancy distributions are determined by the productivity of landscapes and the degree of dominance of species in them, and bimodality is most likely to be found in lower productivity landscapes where a few species dominate resource use (Maurer 1990). (8) Tourist species bring about an inflation in the satellite mode (Nee et al. 1991). (9) Within a given area, better dispersing taxa will have more core species than poorly dispersing taxa, a trend referred to as "organismal scaling" (Collins and Glenn 1997).

In addition to all the above, bimodality has been the subject of debate because its very presence is statistically difficult to verify (Tokeshi 1992). Interpretation of the presence of bimodality in patch occupancy frequency distributions therefore faces problems associated not only with the quantification of bimodality, but also, and perhaps more importantly, with the identification of the mechanisms underlying that bimodality. That is, the pattern may have either an artifactual (mechanisms 1–3 above) or biological origin, and if biological, the mechanism may or may not (mechanisms 4–9 above) involve a strong rescue effect associated with metapopulation dynamics (mechanism 10).

In an attempt to achieve some clarity on the mechanisms that generate patch occupancy frequency distributions, it is helpful to consider the closely related interspecific abundance–range-size relationship. It has been widely documented that abundant species commonly have wider ranges than locally rare species (although the proportion of variation explained is generally low) (Gaston et al. 1997). However, Gaston et al. (1997) showed that these positive relationships may be generated by any of eight principal mechanisms (including both artifactual and biological, of which one is metapopulation based). They also show that none of these mechanisms has unequivocal support and that each is likely to contribute to the relationship to different degrees under different circumstances. Although far less attention has been paid to understanding patch occupancy frequency distributions than has been the case for abundance–range-size relationships, it appears likely that occupancy distributions are likewise not generated by any single or simple combination of mechanisms.

Regardless of the mechanisms involved, bimodal patch occupancy frequency distributions regularly appear (although unimodality is more common) in studies of a variety of taxa at a variety of spatial scales (e.g., Gotelli and Simberloff 1987, Collins and Glenn 1990, 1997, Tokeshi 1992, Pirintsos et al. 1996). One approach to understanding the incidence of this bimodality is to conduct studies on a variety of taxa at a variety of spatial scales, quantifying and comparing the shapes of the occupancy distributions found. Should generalities in the incidence of core–satellite distributions be found from these studies, tests can then be conducted to investigate the mechanisms (be they biological, including metapopulation-based, or artifactual) that generate them.

Here we present the findings of a study of modality patterns for three taxa (dung beetles, birds, and plants) in two habitat types and at four nested spatial scales. First we examine the relationship between distribution and abundance because positive interspecific abundance–range-size relationships are fundamental to most regional metapopulation models (Hanski 1982, 1991, Brown 1984, Kolasa 1989, Collins and Glenn 1997), and metapopulation dynamics is one of the mechanisms proposed to explain bimodality (mechanism 10 above). Next, with respect to the findings of this study, we test (mechanisms 1, 3–5, 9) and examine (mechanisms 2, 6–8, 10) the predictions of each alternative mechanism that has been proposed to explain bimodal occupancy distributions.

Methods

Study area

Field work was undertaken in Tembe Elephant Park (27°01′ S 32°24′ E) and Sileza Nature Reserve (27°06′ S 32°36′ E), on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa. There are two distinct habitat types in these reserves, i.e., sand forest and mixed woodland, and the smaller patches of sand forest are embedded within a larger matrix of mixed woodland (van Wyk 1996; see Plate 1). Sand forest is characterized by tree species such as *Dialium schlechteri* and *Erythrophleum lasianthum* (Caesalpinioideae) (Moll 1977, van Wyk 1996) with a poorly developed understory. The surrounding, more open, mixed woodland is characterized by common, woody

PLATE 1. Photograph showing the two distinct, clearly bounded habitat types in the study areas on the southern Mozambique Coastal Plain of Northern KwaZulu-Natal, South Africa: sand forest (right) and mixed woodland (left). Photo credit: B. J. van Rensburg.

savanna species such as *Acacia burkei, Albizia versicolor,* and *A. adianthifolia* (Mimosoideae). It has a well-developed grass understory represented by *Aristida, Pogonarthria,* and *Perotis* species (Moll 1977, 1980). The soils in both study areas are homogeneous, grey, silicaceous, aerolian sands which are highly leached (dystrophic) and relatively acidic (water pH ≈ 6.1) (van Rensburg et al. 1999).

Sampling

Replicated sampling sites in these reserves were selected from within standardized vegetation communities (sand forest and mixed woodland; van Wyk 1996). Two sand forest sites and two mixed woodland sites were sampled in each reserve, i.e., eight sampling sites, grouped into four reserve–habitat combinations (Tembe sand forest, Tembe mixed woodland, Sileza sand forest, Sileza mixed woodland). Distances between sites and between the areas sampled in the two reserves were, respectively, 1.3–3.1 km and ~18 km.

Bird surveys

Each survey site was comprised of 16 randomly selected fixed survey points. The appropriate number of survey points for these assemblages was determined from a pilot study following the method advocated by Buckland et al. (1994). Distances between the 16 points within a site were at least 150 m. These distances minimized the probability of double detection, ensuring data independence, and provided suitable replicates for the study. Because of terrain difficulties, particularly in the sand forest, sampling points were placed along game and elephant paths. Although this could potentially bias the results, this is unlikely where mobile animals such as birds are surveyed (S. T. Buckland, *personal communication*). Survey points were, however, identified without prior knowledge of bird distributions, and care was taken to ensure that sampling points did not follow more prominent natural features (e.g., forest edges; see Guthery 1988).

Visual and auditory bird surveys were conducted bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were surveyed in alternate months), using point sampling (see Buckland et al. 1994). During one month, each of the four sites was surveyed four times. The 16 sampling points from a single site were surveyed in one morning (10 min per sampling point). Three minutes were spent at each survey point prior to data collection to allow the birds time to adjust to the disturbance caused by the observer. Survey periods were limited to reduce the risk of multiple detection resulting from birds moving out of and back into an observation area, which could lead to substantial density overestimation (Buckland et al. 1994). Thus a compromise between maximization of the probability that individuals in a survey point would be detected (e.g., interval-based bird calls) and minimization of the probability of multiple detection, or of attracting curious species (e.g., Southern Boubou Shrike, *Laniarius ferrugineus*), was sought.

On initial detection, birds were placed into distance categories, demarcated by fixed markers placed at known distances from the observation point (0–4, 5–9, 10–15, 16–30, and 31–50 m) before the study commenced. Although determination of the exact distance at which each bird was detected would have been desirable, this was not practical when many birds were heard and not observed (Buckland et al. 1994). In addition, estimation of exact distances when large numbers of birds are seen over a short period may lead to observational difficulties and a reduction in survey accuracy (Bibby et al. 1985). The distance to a bird in the tree canopy was taken as the distance from the observer to a point directly below the bird on the ground. All birds within 50 m of the survey point, including birds involved in territorial displays, were recorded. Birds flying over the study area were excluded. Records were also categorized as reliable sightings or as bird call records. Unreliable sightings were not included in the database. The number of individuals of each species observed over the course of the study period were summed for each survey point within each site. Survey points within a site were reduced from 16 to 4 by randomly pooling sets of four data points. These four sets are henceforth referred to as "grids" for uniformity of reference with the dung beetle and plant sampling grids.

Beetle sampling

At each sampling site, 30 pitfall traps were set out in five grids of six pitfalls each, with the six pitfalls placed 2 m apart in a 2 × 4 m rectangle. Distances between the five grids within a site were 200 m. Beetles were sampled bimonthly between May 1995 and April 1996, at all four sites in a reserve (the two reserves were sampled in alternative months), using pitfall traps baited with 50 g elephant dung. During each sampling month the pitfalls were set once for 48 h, with rebaiting and the first collection taking place at 24 h, and the second collection at 48 h. Traps were then closed and left in situ until the following sampling month. Specimens were identified by comparing them to identified specimens in the collections of the South African National Insect Collection. The number of individuals of each species trapped over the course of the study period was summed for each sampling grid and each site.

Plant sampling

Twenty 100-m^2 sample grids (10 × 10 m) were distributed in a stratified manner throughout the sampling sites. Sampling was carried out from January to May 1993. The total floristic composition, as well as a cover-abundance value for each species, was recorded using the Braun-Blanquet cover-abundance scale as described by Mueller-Dombois and Ellenberg (1974): R = rare, + = <1%, 1 = 1–5%, 2A = >5–12%, 2B = >12–25%, 3 = >25–50%, 4 = >50–75%, and 5 = >75% (see Matthews et al. 1999 and W. S. Matthews et al., *unpublished manuscript,* for further details of sampling and plant community dynamics at Tembe and Sileza).

Data analysis

Four spatial scales were considered in the analyses; patch (i.e., Tembe sand forest, Tembe mixed woodland, Sileza sand forest, and Sileza mixed woodland, each between 2 and 4.5 km^2 in extent), reserve (Tembe and Sileza: 4.5–6 km^2), habitat (all sand forest and all mixed woodland sites, between 22 and 24 km^2), and local (the full extent of the area sampled; i.e., all sampled sites, ~26 km^2).

Species accumulation curves were compiled for each taxon to establish the degree of sampling representivity. Samples were randomly and sequentially selected without replacement from the full data sets for each taxon until all samples had been selected. This procedure was repeated five times and species accumulation curves compiled from the mean number of species across the five replicates for each sample number.

Ordinary least-squares linear regression was used to establish whether positive interspecific abundance–range size relationships existed, i.e., number of grids in which each species was present vs. their average abundance across those grids, for each of the higher taxa, at each of the four spatial scales sampled in the region.

Tokeshi's (1992) method of determining the exact probability of obtaining an observed frequency value (p_c) for the left- and rightmost classes under the null hypothesis of random occurrence of species in a region was used to quantify modality patterns (see also Collins and Glenn 1997). The probability of obtaining the observed frequency for the left- (p_l) or rightmost (p_r) class can also be calculated separately under the same null hypothesis (Tokeshi 1992): if $P < 0.05$ for both the left- and right-extreme frequency classes then the distribution is bimodal, whereas if $P < 0.05$ for only one of the classes then the distribution is unimodal. This method was used for each taxon at each spatial scale. In all cases the number of grids sampled, and in which species were recorded, was ≥10, and the distribution could thus reasonably be expressed as the proportion of grids occupied by species in 10% grid occupation categories.

To test whether the occupancy distributions found were sample size independent, data from all grids within each habitat type, (1) all sand forest and (2) all mixed woodland grids, were used. Grids were then randomly selected from these data sets until new data sets with sample sizes representing 50% of the original sample size were reached. This procedure was repeated five times for each higher taxon in both sand forest and mixed woodland. The sample size of 50% of the original sample reduced sample sizes to levels equivalent to the smallest sample sizes used in this study (patch scale). The occupancy distributions generated from the smaller randomly selected samples for each taxon were then compared with observed occupancy distributions compiled from similar sample sizes. These sample size reductions were carried out within habitat types only to remove possible habitat heterogeneity effects on the occupancy distributions generated, as far as possible.

Given the prediction that there will be an increase in regionally rare (satellite) species and a decrease in regionally abundant (core) species with an increase in the size of an area sampled (Collins and Glenn 1997), distance scaling was assessed by examining changes in the numbers of core and satellite species from the smallest to largest spatial scales for each taxon.

To test the prediction that bimodal occupancy distributions reflect underlying lognormal or logarithmic series distributions, truncated lognormal and logseries models were fitted to the rank abundance plots of each taxon at each spatial scale (Magurran 1988, Papp 1997).

Organismal scaling was tested by comparing the occupancy distributions of taxa, on the assumption that their rank-order dispersal ability is birds > dung beetles > plants. Here we predict, based on Collins and Glenn's (1997) rationale, that the better dispersing taxa (e.g., birds) will have more core species than the poorer dispersing taxa (e.g., plants). The occupancy distributions of each taxon within each spatial scale were also compared to each other using Kolmogorov-Smirnov two-sample tests (Siegel 1956). To further test Collins and Glenn's (1997) organismal scaling prediction of better dispersing taxa (i.e., those with larger ranges) in the core mode, we used the bird data collected here and examined the broader southern African distributions (percentage of 25-km^2 grid cells in which species has been recorded in southern Africa, extracted from Harrison et al. 1997) of those species in the core and satellite categories of the distributions generated by this study. The prediction here is, if core mode species are better dispersers they should be subregionally widespread, whereas if satellite species are poor dispersers they should have narrow subregional distributions.

Results

The number of species recorded in each taxon across scales ranged between 65 and 112 for birds, 35 and 68 for dung beetles, and 95 and 501 for plants (Table 1). The species accumulation curves showed that the species richness of the dung beetle and bird assemblages reached an asymptote well within the sample size used in this study (Fig. 1). The plant assemblage required a far larger sample size before representivity was achieved; however, this assemblage also reached an asymptote within the sample size used (Fig. 1). All three assemblages sampled were thus highly representative of the area.

The relationship between number of sites occupied and average abundance was positive for all and significant for 24 of the 27 taxon–spatial scale combinations (Table 1). The three nonsignificant relationships were all at the patch scale. Nonetheless, the metapopulation assumption (Hanski 1982), or prediction (Hanski and Gyllenberg 1993), of a positive relationship between distribution and abundance was largely met.

Significant bimodality was detected in just under 50% of the cases examined and was present in occupancy distributions of all three taxa (Fig. 2). However, there was a clear tendency for decreasing frequency of bimodality with increasing spatial scale (from Fig. 2A–D). Evidence of distance scaling was also stronger within, rather than across, habitat types (Fig. 2). When moving from a particular habitat at the patch scale (Fig. 2A) directly to the same habitat type at the larger, habitat scale (skipping the reserve scale) (Fig. 2C), the switch from bimodal to unimodal was clearer than when including the intermediate reserve scale (Fig. 2B) that combines data for both habitat types.

The reduction of sample sizes by 50% did not change largely the shape of the patch occupancy distributions (Table 2). At the habitat scale all observed occupancy distributions were unimodal (Fig. 2). Reducing these data sets to sample sizes equivalent to those used at the smallest (i.e., patch) spatial scale did not change the distributions from unimodal to bimodal (with the exception of two replicates of the mixed woodland dung beetle assemblage; Table 2). The presence of bimodality at the patch scale therefore could not be attributed to the smaller sample sizes used at this scale.

Within each of the three taxa examined there were fewer species in the core modes at the larger local and habitat scales than at the smaller patch and, in some cases, reserve scales (Fig. 2, Table 3). The number of satellite species, in contrast, increased from patch to local scales for dung beetles. The increase was less clear for birds, and neither an increase nor a decrease in the number of species with increasing spatial scale was evident for plants (Table 3). Distance scaling was thus clear for core, but not satellite, species in the three taxa tested. The bimodality detected at patch and reserve scales thus resulted from the presence of a core mode, and although there were some signs of an increase in the satellite mode with increasing spatial scale these did not contribute to the change in distribution from unimodal to bimodal.

Dung beetle assemblages fitted the logarithmic series distribution at all spatial scales (Table 4), regardless of the shape of the corresponding occupancy distribution (Fig. 2). Therefore logarithmic series were found to underlie both unimodal and bimodal occupancy distributions. Similar results were found for birds and plants, although only in some instances did the rank abundance distributions fit the logarithmic series (Table 4). However, those that did fit the series were never exclusively associated with bimodal occupancy distributions (Fig.

TABLE 1. Relationship between number of sites occupied (N) and average abundance for each taxon group at each spatial scale using least-squares linear regression (all were positive) in Tembe Elephant Park and Sileza Nature Reserve in South Africa.

Spatial scale	Taxon	S	N	R^2	P
Patch					
Tembe sand forest	Birds	65	15	0.81	<0.001
	Dung beetles	48	10	0.31	0.089
	Plants	95	10	0.87	<0.001
Sileza sand forest	Birds	63	16	0.75	<0.001
	Dung beetles	35	10	0.54	0.014
	Plants	107	10	0.77	0.053
Tembe mixed woodland	Birds	85	16	0.76	<0.001
	Dung beetles	54	10	0.45	0.035
	Plants	292	20	0.39	<0.01
Sileza mixed woodland	Birds	74	15	0.65	<0.001
	Dung beetles	63	10	0.34	0.074
	Plants	156	17	0.43	<0.01
Reserve					
Tembe	Birds	94	25	0.76	<0.001
	Dung beetles	65	20	0.35	<0.01
	Plants	230	28	0.59	<0.01
Sileza	Birds	90	27	0.71	<0.01
	Dung beetles	56	16	0.28	0.036
	Plants	197	20	0.56	<0.01
Habitat					
Sand forest	Birds	87	27	0.74	<0.001
	Dung beetles	52	15	0.41	0.0101
	Plants	159	14	0.48	<0.01
Mixed woodland	Birds	99	29	0.72	<0.001
	Dung beetles	68	20	0.30	0.0126
	Plants	343	40	0.47	0.0279
Local					
	Birds	112	43	0.70	<0.001
	Dung beetles	68	29	0.28	<0.01
	Plants	501	54	0.56	0.0122

Notes: Average abundances were calculated from the number of occupied sites rather than the total number of sites. S = number of species. Table-wide $\alpha = 0.05$ for birds, dung beetles, and plants using the sequential Bonferroni technique (Rice 1988).

2). The bird and plant assemblages were almost exclusively truncated lognormally (Table 4), again regardless of the shape of the corresponding occupancy distribution (Fig. 2).

Little evidence of organismal scaling (larger core modes for better dispersing taxa) according to the proposed rank dispersal ability of the three taxa examined (i.e., birds > dung beetles > plants) was found (Table 3). Dung beetles had the largest core mode percentages at all patch and reserve scales. Although at the larger habitat and local scales birds did have higher core percentages than the other two taxa (Table 3), none of these occupancy distributions were significantly different from each other (Table 5). The distributions of the three taxa were therefore almost exclusively similar within each scale examined (Table 5) (in spite of large differences in the species richness of the three assemblages; Fig. 2). These results therefore provide no support for the effect of organismal scaling on the shape of occupancy distributions.

In addition, bird species in each of the core and satellite categories in this study (Fig. 2A) included species with both narrow and wide ranges in southern Africa (Fig. 3). This was true of core and satellite categories at patch, habitat, and local scales. For example, at the sand forest habitat scale, satellite species included species that occur in 0.04–70% of the grid cells in southern Africa, i.e., the satellite mode included both subregionally restricted and widespread species. Within the core category in the same habitat there were species that are found in 2.2–32.7% of the quarter-degree grid cells in southern Africa, i.e., the core category included species with narrow to moderately wide subregional distributions. Therefore, neither core nor satellite modes contained species with either exclusively narrow or wide distribution ranges in southern Africa.

DISCUSSION

After testing, and elsewhere less formally examining, the mechanisms that have been proposed to explain bimodality and the variability in its incidence (outlined in *Introduction*), a number appear invalid or inapplicable, whereas a few find support, in light of the results found here.

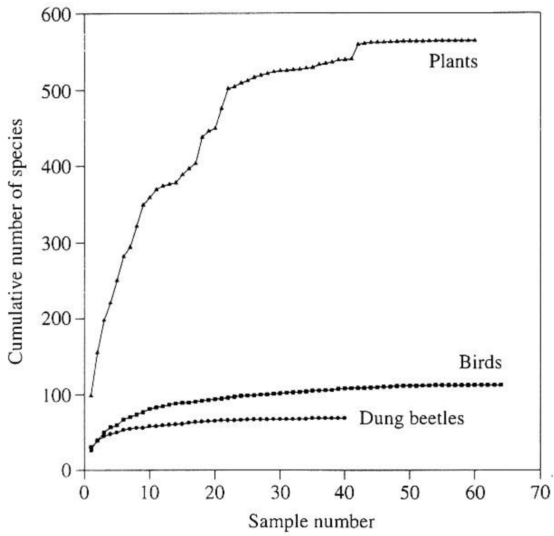

FIG. 1. Species accumulation curves for dung beetle, bird, and plant assemblages in Tembe Elephant Park and Sileza Nature Reserve in South Africa. Each point on the curve represents the mean of five randomly selected samples from the full data set for the higher taxon in question.

Artifactual mechanisms

(1) If bimodality occurs because occupancy is constrained to lie between zero and one (Raunkiaer 1934, Williams 1950), then this mechanism should apply equally across all spatial scales. This was not the case here.

(2) Considering sampling representivity and the possible effect of undersampling rare species on occupancy distributions, the assemblages of the three taxa sampled in this study are based on data accumulated over 12 mo and were highly representative of the area (as compared to species lists for these areas and as evident from the species accumulation curves that were compiled). Although representative, it is possible that rare species in these assemblages were sampled at fewer sites than at which they actually occur, bringing about an inflation in satellite modes. The overwhelming majority of occupancy distributions, and indeed species abundance distributions, even in the most well-sampled assemblages, have a peak in the lowest abundance class, or are right skewed (Gaston and Lawton 1990). Although undersampling may inflate the satellite mode, the observed rare species mode in such distributions is so common that there can be little doubt as to its existence (Tokeshi 1992). Nonetheless, it is the disappearance of the core mode at larger scales, rather than any change in the satellite mode, that converted the occupancy distributions from bimodal at small scales to unimodal at larger scales in this study. To test the extent of this rare species effect on the satellite mode, it would be necessary to quantify the change in occupancy patterns of the rare species with increasing sample effort.

(3) The presence of bimodality in this study could not be attributed to Williams' (1964) demonstration that the fewer sites sampled, the higher the fraction of species present in the core mode, because random sample size reductions did, by and large, not produce bimodal distributions. Gotelli and Simberloff (1987) also showed that the predicted reduction in the proportion of core species across an increase of 100 sampled quadrates was only ~2–3%. The observed reduction in core species across the 100 quadrates, in contrast, was ~16% (see Gotelli and Simberloff 1987: Fig. 6). Similarly, in this study there was a reduction of 13–15% in core species between smallest to largest scales, with an average increase of only 40 sample sites (see Tables 1 and 4). The reduction in percentage of core species is therefore greater than may be expected to result purely from an increase in sample size.

Biological mechanisms

(4) We did find that patch occupancy frequency distributions were sensitive to the spatial scale of observation, and furthermore, that there appears to be a systematic pattern to this sensitivity, i.e., that there is some form of distance scaling. Occupancy distributions were bimodal at the smallest spatial scales examined here (2–4.5 km^2), becoming unimodal at larger spatial scales. As found in similar empirical studies to date (e.g., Gotelli and Simberloff 1987, Collins and Glenn 1990, 1997, Pirintsos et al. 1996), the incidence of bimodality in the frequency distributions in this study was high (50%) (although see Tokeshi 1992). However, unlike other studies, for all taxa we found a decreasing incidence of bimodality with an increase in the spatial extent covered. Although Collins and Glenn (1997) found a similar change across two scales, their small scale (36 km^2) was somewhat larger than the largest, local scale (26 km^2) in this study. In addition, the larger scale Collins and Glenn (1997) examined covered a different geographic area to the smaller scale they examined, with variable spatial extents for each taxon (they do not provide areas of coverage). Therefore, in their study within each taxon the species set at the smaller scale was not a geographic subset of the assemblage at the larger scale, and it is unclear to what extent, if any, the species composition of the assemblages at the two scales overlap. The study presented here, in contrast, examines true distance scaling where each smaller spatial scale is a geographic subset of the next larger one. Nonetheless we too find a decrease in the frequency of bimodality with increasing spatial extent, although across four rather than two spatial scales. Furthermore, we find that this pattern is stronger within (from almost exclusively bimodal at the habitat–patch scale [2–4 km^2] to exclusively unimodal at the larger habitat scale [22–24 km^2]), than across, habitat types (see also Raunkiaer 1934, Gotelli and Simberloff

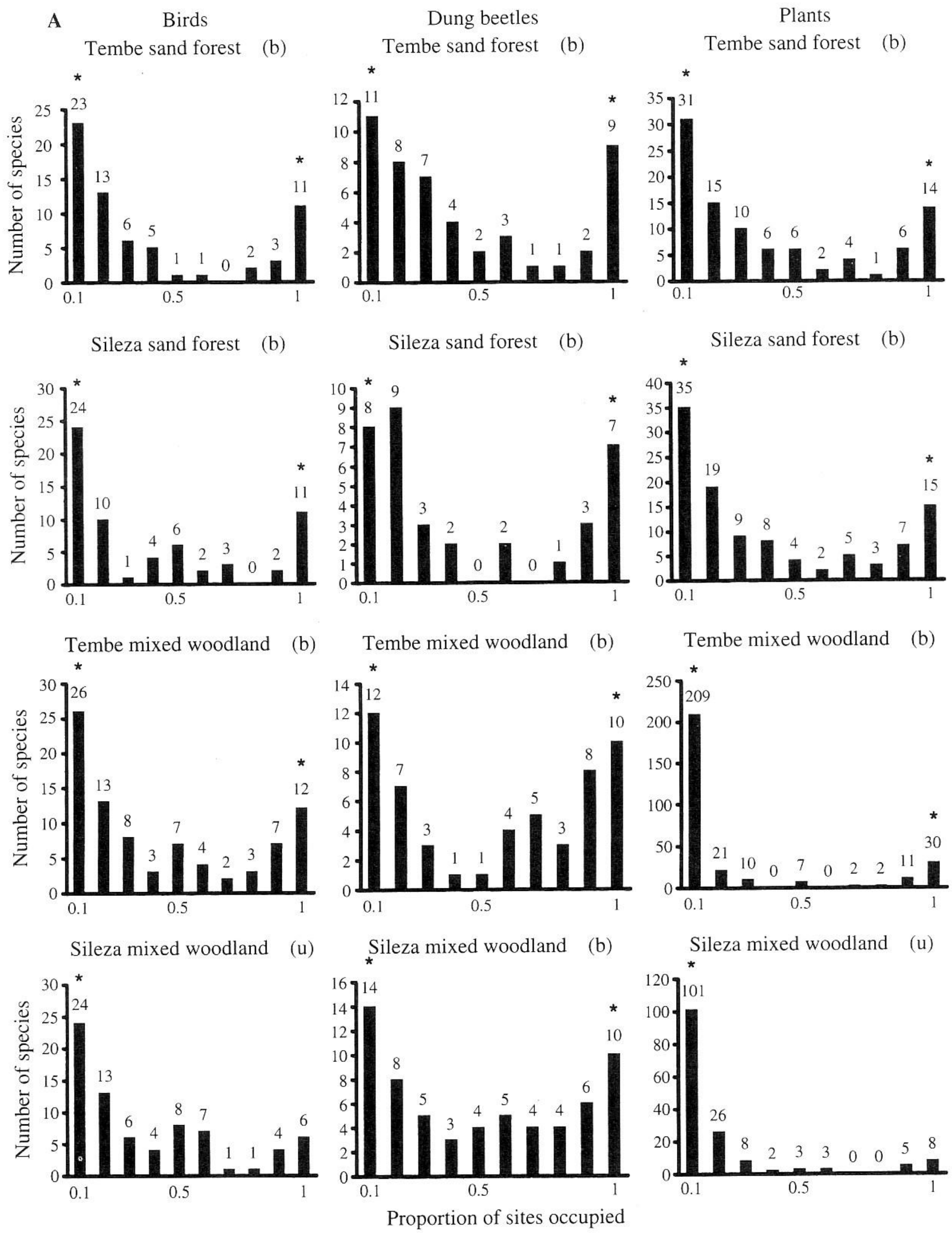

FIG. 2. Patch occupancy frequency distributions of the three taxa at (A) patch, (B) reserve, (C) habitat, and (D) local scales. All distributions were significantly different from random ($p_c < 0.001$); Stars (★) associated with core and satellite classes denote modes significant at $P < 0.005$; b = bimodal, u = unimodal distribution.

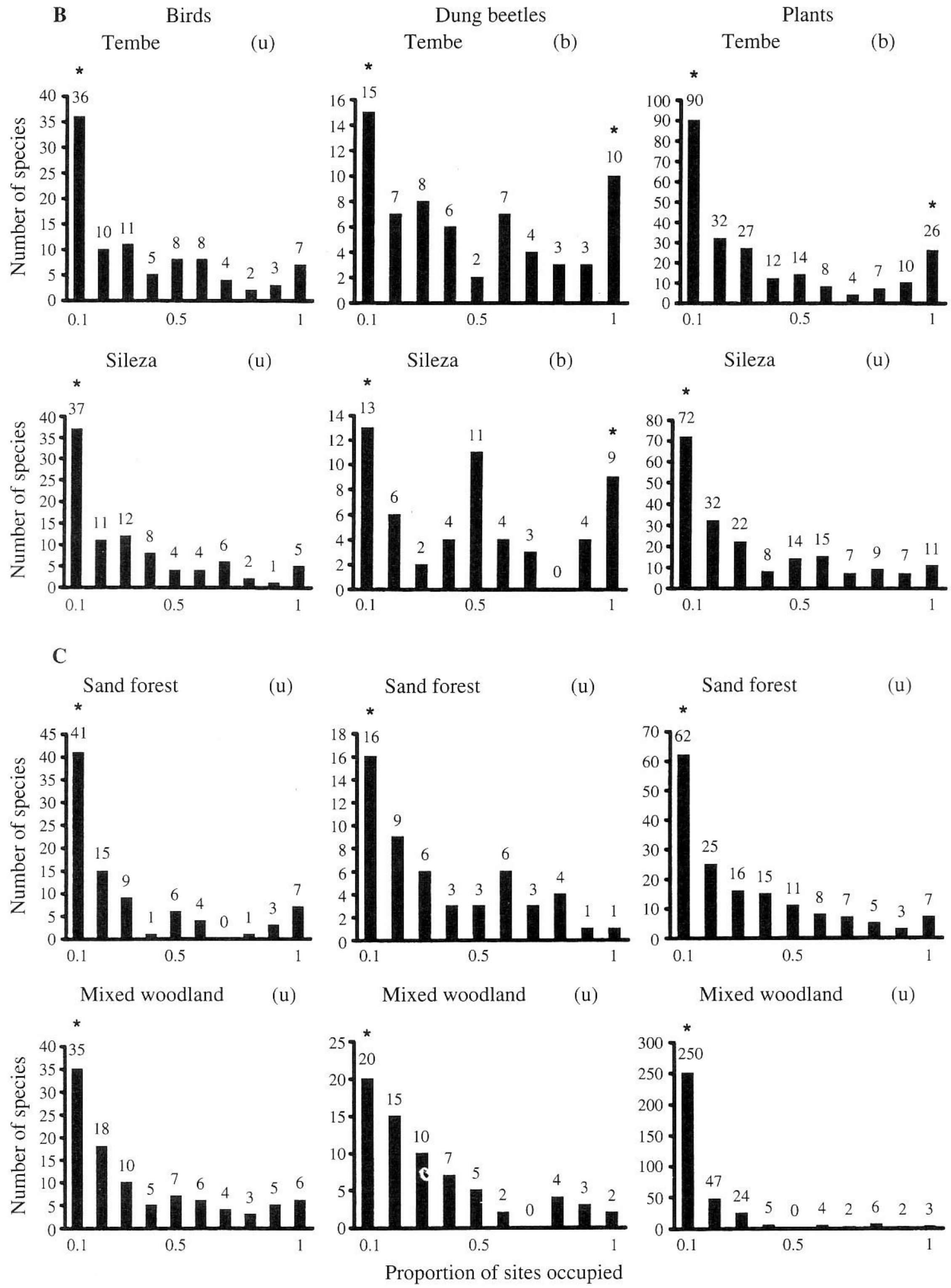

FIG. 2. Continued.

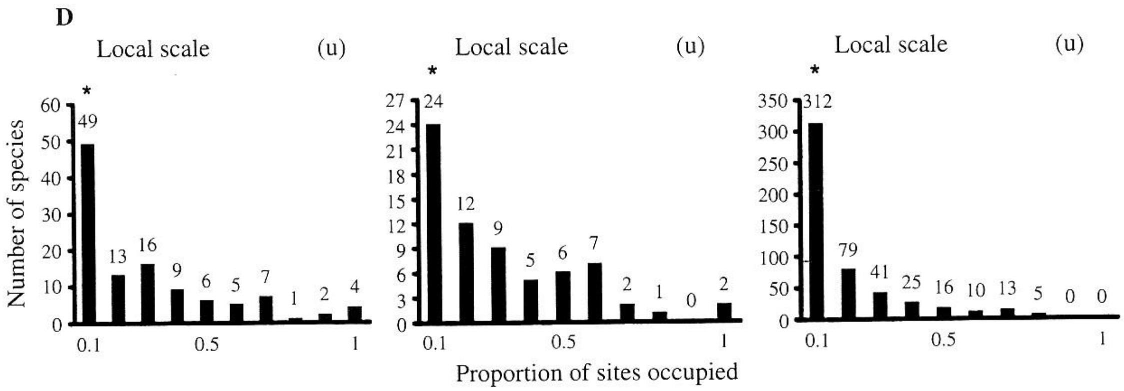

FIG. 2. Continued.

1987). Bimodal and unimodal distributions were equally frequent at the smaller (across habitat) reserve scale (4–6 km^2, including two habitat types) becoming unimodal at the local (26 km^2) scale. Other studies of Tembe Elephant Park and Sileza Nature Reserve show significant differences in the bird (van Rensburg et al. *unpublished manuscript*) and dung beetle (van Rensburg et al. 1999) assemblages of the two habitats (sand forest and mixed woodland). This may explain the incidence of unimodality at smaller, across habitat (i.e., reserve) scales, where inclusion of a new habitat type and different species assemblage leads to a more rapid

TABLE 2. Patch occupancy frequency distributions of samples of grids randomly selected from each habitat type.

Habitat/taxon	N	N_r	R	p_c	p_l	p_r	Diagnosis
Sand forest							
Birds	32	16	1	<0.0001	<0.0001	0.13	unimodal
			2	<0.0001	<0.0001	0.13	unimodal
			3	<0.0001	<0.0001	0.16	unimodal
			4	<0.0001	<0.0001	0.24	unimodal
			5	<0.0001	<0.0001	0.07	unimodal
Dung beetles	20	10	1	<0.0001	<0.0001	0.10	unimodal
			2	<0.0001	<0.0001	0.32	unimodal
			3	<0.0001	<0.0001	0.08	unimodal
			4	<0.0001	<0.0001	0.18	unimodal
			5	<0.0001	<0.0001	0.33	unimodal
Plants	20	10	1	<0.0001	<0.0001	0.22	unimodal
			2	<0.0001	<0.0001	0.21	unimodal
			3	<0.0001	<0.0001	0.23	unimodal
			4	<0.0001	<0.0001	0.20	unimodal
			5	<0.0001	<0.0001	0.21	unimodal
Mixed woodland							
Birds	32	16	1	<0.0001	<0.0001	0.33	unimodal
			2	<0.0001	<0.0001	0.27	unimodal
			3	<0.0001	<0.0001	0.37	unimodal
			4	<0.0001	<0.0001	0.26	unimodal
			5	<0.0001	<0.0001	0.33	unimodal
Dung beetles	20	10	1	<0.0029	<0.05	0.02	bimodal
			2	<0.002	<0.17	0.003	unimodal
			3	<0.014	<0.069	0.124	no mode
			4	<0.004	<0.014	0.119	unimodal
			5	<0.003	<0.032	0.031	bimodal
Plants	40	20	1	<0.0001	<0.0001	0.20	unimodal
			2	<0.0001	<0.0001	0.22	unimodal
			3	<0.0001	<0.0001	0.22	unimodal
			4	<0.0001	<0.0001	0.23	unimodal
			5	<0.0001	<0.0001	0.24	unimodal

Notes: The final sample size (N_r) used for each taxon represents a sample size reduction of 50% of the original sample size (N). R = replicate number; p_c, p_l, and p_r are the exact probabilities of obtaining the observed frequency value for the left- and rightmost classes combined, the leftmost class, and the rightmost class, respectively (see *Methods: Data analysis*).

TABLE 3. Percentage of species in the satellite and core modes (those species occupying between 1% and 10% and between 91% and 100% of grids, respectively) for each taxon (Pl = plants, Db = dung beetles, Bi = birds) at the different spatial scales.

	Percentage of satellite species			Percentage of core species		
Scale	Pl	Db	Bi	Pl	Db	Bi
Patch						
Tembe sand forest	32	22	35	15	18	17
Sileza sand forest	32	22	38	14	19	17
Tembe mixed woodland	71	22	30	10	18	14
Sileza mixed woodland	64	22	32	5	16	8
Reserve						
Sileza	36	23	41	6	16	5
Tembe	39	23	38	11	15	7
Habitat						
Sand forest	39	30	47	4	2	8
Mixed woodland	73	29	35	1	3	6
Local	62	35	44	0	3	4

Notes: Spatial scales are ranked from smallest to largest. Comparisons down columns for each taxon = distance scaling. Comparisons across taxa within rows = organismal scaling.

increase in species in the satellite mode, than would the addition of a patch of the original habitat type. Because the core–satellite hypothesis attempts to explain the distribution of species that can potentially occupy all sites (i.e., considers occupancy frequency distributions within homogenous sets of patches) (Hanski and Gyllenberg 1993), it is important to consider the possible effects of including different habitats on the shape of occupancy distributions (see also Raun-

TABLE 5. Differences in patch occupancy frequency distributions between taxa at each spatial scale based on pairwise Kolmogorov-Smirnov two-sample tests

Spatial scale/taxon group	Taxon group: Plants	Taxon group: Birds
Patch		
Tembe sand forest		
Birds	NS	
Dung beetles	NS	NS
Sileza sand forest		
Birds	NS	
Dung beetles	NS	NS
Tembe mixed woodland		
Birds	NS	
Dung beetles	<0.05	NS
Sileza mixed woodland		
Birds	NS	
Dung beetles	NS	NS
Reserve		
Tembe		
Birds	NS	
Dung beetles	NS	NS
Sileza		
Birds	NS	
Dung beetles	<0.05	NS
Habitat		
Sand forest		
Birds	NS	
Dung beetles	NS	NS
Mixed woodland		
Birds	NS	
Dung beetles	NS	NS
Local		
Birds	NS	
Dung beetles	NS	NS

Note: Table entities are *P* values.

TABLE 4. Logarithmic and truncated lognormal series chi-square goodness-of-fit tests of the rank abundance distributions of each taxon at each spatial scale.

	Logseries									Truncated lognormal					
	Dung beetles			Birds			Plants			Dung beetles		Birds		Plants	
Scale	χ^2	df	*P*	χ^2	df	*P*	χ^2	df	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Patch															
TSF	9.92	10	NS	3.40	8	NS	9.32	7	NS	23.75	**	8.39	NS	4.75	NS
SSF	10.29	10	NS	4.07	8	NS	13.96	6	*	20.05	*	8.52	NS	11.29	NS
TMW	16.70	10	NS	11.22	8	NS	6.29	8	NS	19.92	*	9.75	NS	4.76	NS
SMW	9.59	10	NS	7.81	7	NS	17.21	8	*	15.62	*	4.40	NS	6.77	NS
Reserve															
TEM	10.22	10	NS	17.26	9	*	9.38	8	NS	14.97	NS	12.85	NS	6.23	NS
SIL	6.38	10	NS	4.90	9	NS	45.67	8	***	14.74	NS	6.56	NS	14.45	NS
Habitat															
SF	13.81	10	NS	7.44	9	NS	19.75	7	**	23.16	**	16.72	*	3.16	NS
MW	10.12	10	NS	10.25	8	NS	52.02	8	***	10.09	NS	5.53	NS	42.16	**
Local	14.15	10	NS	12.85	10	NS	143.42	8	***	12.34	NS	8.52	NS	46.05	**

Note: TSF and SSF = Tembe and Sileza sand forests, TMW and SMW = Tembe and Sileza mixed woodlands, TEM = Tembe Elephant Park, SIL = Sileza Nature Reserve, SF = sand forest, MW = mixed woodland.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; significant difference between the model and observed series. NS = no significant difference between the model and observed series.

† df = 10 throughout for truncated lognormal tests.

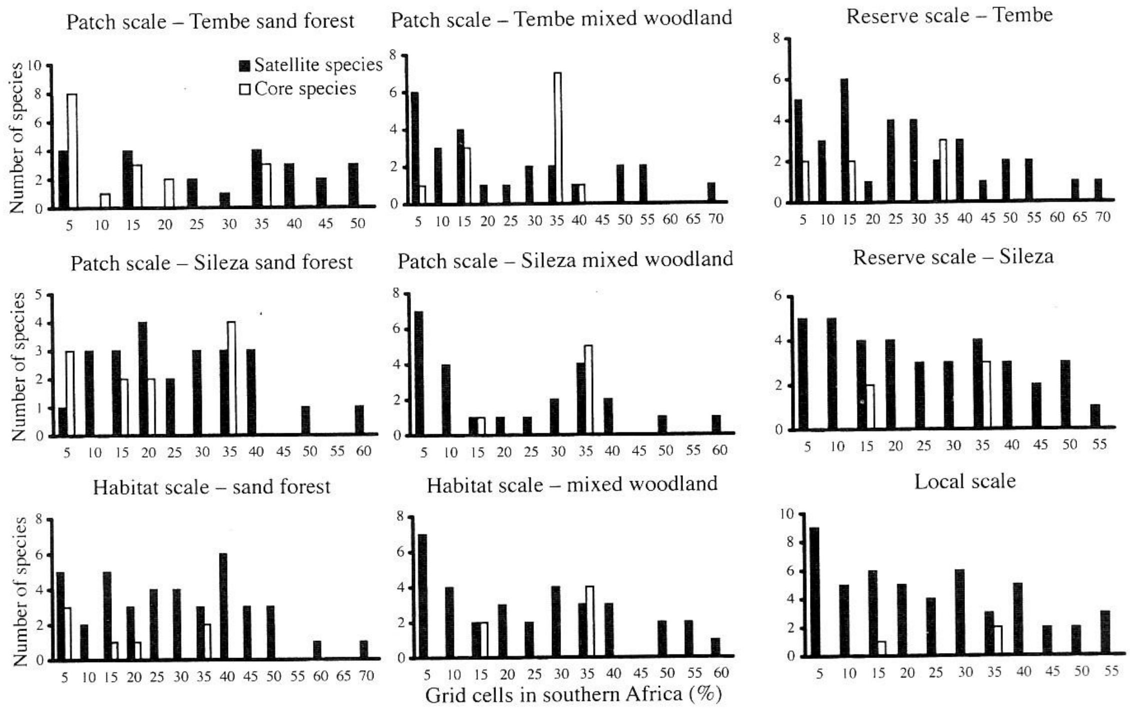

FIG. 3. Percentage of quarter degree (25 km^2) grid cells in which the core and satellite bird species, identified at four spatial scales in the present study, are found in southern Africa.

kiaer 1934, Gotelli and Simberloff 1987). It is thus critical to have information on the heterogeneity of an area before attempting to quantifying occupancy distributions. In spite of occupancy distributions being examined across habitat types for part of the analyses presented here, bimodality remained more frequent at smaller than at larger scales for this part of the analysis.

The distance scaling of occupancy distributions discussed above may be related to the nature of range-size frequency distributions, which are commonly unimodal and right skewed (Gaston 1998), and an associated area effect. Because the majority of species have small range sizes, as the size of an area sampled increases it will increasingly extend beyond the distribution ranges of species in the assemblage being sampled. Therefore, the larger the area sampled the fewer species one would expect to occupy >90% of the patches within it (see also Brown 1984). This would lead to the observed decrease in the size of the core mode with increasing spatial scale. At 50% the frequency of bimodality in this study was high (compared to studies in general; Tokeshi 1992). However, this may be expected considering the relatively small scale at which it was conducted (2–26 km^2).

(5) Papp (1997) predicted that bimodal occupancy distributions arise from underlying lognormal or logarithmic series rank abundance distributions. Although Papp (1997) showed that these distributions generate bimodal occupancy distributions, he did not consider possible alternative mechanisms that may also generate bimodality, nor did he suggest which form of rank abundance series underlies unimodal frequency distributions. Here we found no relationship between the presence of bimodality and either logseries or truncated lognormal distributions.

(6) As outlined by Hanski and Gyllenberg (1993), Brown's (1984) specialist–generalist explanation for bimodality does not hold within patches of similar habitat, because all species can potentially occupy all sites. In this study bimodality was found predominantly within homogenous sets of patches (i.e., at the patch scale) and the assumption that all species could occupy all areas within these patches appears sound. However, the assumptions of Brown's (1984) model may be violated at the restricted spatial scale examined in this study. It should perhaps rather be tested at scales more representative of the range sizes of the species in question and using assemblages where specialist and generalist species can be readily identified.

(7) Commenting on the core mode, Maurer (1990) predicted that bimodality is associated with high dominance in assemblages in low productivity habitats. Although we cannot comment on the productivity of the habitats sampled, at the patch scale the dung beetle and bird assemblages of Sileza sand forest had the highest percentage dominance (52%), and Tembe mixed woodland had the lowest dominance (28%) (van Rensburg et al. 1999; B. J. van Rensburg, *personal observations*).

In spite of this 24% difference in dominance between habitats, and comparatively low degree of assemblage dominance in both, the occupancy distributions for dung beetles and birds in both of these patches were bimodal. The degree of dominance of assemblages therefore did not explain the bimodality found here. To test Maurer's (1990) hypothesis comparisons should be made between matched assemblages in habitats with known, different productivity levels.

(8) Tourist species may indeed bring about an inflation in the satellite mode, but again it is the presence or absence of a core (see point 2 above), rather than a satellite, mode that identifies the occupancy distributions here as either bi- or unimodal. In addition, uniform distributions or unimodal distributions with the mode in the core category are generally uncommon (Tokeshi 1992). The identification of tourist species is controversial (Gaston 1994). However, if methods were developed by which they could be objectively designated (such as that suggested by McGeoch and Chown 1998), then their effect on the shape of occupancy distributions could be quantified.

(9) The prediction of higher proportions of core species for taxa with better dispersal abilities, based on the assumption that birds are better dispersers than dung beetles and dung beetles better than plants, was not realized in this study. Little evidence of an organismal effect on the shape of occupancy distributions was thus found (similar to the findings of Collins and Glenn 1997), and such an effect is unlikely in this type of study (i.e., partial analyses, sensu Gaston and Blackburn 1996, and a snapshot of species distributions that have accumulated over time). On further consideration it appears unlikely that any conclusions can be made about the dispersal abilities of species in core and satellite modes when sampling is conducted as it was in both this study and that of Collins and Glenn (1997). When representative samples are taken of an assemblage from a patch, habitat, or local area (as was the case here), the occurrence of a species at a certain number of sites represents the distribution of that species in the area sampled. Given that over evolutionary time most species have had the opportunity to colonize and occupy all suitable patches (and this is a reasonable assumption in the areas sampled here and areas of a similarly small size), then the occupancy distributions represent snapshots of accumulated distributions over evolutionary time. In this instance better dispersers may not necessarily be expected to occur at more sites than poorly dispersing species. However, if the actual colonization of an area, particularly an island, is being monitored over time (such as is the case in the study by Nieminen and Hanski 1998), it is likely that better dispersing species will shift more rapidly from the satellite to core mode of occupancy distributions than species with poorer dispersal abilities. Of course, this may also be true of highly fragmented or very patchy habitats (With and Crist 1995). Given sufficient time in comparatively unfragmented habitats, however, the core–satellite distribution will again represent only those species that are either patchily or locally rare or abundant, without encompassing any information on the dispersal abilities of the species concerned. This argument is supported by the occurrence of both widely and narrowly distributed bird species in southern Africa in each of the core and satellite modes of the occupancy distributions generated by sampling sand forest and mixed woodland in Tembe and Sileza. Assumptions of the relative dispersal abilities of higher level taxonomic groups is also problematic. For example, it has recently been shown that the rate of spread of tree species may be far more rapid than previously thought (Clark 1998). It is thus clear that the species in core categories do not exclusively demonstrate greater "dispersal abilities," if one uses, as suggested by Collins and Glenn (1997), the number of sites at which a species is present as an indication of its dispersal ability.

The final mechanism (10) proposed to explain bimodality is of course a strong rescue effect associated with metapopulation dynamics. With no information on the population structure and dynamics of any of the species in the three assemblages examined, we were unable to test this hypothesis. However, the shape of empirically derived occupancy distributions is commonly used as an indirect indication of the possible presence of metapopulation dynamics (Gotelli and Simberloff 1987, Gaston and Lawton 1989, Collins and Glenn 1990, 1997). If there is no bimodality there should be no strong rescue effect. We could therefore predict, based on the findings of this study, that metapopulation dynamic processes are not generating the occupancy distributions at larger scales (22–26 km^2) for the three taxa we examined. Bimodality at the patch level on the other hand was pervasive. Therefore, the presence of a strong, metapopulation dynamics-associated rescue effect for dung beetles, birds, and plants within scales of 2–4.5 km^2 in Tembe and Sileza cannot be ruled out without having quantified the immigration and extinction dynamics of these taxa. Very little evidence exists in the literature in support of plant or vertebrates exhibiting metapopulation dynamics (Pfister 1988, Gotelli and Kelley 1993, Harrison et al. 1995, Gaston et al. 1997, Scheiner and Rey-Benayas 1997), and only some evidence has been found for insect species (e.g., Harrison et al. 1988, Kindvall and Ahlén 1992, Hanski 1994, but see Gaston and Lawton 1989). Birds, for e.g., appear unlikely to exhibit metapopulation dynamics because the dispersal ranges of the vast majority of species are so large (Blackburn et al. 1997). Nonetheless, both bird and dung beetle assemblages are known to differ significantly between mixed woodland and sand forest habitats (van Rensburg et al. 1999; B. J. van Rensburg, S. L. Chown, A. S. van Jaarsveld, and M. A. McGeoch, *unpublished manuscript*), and sand forest characteristically exists as distinct patches of varying sizes within a matrix of mixed woodland (van Wyk 1996, van Rensburg et al. 1999). At the patch scale bimodality was found for all sand forest assemblages, whereas the two unimodal occupancy distributions at this scale were associated with mixed woodland. The natural patchiness of the mixed woodland–sand forest system may therefore contribute to the bimodality found, and metapopulation dynamics cannot be ruled out as a possible mechanism at this scale.

The results presented here relate to mechanisms responsible for the presence or absence of bimodality in occupancy distributions within and across comparatively small spatial scales. However, processes affecting patch occupancy patterns may change as the sampling extent incorporates increasingly larger spatial scales, until the point where the geographic ranges of species are encompassed by the sample area. Therefore, some of the mechanisms that were found to contribute to the shape of occupancy distributions in this study may change as larger spatial scales are examined. However, the approach to testing the mechanisms used here can similarly be applied at and across any combination of spatial scales.

Conclusion

Although undersampling of rare species may play a role in other studies where the satellite mode is responsible for generating the bimodality, unimodal and left-skewed distributions are uncommon and right-skewed occupancy distributions (such as those in this study) are pervasive (Tokeshi 1992). It was certainly the behavior of the core mode within and across taxa and spatial scales, rather than the satellite mode, that was of interest across the relatively small extent of the sample area examined here. Therefore, two of the ten mechanisms said to account for bimodality were identified as possible and/or likely candidates explaining the bimodal occupancy distributions found at this scale. Of these, right-skewed range-size frequency distributions and an area effect, explaining the decrease in the size of the core mode from small to large scales, appear most likely. Finally, metapopulation dynamics associated with a strong rescue effect remains a possibility, and this study highlights the importance of considering habitat heterogeneity and area effects when testing metapopulation models.

Acknowledgments

The KwaZulu Department of Nature Conservation provided accommodation in Tembe, and financial and logistic support. The Park Warden and Chief Nature Conservator of Tembe Elephant Park, Mr. E. W. Ostrosky, is thanked for assisting B. J. van Rensburg in Tembe. Adrian Davis (University of Pretoria) and Riaan Stals (National Collection of Insects) are thanked for assistance with the beetle identifications. This work was partially supported by grants to A. S. van Jaarsveld and S. L. Chown from the Foundation for Research Development and the University of Pretoria. The Mazda Wildlife Fund provided logistic support to S. L. Chown.

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ANNEXURE 3

Table showing the volumes removed by elephant, preference index and densities per ha for each woody species in each habitat type in Tembe Elephant Park.. The species are grouped (thick dashed line) in terms of the volume utilized and the volume available, and then in terms of selection in all habitats combined (see text). Abbreviations are: SF – Sand Forest, Th – Thicket, ThC – Thicket on Clay, CW – Closed Woodland, OW- Open Woodland, OWA – Open Woodland with high *A. adianthifolia* densities, SW – Sparse Woodland, AHC – All Habitats Combined, VPD – Volume in Cubic Metres/Preference/Density per ha, CLS – Utilization Class. For the volumes removed H – High, M – Moderate, L – Low, T – Trace. For the Preferences S – Selected, N – Neutral Use, R – Rejected. For the Densities Available H – High Densities, M – Moderate, L – Low, R – Rare. * indicates samples of less than 3 individuals. # indicates those species where the All Habitats Combined data result in a classification which is different to that for most of the separate habitats. The figures surrounded by a light dotted line indicate where the utilisation of a particular species in a particular habitat type differs substantially from the intensity of use in other habitats types.

Species	SF	Th	ThC	CW	OW	OWA	SW	AHC	VPD	CLS
Albizia adianthifolia	258 / 4.2/6.4	121 / 2.5/0.4*	20 / 2.4/0.8*	171 / 2/0.3*	3752 / 2.1/2.1	15365 / 1.5/11.5	/ /	19688 / 2.1/3.1	HSL	i
Albizia versicolor	/ /	95 / 2.5/4.3*	343 / 2/9.9	1168 / 2/3	1670 / 1.9/6.8	6081 / 1.5/13	226 / 1.7/4.7	9583 / 1.9/6	HSL	i
Sclerocarya birrea sub. caffra	145 / 2.4/26.3	975 / 1.9/10.2	1265 / 2/7.1	518 / 1.8/26.3	2294 / 1.9/3.5	755 / 1.2/3.5	619 / 1.5/2.2	6571 / 1.8/11.3	HSM	i
Terminalia sericea	44 / 4.2/8.1*	560 / 2.1/38.6	1051 / 1.5/67	1372 / 1.6/127.9	4368 / 1.6/42.5	5841 / 1.2/59.2	1103 / 1.4/87.2	14340 / 1.6/61.5	HSH	i
Acacia burkei	304 / 1.4/19	2898 / 1.4/85.9	790 / 1/104.4	992 / 0.9/62.5	2051 / 0.6/46.5	447 / 0.7/9.9	435 / 0.7/17.7	7916 / 0.8/49.4	HNH	ii
Acacia robusta sub. clavigera	39 / 2.8/24.5	29 / 2.5/0.4*	1354 / 2.1/14.5	101 / 2/0.9	/ /	1104 / 0.8/1	/ /	2627 / 1.7/5.9	MSL	iii
Afzelia quanzensis	38 / 1.4/9.9	189 / 1.9/1.7	382 / 1.9/6.6	439 / 0.9/29.3	429 / 1.8/1.9	1278 / 1.3/2.8	48 / 2/0.1*	2804 / 1.4/7.5	MSL#	iii
Trichilia emetica	98 / 4.2/5.2*	/ /	25 / 1.2/3*	353 / 1.4/2	1509 / 2.1/3.2	/ /	98 / 2/0.3*	2084 / 2/2	MSL	iii
Combretum molle	0 / 0/5.2*	288 / 1.3/60.4	249 / 1.7/9.1	781 / 1.1/145.3	212 / 1/14.9	1643 / 1/21.2	14 / 1.2/11.4	3187 / 1.2/38.2	MNM	iv
Dialium schlechteri	639 / 1.7/46.2	1087 / 1.3/93.8	10 / 1.6/6.5	429 / 0.5/20.4	646 / 0.9/6.9	1584 / 1/6.8	0 / 0/18.3	4395 / 0.9/28.4	MNM	iv
Strychnos madagascariensis	6 / 2.1/5.2*	662 / 2.1/141.3	28 / 1.4/11.7	173 / 1.3/58.3	710 / 0.9/65.5	1417 / 1.1/110.2	322 / 1.2/71.7	3317 / 1.3/66.3	MNH#	iv
Galpinia transvaalica	2 / 4.2/10.3*	/ /	330 / 2.4/0.2*	/ /	/ /	/ /	/ /	332 / 2.1/1.5	LSL	v
Garcinia livingstonei	/ /	/ /	3 / 2.4/2.2*	73 / 2/2	145 / 1.3/3	265 / 1/7.4	13 / 2/0.2*	499 / 1.5/2.1	LSL	v
Antidesma venosum	/ /	/ /	26 / 0.8/5.3	47 / 1.2/14.4	31 / 1.8/2.9	241 / 1.3/6.5	/ /	344 / 1.6/4.2	LSL	v
Manilkara discolor	201 / 1.8/42.1	/ /	0 / 2.4/5.6*	/ /	/ /	/ /	/ /	201 / 1/6.8	LSL*	v

Newtonia hildebrandtii	638 / 2.6/9.3	/ /	/ /	/ /	/ /	/ /	/ /	638 / 1.3/1.3	LSL	v
Wrightia natalensis	192 / 1.4/3.5	/ /	/ /	/ /	/ /	/ /	/ /	192 / 0.7/0.5	LSL	v
Ficus stuhlmannii	/ /	/ /	/ /	/ /	147 / 2.1/0.2*	/ /	/ /	147 / 2.1/0	LSR	v
Syzygium cordatum	/ /	/ /	145 / 0.8/1	143 / 1.2/2	118 / 1.8/1.1	37 / 1.6/0.1*	22 / 2/0.1*	464 / 1.4/0.6	LSR	v
Erythrophleum lasianthum	60 / 0.7/7	/ /	/ /	/ /	/ /	51 / 1.6/1.8	/ /	111 / 0.9/1.3	LNL	vi
Sapium integerrimum	17 / 2.1/5.2*	0 / 0/7.6*	/ /	37 / 1.1/15.9	93 / 0.9/5.7	234 / 0.9/12.6	/ /	380 / 1.1/6.7	LNL	vi
Ziziphus mucronata	/ /	0 / 0/0.4*	362 / 1.3/10.4	11 / 2/0.7*	8 / 0.7/6.6	93 / 0.7/3.8	0 / 0/3.7*	475 / 0.9/3.7	LNL	vi
Balanites maughamii	0 / 0/9.9	372 / 2/2.1	0 / 0/1*	0 / 0/0.6*	34 / 2.1/0.1*	312 / 0.5/1.6	/ /	717 / 0.7/2.2	LNL	vi
Commiphora neglecta	0 / 0/38.6*	95 / 1.4/42.5	16 / 1.8/15.6	0 / 0/54.9	14 / 1.1/2.1*	/ /	/ /	125 / 0.8/22	LNM[#]	vi
Psydrax fragrantissima	264 / 1.7/106.1	/ /	/ /	/ /	/ /	/ /	/ /	264 / 0.9/15.2	LNM	vi
Pteleopsis myrtifolia	411 / 2.4/102.4	12 / 0.8/21.6	/ /	/ /	/ /	0 / 0/1.2*	/ /	423 / 1.1/17.9	LNM[#]	vi
Spirostachys africana	212 / 2.8/3.5	29 / 1.7/18.8	1110 / 0.9/33.7	62 / 0.8/15.5	255 / 1.2/3	17 / 0.3/2.9	84 / 0.7/0.2	1769 / 0.9/11.1	LNM[#]	vi
Strychnos spinosa	0 / 2.1/38.6*	66 / 1.2/114	8 / 0.5/38.8	25 / 0.6/29.9	134 / 0.9/23.7	95 / 0.8/14.4	12 / 1/7.7	341 / 0.9/38.1	LNM[#]	vi
Cordia caffra	/ /	/ /	166 / 2.4/0.2*	0 / 0/1.7*	/ /	/ /	/ /	166 / 1.1/0.3	LNR	vi
Cleistanthus schlechteri v. schlecteri	29 / 0.3/39.6	/ /	/ /	/ /	/ /	301 / 1.1/2.7	/ /	331 / 0.6/6.1	LRL	vii
Acacia senegal v. rostrata	/ /	/ /	152 / 0.7/22.8	/ /	/ /	/ /	/ /	152 / 0.6/3.3	LRM	vii
Psydrax locuples	70 / 2.8/18.4	59 / 0.7/249.6	7 / 0.2/36.2	53 / 1.8/17.2	0 / 1.1/2.1*	12 / 0.8/1.5*	/ /	201 / 0.8/46.4	LRM[#]	vii
Tabernaemontana elegans	19 / 0.8/48	1 / 0.5/50.7	0 / 0/13.4	47 / 1.5/9	27 / 0.6/7.6	22 / 0.5/7.4	/ /	116 / 0.7/19.4	LRM[#]	vii
Dichrostachys cinerea	21 / 2.8/97.8	20 / 1.5/84.6	5 / 0.3/43.5	4 / 2/10.6*	26 / 0.6/15.8	49 / 0.6/8.3	0 / 0/91.7	124 / 0.5/50.3	LRM[#]	vii
Euclea natalensis	0 / 0/59.2	20 / 0.6/87.4	154 / 0.5/38.1	0 / 0/39.6	6 / 0.1/13.2	0 / 0/4.5	0 / 0/3.7*	180 / 0.2/35.1	LRM	vii
Hymenocardia ulmoides	1218 / 1/166.7	57 / 1/46.7	/ /	/ /	/ /	11 / 0.2/13.6	0 / 0/3.7	1286 / 0.5/33	LRM	vii
Vepris lanceolata	142 / 0.7/33.7	379 / 0.3/139.8	0 / 0/8.6	15 / 0.7/22.5	/ /	0 / 0/1.2*	/ /	537 / 0.3/29.4	LRM	vii
Drypetes arguta	109 / 0.3/403.4	0 / 0/42.4	/ /	/ /	/ /	/ /	/ /	109 / 0.1/63.7	LRH	vii
Hyperacanthus microphyllus	/ /	4 / 2.5/14*	/ /	/ /	/ /	/ /	/ /	4 / 2.1/2	TSL*	viii
Warneckea sousae	2 / 1.4/24.6*	/ /	/ /	/ /	/ /	/ /	/ /	2 / 0.7/3.5	TSL*	viii
Tricalysia junodii var. junodii	2 / 2.1/19.3*	/ /	/ /	/ /	/ /	/ /	/ /	2 / 1.1/2.8	TSL*	viii
Elaeodendron transvaalensis	/ /	/ /	72 / 2.4/1.8*	/ /	/ /	/ /	/ /	72 / 2.1/0.3	TSR*	viii
Euphorbia tirucalli	/ /	/ /	60 / 2.4/0.2*	/ /	/ /	/ /	/ /	60 / 2.1/0	TSR*	viil
Kigelia africana	/ /	/ /	/ /	9 / 2/0.7*	7 / 2.1/0.2*	/ /	/ /	16 / 2.1/0.1	TSR*	viii
Phyllanthus reticulatus	/ /	/ /	/ /	2 / 2/1.7*	/ /	/ /	/ /	2 / 2.1/0.2	TSR*	viii

Boscia foetida sub. rehmanniana	/ /	6 / 1/37	7 / 2.4/0.8*	/ /	/ /	/ /	/ /	12 / 1.1/5.4	TNL*	ix
Canthium setiflorum sub. setiflorum	/ /	0 / 0/14*	/ /	12 / 1/7	/ /	/ /	0 / 0/3.7*	12 / 0.7/3.5	TNL*	ix
Euclea divinorum	/ /	12 / 0.8/12.9	30 / 1.6/8.6	/ /	/ /	/ /	/ /	42 / 1.1/3.1	TNL[#]	ix
Mimusops caffra	65 / 2.4/16.8	/ /	/ /	0 / 0/12.9	/ /	/ /	/ /	65 / 0.7/4.2	TNL[#]	ix
Rothmannia fisheri sub. moramballae	2 / 1.4/48.9	/ /	/ /	/ /	/ /	/ /	/ /	2 / 0.7/7	TNL	ix
Sideroxylon inerme	/ /	/ /	48 / 1/18.2	/ /	/ /	/ /	/ /	48 / 0.9/2.6	TNL	ix
Tricalysia delagoensis	0 / 0/29.6*	/ /	/ /	0 / 2/8.9*	/ /	/ /	/ /	0 / 1.1/5.5	TNL*	ix
Drypetes natalensis	22 / 1.7/41.7	/ /	/ /	/ /	/ /	/ /	/ /	22 / 0.9/6	TNL	ix
Bridelia cathcartica	5 / 1.4/39.9	0 / 0/7.2*	4 / 0.8/16.7	12 / 0.9/50.2	24 / 0.9/4.3	1 / 0.5/6.6	/ /	45 / 0.8/17.8	TNM	ix
Lagynias lasiantha	10 / 1.4/88.8	/ /	/ /	/ /	/ /	/ /	/ /	10 / 0.7/12.7	TNM	ix
Rhus gueinzii	55 / 2.8/18.4	0 / 0/28.1*	0 / 0.6/22.3	28 / 1.5/14.1	10 / 0.8/3.1	0 / 0/2.9	/ /	94 / 0.8/12.7	TNM[#]	ix
Acacia nilotica sub. kraussiana	0 / 0/4*	/ /	4 / 0.9/17.9	55 / 1/1.3*	/ /	23 / 1.6/2	/ /	83 / 1.2/3.6	TNR	ix
Berchemia zeyheri	/ /	/ /	91 / 1.2/3*	/ /	/ /	/ /	/ /	91 / 1.1/0.4	TNR	ix
Combretum mkuzense	/ /	/ /	/ /	/ /	/ /	33 / 1/2.7	/ /	33 / 1.3/0.4	TNR	ix
Ekebergia capensis	/ /	/ /	38 / 2.4/0.2*	0 / 0/1.7*	/ /	/ /	/ /	38 / 1.1/0.3	TNR*	ix
Schotia brachypetala	/ /	/ /	34 / 1.2/0.3*	37 / 2/0.3*	/ /	0 / 0/0.1*	/ /	71 / 1.1/0.1	TNR	ix

Canthium inerme	0 / 0/48.9	/ /	0 / 0/7.8*	22 / 2/12.3	0 / 0/0.4*	/ /	/ /	22 / 0.7/9.9	TRL[#]	x
Monodora junodii	0 / 0/50.7	0 / 2.5/14*	/ /	/ /	/ /	/ /	/ /	0 / 0.4/9.3	TRL	x
Acalypha glabrata	4 / 2.1/38.6*	/ 0/28.1*	/ /	/ /	/ /	/ /	/ /	4 / 0.5/9.5	TRL	x
Acridocarpus natalitius v. linearifolius	0 / 0/19.3*	/ /	/ /	/ /	/ 0/4.3	0 / 0.5/3.6	/ /	0 / 0.3/3.9	TRL	x
Ancylanthos monteiroi	/ /	/ 0/21.6	/ /	/ /	1 / 1.1/0.6*	/ /	/ /	1 / 0.4/3.2	TRL	x
Dovyalis longispina	0 / 0/19.3*	/ /	0 / 0/5.6*	2 / 1/10.6*	/ /	/ /	/ /	2 / 0.5/5.1	TRL	x
Erythroxylum delagoense	11 / 2.1/20.6*	/ /	/ /	0 / 0/26.6	0 / 0/0.4*	18 / 1.6/0.3*	/ /	28 / 0.6/6.8	TRL	x
Grewia microthyrsa	/ /	0 / 0/42.4	14 / 2.4/7.8*	/ /	3 / 0.5/3.6	0 / 0/3.6	/ /	18 / 0.5/8.2	TRL	x
Margaritaria discoidea	/ /	0 / 0/28.1*	/ /	2 / 1/10.6*	0 / 0/1.1*	/ /	/ /	2 / 0.4/5.7	TRL	x
Maytenus senegalensis	/ /	12 / 2.5/7.2*	0 / 0/33.5	0 / 0/8.9*	1 / 0.5/4.3	0 / 0/2.4*	/ /	13 / 0.3/8	TRL	x
Ozoroa engleri	/ /	/ /	/ /	0 / 0/8.9*	47 / 0.2/8.9	8 / 0.3/7.3	0 / 0/14.7	54 / 0.2/5.7	TRL	x
Pavetta catophylla	/ /	0 / 0/14*	1 / 1.2/11.2*	/ /	/ /	0 / 0/2.4*	/ /	1 / 0.4/3.9	TRL	x
Phoenix reclinata	0 / 0/10.3*	/ /	23 / 0.4/31.3	1 / 2/8.9*	/ /	/ /	/ /	23 / 0.5/7.2	TRL	x
Ptaeroxylon obliquum	0 / 0/68.4	0 / 0/18.3*	11 / 0.6/5.4	3 / 2/1.7*	/ /	0 / 0/0.3*	/ /	15 / 0.3/13.5	TRL	x
Vangueria esculenta	0 / 0/10.3*	/ /	0 / 0/2.2*	/ /	1 / 0.4/4	0 / 0/1.7*	3 / 2/0.2*	18 / 0.4/2.6	TRL	x
Xylotheca kraussiana	0 / 0/29.6*	0 / 0/14*	0 / 0/5.6*	2 / 2/8.9*	/ /	0 / 0/2.4*	/ /	2 / 0.3/8.6	TRL	x
Zanthoxylum capense	0 / 0/10.3*	7 / 1.7/21.6	17 / 2.4/0.8*	3 / 0.7/4.2	0 / 0/3.1	0 / 0/0.8*	/ /	27 / 0.6/5.8	TRL	x
Acacia borleae	/ /	/ /	0 / 0/33.5	/ /	/ /	/ /	/ /	0 / 0/4.8	TRL	x
Grewia caffra	23 / 2.1/28.6	3 / 0.5/56.5	0 / 0/11.2*	/ /	0 / 0/1.1*	0 / 0/4.1	/ /	26 / 0.4/14.5	TRM[#]	x
Hyphaene coriacea	3 / 0.6/53.3	/ /	0 / 0/92.6	3 / 0.5/44.1	0 / 0/3.7	0 / 1.6/1.2	11 / 0.7/8.1	18 / 0.3/29	TRM[#]	x

Salacia leptoclada	5 / 0.4/115.2	/ /	/ /	/ /	/ /	/ /	/ /	5 / 0.2/16.5	TRM	x
Strychnos decussata	39 / 1.4/24.6	18 / 0.5/44.9	2 / 0.8/3.8	/ /	0 / 0/1.1*	/ /	/ /	60 / 0.5/10.6	TRM#	x
Teclea gerrardii	9 / 0.4/108.4	0 / 0/70.9	0 / 0/5.6*	0 / 0/3.1	/ /	0 / 0/2.2	/ /	9 / 0.1/27.2	TRM	x
Todalliopsis bremekampii	7 / 0.6/195.8	/ /	/ /	/ /	/ /	/ /	/ /	7 / 0.3/28	TRM	x
Tricalysia capensis	0 / 0/52.9	9 / 1/46.7	2 / 1.2/7.8*	0 / 0/8.9*	/ /	0 / 0/2.4*	/ /	12 / 0.5/17	TRM	x
Vangueria infausta sub. infausta	0 / 0/19.3*	5 / 0.6/56.1	17 / 1.9/17.9	22 / 1/17.6	13 / 0.4/28.8	7 / 0.2/13.6	1 / 0.5/11.2	66 / 0.5/23.5	TRM#	x
Catunaregam spinosa sub. spinosa	4 / 1.2/117.1	0 / 0/77.4	0 / 0/7.8*	3 / 0.3/175.2	0 / 0/11.4	0 / 0/3.6	0 / 0/14.7	8 / 0.2/58.2	TRH#	x
Cola greenwayi	27 / 0.3/498.5	/ 0/7.2*	/ /	/ /	/ /	/ /	/ /	27 / 0.1/72.2	TRH#	x
Brachylaena huillensis	13 / 0.4/337.8	2 / 0.4/84.2	0 / 0/11.2*	0 / 0/26.6	0 / 0/5.3	1 / 0.2/10.2	0 / 0/66	16 / 0.1/77.3	TRH#	x
Croton pseudopulchellus	16 / 0.4/581.6	0 / 0/28.1*	0 / 0/5.6*	/ /	/ /	/ /	/ /	16 / 0.2/87.9	TRH#	x

Clausena anisata	0 / 0/29.6*	0 / 0/28.1*	0 / 0/5.6*	0 / 0/53.1	0 / 0/3.2	0 / 0/7.8	/ /	0 / 0/18.2	CM	xi
Coddia rudis	0 / 0/19.3*	0 / 0/56.1	0 / 0/39.1	0 / 0/8.9*	0 / 0/1.1*	0 / 0/1.7*	/ /	0 / 0/18	CM	xi
Plectroniella armata	0 / 0/23.3*	/ /	0 / 0/13.4	0 / 0/35.4	/ /	0 / 0/1.2*	/ /	0 / 0/10.5	CM	xi

Coffea racemosa	/ /	/ /	0 / 0/11.2*	/ /	/ /	/ /	/ /	0 / 0/1.6	CL*	xii
Diospyros inhacaensis	0 / 0/19.3*	/ /	/ /	0 / 0/8.9*	/ /	/ /	/ /	0 / 0/4.6	CL*	xii
Ehretia rigida	/ /	0 / 0/14*	0 / 0/5.6*	/ /	/ /	/ /	/ /	0 / 0/2.8	CL*	xii
Euphorbia ingens	/ /	0 / 0/8.9	0 / 0/0.3*	0 / 0/0.7*	0 / 0/0.1*	0 / 0/0.1*	/ /	0 / 0/1.4	CL	xii
Gardenia volkensii	/ /	/ /	0 / 0/5.6*	/ /	/ /	/ /	/ 0/3.7	0 / 0/1.3	CL*	xii
Haplocoelum gallense	0 / 0/3.5	0 / 0/14*	/ /	/ /	/ /	/ /	/ /	0 / 0/2.5	CL*	xii
Hyperacanthus amoenus	0 / 0/24.6	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/3.5	CL*	xii
Mundulia sericea	/ /	/ /	/ /	0 / 0/35.4	0 / 0/12.8	0 / 0/8.7	0 / 0/3.7*	0 / 0/8.7	CL	xii
Ochna arborea var. arborea	0 / 0/4*	0 / 0/7.2*	/ /	/ /	/ /	/ /	/ /	0 / 0/1.6	CL*	xii
Ochna barbosae	0 / 0/38.6*	/ /	/ /	/ /	/ /	0 / 0/1.2*	/ /	0 / 0/5.7	CL	xii
Ochna natalitia	/ /	0 / 0/14*	0 / 0/16.7	0 / 0/17.7*	0 / 0/2.1*	0 / 0/3.6	/ /	0 / 0/7.7	CL	xii
Oxyanthus latifolius	0 / 0/10.3*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/1.5	CL*	xii
Strychnos henningsii	0 / 0/27.4	/ /	/ /	/ /	0 / 0/1.1*	/ /	/ /	0 / 0/4.1	CL	xii
Suregada zanzibariensis	0 / 0/19.3*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/2.8	CL*	xii
Tarenna junodii	0 / 0/19.3*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/2.8	CL*	xii
Vitex amboniensis	0 / 0/18.4	/ /	/ /	/ /	0 / 0/1.1*	0 / 0/2.4*	/ /	0 / 0/3.1	CL	xii
Acacia karroo	/ /	/ /	0 / 0/4.5*	/ /	/ /	/ /	/ /	0 / 0/0.6	CR*	xii
Albizia forbesii	/ /	0 / 0/0.8	/ /	/ /	/ /	/ /	/ /	0 / 0/0.1	CR*	xii
Casearia gladiiformis	/ /	/ /	/ /	0 / 0/1.7*	/ /	/ /	/ /	0 / 0/0.2	CR*	xii
Cassipourea mossambicensis	0 / 0/5.2*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/0.7	CR*	xii
Combretum celastroides sub. orientale	0 / 0/5.2*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/0.7	CR*	xii

Erythroxylum emarginatum	/ /	/ /	0 / 0/5.6*	/ /	/ /	/ /	/ /	0 / 0/0.8	CR*	xii
Euclea schimperi	/ /	/ /	/ /	/ /	/ /	0 / 0/0.3*	/ /	0 / 0/0	CR*	xii
Eugenia natalitia	/ /	0 / 0/7.2*	/ /	/ /	/ /	/ /	/ /	0 / 0/1	CR*	xii
Euphorbia grandidens	/ /	/ /	/ /	0 / 0/0.7*	/ /	/ /	/ /	0 / 0/0.1	CR*	xii
Lannea antiscorbutica	0 / 0/2.3*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/0.3	CR*	xii
Manilkara concolor	/ /	/ /	/ /	0 / 0/0.3*	/ /	/ /	/ /	0 / 0/0	CR*	xii
Maytenus undata	/ /	/ /	/ /	0 / 0/1.7*	/ /	0 / 0/1.2*	/ /	0 / 0/0.4	CR*	xii
Premna mooiensis	/ /	/ /	/ /	/ /	/ /	0 / 0/1.2*	/ /	0 / 0/0.2	CR*	xii
Pseudobersama mossambicensis	0 / 0/19.3*	/ /	/ /	/ /	/ /	/ /	/ /	0 / 0/2.8	CR*	xii
Thespesia acutiloba	/ /	/ /	0 / 0/6.4*	/ /	/ /	/ /	/ /	0 / 0/0.9	CR*	xii
Totals	5501 / /4479.3	8095 / /2290.2	8477 / /1029.3	7231 / /1352.4	18786 / /396.1	37347 / /436.8	3012 / /450.2	88465 / /1490.6		